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Évolution de l'organisation sociale et sa variabilité chez les mammifères

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À mes parents et à toutes mes petites abeilles travailleuses…

> *« Merci pour les roses, merci pour les épines »*
>
> Jean d’Ormesson

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Vulgarisations scientifiques:

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Olivier, C. A. & Schradin, C. (17 mars 2022). Les musaraignes-éléphants ne vivent pas toujours en couple. Article parut dans l'INEE-CNRS, Rubrique actualité et résultat scientifique. https://www.inee.cnrs.fr/fr/cnrsinfo/les-musaraignes-elephants-ne-vivent-pas-toujours-en-couple

Olivier, C. A., Makuya, L., Qiu, J. (2021). Frontiers in Social Evolution (FINE). *EthoNews, newsletter of the Ethologische Gesellschaft e.V.*. available at https://www.researchgate.net/publication/356604539_Frontiers_in_Social_Evolution_FINE.

Table des matières

Abréviations

SEM: Socio-ecological model

IVSO: Intra-Specific Variation in Social Organization

MF: Pair-living

MFF: One male with multiple females group

MMF: One female with multiple males group

MMFF: Multi males multi females group

SO: Social Organization

Pop: Population

Sp: Species

e.g.: for example

i.e.: that is

Résumé

La compréhension des systèmes sociaux est un sujet clé de l'écologie comportementale et l'un des objectifs majeurs de la biologie évolutive. Le système social d'une espèce est décrit par quatre composantes qui sont liées les unes aux autres : la structure sociale, le système de soins, le système d'accouplement et l'organisation sociale (Kappeler, 2019). La structure sociale décrit les interactions entre individus, le système de soins qui s'occupe de la progéniture et le système d'accouplement est lié à qui se reproduit avec qui. La quatrième composante, l'organisation sociale, détermine la taille, la composition sexuelle et la cohésion spatio-temporelle du groupe. C'est la composante qui est la plus souvent rapportée dans les études de terrain et elle peut également influencer la structure sociale, le système de soins et le système d'accouplement. Ainsi, l'organisation sociale offre le plus de données pour les études comparatives sur l'évolution sociale.

Au sein du règne animal, les espèces présentent une grande variété d'organisations sociales, allant de la vie solitaire chez de nombreux invertébrés, carnivores et musaraignes, à la vie en couple chez certains cichlidés et la plupart des oiseaux, en passant par des groupes d'éléphants, de loups, de pinsons et même des espèces eusociales comme les abeilles, les fourmis et les rats-taupes nus. Les mammifères, en particulier, constituent une classe très intéressante à étudier car ils sont présents dans tous les habitats terrestres, marins et certains peuvent même voler. Ils ont fait l'objet d'études approfondies (Kleiman et Malcolm 1981; Lukas et Clutton-Brock 2013; Thierry et al. 2000). Il a été démontré que la phylogénie, les traits d’histoire de vie et les facteurs écologiques peuvent être liés à l'organisation sociale et ainsi expliquer une partie significative de la variation observée entre les espèces. Les traits

d'histoire de vie, tels que la masse corporelle ou le rythme d'activité sont étroitement liés à la socialité (Bekoff et al Mitton, 1981). Des facteurs écologiques, tels que le risque de prédation ou la compétition pour les ressources, peuvent également façonner l'organisation sociale en déterminant les formes de regroupement des individus (Wrangham 1980 ; van Schaik 1989).

Expliquer l'évolution de l'organisation sociale a été fondamental pour comprendre la socialité humaine et plus largement l'évolution sociale. Des études comparatives récentes ont abordé des questions essentielles sur les origines évolutives des différentes organisations sociales (Lukas et Clutton-Brock 2013; Lukas et Clutton-Brock 2012). Ces études ont soutenu que le premier mammifère placentaire était solitaire et que des formes plus complexes d'organisation sociale étaient apparues plus tard (Lukas et Clutton-Brock 2013, Gebo 2004). Cependant, dans ma thèse, je remets en question ces affirmations avec de nouvelles analyses modernes. Si l'organisation sociale est variable entre les espèces, il est moins connu qu'elle varie aussi souvent au sein d'une même espèce (Lott 1984; Schradin et al. 2018).

Autrefois, il était largement admis que chaque espèce avait une organisation sociale spécifique. Cependant, la variation intra-spécifique de l'organisation sociale (IVSO) a été constatée chez de nombreux taxons de mammifères, y compris les Artiodactyles (Jaeggi et al. 2020), Strepsirrhini (Agnani et al. 2018), Eulipotyphla (Valomy et al. 2015) et Carnivora (Dalerum 2007), ce qui suggère que l'organisation sociale variable chez les mammifères pourrait être plus courante que nous le pensions. Toutefois, bien que cette variation ait été répertoriée chez de nombreux taxons de mammifères, des études approfondies manquent encore pour plusieurs taxons. Ainsi, une prise en compte de l'IVSO pourrait transformer notre compréhension de l'évolution sociale des mammifères (Jaeggi et al. 2020 ; Schradin et al. 2018).

L'objectif de ma thèse est de mieux comprendre l'évolution de l'organisation sociale chez les mammifères, en posant les questions suivantes : 1. Quelle est l'ampleur de la variation de l'organisation sociale chez les mammifères au niveau de l'espèce et de la population ? 2. Notre compréhension de l'organisation sociale ancestrale change-t-elle lorsque nous prenons en compte la variation ? 3. Quels facteurs écologiques et traits d’histoire de vie sont associés aux différentes formes d'organisation sociale (variation comprise) ? 4. Quelle était l'organisation sociale ancestrale de tous les mammifères ? Ma thèse contient donc trois chapitres et une revue dans lesquels j'ai étudié différents ordres de mammifères, en commençant par un ordre comportant peu d'espèces et en terminant par une étude de tous les ordres de mammifères existants.

Dans le premier chapitre, j'ai étudié les musaraignes éléphants (Macroscelidea), un ordre de mammifères ne comptant que 19 espèces. Il a été considéré comme le seul ordre de mammifères où toutes les espèces étaient supposées être monogames (système d'accouplement) en raison des observations de leur vie en couple (organisation sociale) **(Olivier, C. A., Jaeggi, A. V., Hayes, L. D., & Schradin, C. (2022). Revisiting the components of Macroscelidea social systems: Evidence for variable social organization, including pair-living, but not for a monogamous mating system. *Ethology*, *128*(5), 383–394)**. J'ai examiné la littérature primaire sur les quatre composantes des systèmes sociaux (organisation sociale, système d'accouplement, structure sociale et système de soins) chez les musaraignes éléphants afin d'évaluer si elles sont réellement monogames quand la variation possible est considérée. Afin d'identifier le manque de connaissance concernant leur système social, j'ai examiné les preuves d'une vie en couple, de la fidélité du partenaire (système d'accouplement), des liens de couple (structure sociale) et des soins biparentaux (système de soins). Sur les 19 espèces qui composent l'ordre des Macroscelidea, j'ai trouvé des informations sur leur organisation sociale pour huit espèces, et sept d'entre elles étaient souvent en couple. Cependant, ces sept espèces présentaient des variations intra-spécifiques dans l'organisation sociale : deux de ces espèces vivaient également de manière solitaire, deux espèces vivaient aussi en groupe, et les trois espèces restantes étaient à la fois solitaires et en groupe. La huitième espèce était exclusivement solitaire. J'ai ensuite reconstitué l'organisation sociale ancestrale des Macroscelidea à l'aide de modèles phylogénétiques bayésiens à effets mixtes et j'ai constaté qu'une organisation sociale variable, plutôt que la vie en paire exclusive, était l'état ancestral le plus probable. Aucun facteur socio-écologique (taille du corps, densité de population et habitat) ne prédisait une organisation sociale spécifique. Les observations d'accouplement ont été rares, de sorte qu'aucune déclaration ferme ne peut être faite. Cependant, une étude non publiée a indiqué des niveaux élevés d'extra-paire paternité. En ce qui concerne la structure sociale, il n'y a pas de signe de l'existence d'un lien entre les couples, mais il y a des preuves de surveillance du compagnon. Seuls les soins maternels ont été observés, les femelles ayant des périodes d'allaitement très courtes. Les données suggèrent donc qu'en dépit d'une forme d'organisation sociale souvent de type couple, les Macroscelidea ne devraient pas être décrits comme un ordre monogame car peu ou pas de preuves soutiennent la désignation de leur système d'accouplement comme tel, de même qu'ils ne vivent pas exclusivement en couple (organisation sociale). Nous demandons donc que des études de terrain supplémentaires sur les systèmes sociaux des Macroscelidea soient faites afin de pouvoir avoir une idée beaucoup plus précise de leur système d'accouplement.

J'ai ensuite étudié l'ordre des mammifères le plus étudié et nos plus proches parents, les primates. Il est fondamental d'expliquer l'évolution de l'organisation sociale des primates pour comprendre la socialité humaine et, plus largement, l'évolution sociale. Il a souvent été suggéré que l'ancêtre de tous les primates était solitaire et que d'autres formes d'organisation sociale ont évolué par la suite (Kappeler et Pozzi 2019; Lukas et Clutton-Brock 2013; Shultz et al. 2011). Cependant, les recherches précédentes incluaient l'hypothèse que de nombreuses espèces de primates non-étudiées étaient solitaires, trouvant ensuite que les transitions vers des systèmes sociaux plus complexes étaient déterminées par divers traits d'histoire de vie et facteurs écologiques. J'ai construit une base de données à partir de littérature primaire (menées sur le terrain) quantifiant le nombre d'individus (unités sociales) exprimant différentes organisations sociales dans chaque population. En utilisant des modèles phylogénétiques bayésiens à effets mixtes, nous avons déduit la probabilité de chaque organisation sociale, basée sur plusieurs prédicteurs socio-écologiques, dans la population ancestrale. Dans ce chapitre, et contrairement au premier, j'ai utilisé des statistiques plus avancées afin de prendre en compte l'IVSO comme une variable continue. Nous avons constitué une base de données sur l'organisation sociale de 499 populations de 216 espèces de primates observées sur le terrain. Je montre pour la première fois que lorsque la variation intra-spécifique est prise en compte, l'organisation sociale ancestrale des primates est variable. L'organisation sociale la plus courante étant la vie en couple, avec environ 15 à 20 % des unités sociales de la population ancestrale qui s'écartent de ce modèle en vivant solitairement. De plus, la taille du corps et les rythmes d'activité avaient des effets significatifs sur les transitions entre les types d'organisations sociales. Nos résultats remettent en question l'hypothèse selon laquelle l’ancêtre des primates était solitaire et le fait que la vie en couple ait évolué par la suite. Au contraire, la vie en couple semble très ancienne dans l'évolution, probablement en raison des avantages reproductifs tels que l'accès aux partenaires et la réduction de la compétition intra-sexuelle. Des structures sociales plus complexes (liens entre couples) et des systèmes de soins (soins biparentaux et allo-parentaux) sont apparus plus tard. Cette étude a été soumise **(Olivier, C. A., Martin, J. S., Pilisi, C., Agnani, P., Kauffmann, C., Hayes, L., Jaeggi, A.V. & Schradin, C. Primate Social Organization Evolved from a Flexible Pair- Living Ancestor).**

Afin d'avoir une vue d'ensemble de toutes les espèces actuelles de mammifères, j'ai créé une base de données avec l'ensemble des informations que j'ai pu trouver dans la littérature primaire sur leur organisation sociale (au niveau de l'espèce et de la population). Le but de cette étude était de 1. Créer une base de données sur l'organisation sociale des mammifères 2. Prendre en compte l'IVSO 3. Déterminer l'organisation sociale ancestrale de tous les mammifères et 4. Rechercher quels facteurs environnementaux ou traits d'histoire de vie sont liés à une certaine organisation sociale. Jusqu'à présent, on pensait que l'organisation sociale ancestrale des mammifères était la vie solitaire et que la vie en couple et en groupe en découlait (Kappeler et Pozzi 2019 ; Lukas et Clutton-Brock 2013). Par exemple, Lukas et Clutton-Brock (2013) ont constaté dans leur étude comparative que l'ancêtre de tous les mammifères était solitaire et suggèrent d'importantes transitions sociales à partir de cet état primitif. Cependant, les preuves fossiles indiquent un mode de vie grégaire chez certains mammifères primitifs et même chez les mammifères souches (cynodontes), ancêtres des premiers mammifères. Sur les 5740 espèces de mammifères, j'ai trouvé des informations sur leur organisation sociale pour 806 espèces et 1622 populations. Par ailleurs, 412 espèces et 631 populations avaient une organisation sociale variable. En utilisant un modèle bayésien et en tenant compte de la variation intra-spécifique, je montre que l'organisation sociale ancestrale des mammifères n'était pas exclusivement solitaire, mais variable, incluant la vie en couple et en groupe. Ainsi, notre étude transforme notre compréhension de l'évolution sociale des mammifères, et notamment sur le fait de considérer la vie solitaire chez les mammifères comme un simple état ancestral ou une adaptation particulière **(Olivier, C.A., Jaegi, A.V., Hayes. L., Martin, J.S., Qui, J., Makuya, L. & Schradin, C. Was the ancestral mammal really solitary living? (*en préparation*)).** Cette thèse a fourni une nouvelle perspective sur l'évolution de l'organisation sociale en 1. Se concentrant uniquement sur les espèces étudiées dans leur environnement naturel, 2. Prenant en compte pour la première fois l'IVSO et 3. Utilisant de nouvelles méthodes statistiques et en considérant pour la première fois l'IVSO comme une variable continue. Les principaux résultats sont les suivants 1. Cette base de données a révélé qu'il existe une variation, entre et au sein, des espèces pour les macroscelidea, les primates et les mammifères de manière générale. 2) Les facteurs liés à l'histoire de la vie, tels que la masse corporelle et les rythmes d'activité, ont des effets importants sur les organisations sociales des primates. 3) Considérant l'IVSO, l'organisation sociale ancestrale de tous les mammifères était variable.

En somme, mes résultats soulignent l'importance de n'utiliser que des données de terrain et de prendre en compte la variation intra-spécifique. La prise en compte de cette variation dans l'estimation de l'organisation sociale ancestrale a fourni de nouvelles perspectives sur l'évolution des mammifères et sur notre propre ancêtre. Cependant, l'examen des études de terrain a également montré que seule une minorité d'espèces a été étudiée et que, pour la plupart des espèces de mammifères, nous manquons d'informations sur leur organisation sociale. Nous appelons donc à davantage d'études de terrain concernant leur organisation sociale. En effet, davantage d'espèces doivent être étudiées dans leur habitat naturel afin de déduire de manière fiable la forme ancestrale de l'organisation sociale et les facteurs écologiques et d'histoire de vie liés à l'évolution sociale des mammifères. L'étude de l'évolution de l'organisation sociale est un sujet important car elle peut également nous aider à comprendre comment les espèces modifient leur comportement face aux changements globaux. Cela pourrait nous aider à proposer des plans de conservation adaptés (Olivier, C. A., Schradin, C., & Makuya, L. (2022). Global Change and Conservation of Solitary Mammals. *Frontiers in Ecology and Evolution*, *10*, 906446).

I. General Introduction

I.1 Social system

I.1.1 General background

Animals exhibit a stunning diversity in social behavior and resulting social systems. Understanding this diversity of animal social systems is a key subject in behavioral ecology and has been one of the aims in evolutionary biology (Clutton-Brock and Janson 2012; Kappeler et al. 2013; Rubenstein and Abbot 2017). Within the animal kingdom, species display a wide variety of social systems ranging from solitary living in many invertebrates, fish, carnivores and shrews, over pair-living in some cichlids, song-birds, jackals and prairie voles, to groups of elephants, wolves or flocks of finches and even eusocial species like bees, ants, or naked mole rats. This extraordinary level of behavioral complexity has been studied in a wide variety of taxa over the past decades (Dew et al. 2016; Rubenstein and Abbot 2017; Jordan et al. 2021). With this increasing number of studies and with the great diversity of taxonomic groups, a vocabulary has arisen to describe behavior and social systems in particularly (Rubenstein and Abbot 2017). However, as the study of sociality has been developed in different ways in invertebrates and vertebrates, researchers studying the social systems of these different taxa have not always used the same vocabulary and definitions, resulting in a large number of terms (**Figure I-1**; Rubenstein and Abbot 2017).

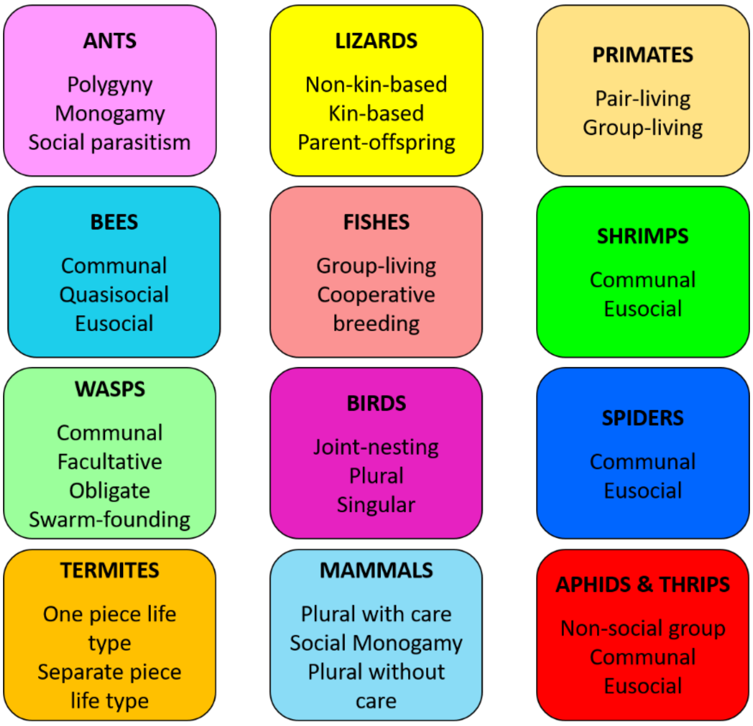


__Figure I-1:__ Different terms used to describe social systems in different taxa, as used in the current literature (reviewed by *Rubenstein's book "Comparative Social Evolution", 2017).*

As it was the case with the taxonomic classification, a homogenisation of the vocabulary of social systems was proposed. The inconsistent definitions of social system components coupled with differences in the methodological approaches used to study vertebrate and invertebrate social systems have hindered progress in the study of social evolution (Kappeler 2019). Considering the needs for alignment on definitions used in the study of animal sociality, Kappeler and van Schaik proposed a classification of social systems in 2002, which Kappeler modified and clarified in 2019. This classification is based on four inter-related components: the social structure, the mating system, the care system and the social organization (**Figure I-2**). My thesis is based on his classification which I review here to show its advantage by giving clarity on which aspect one is actually studying.

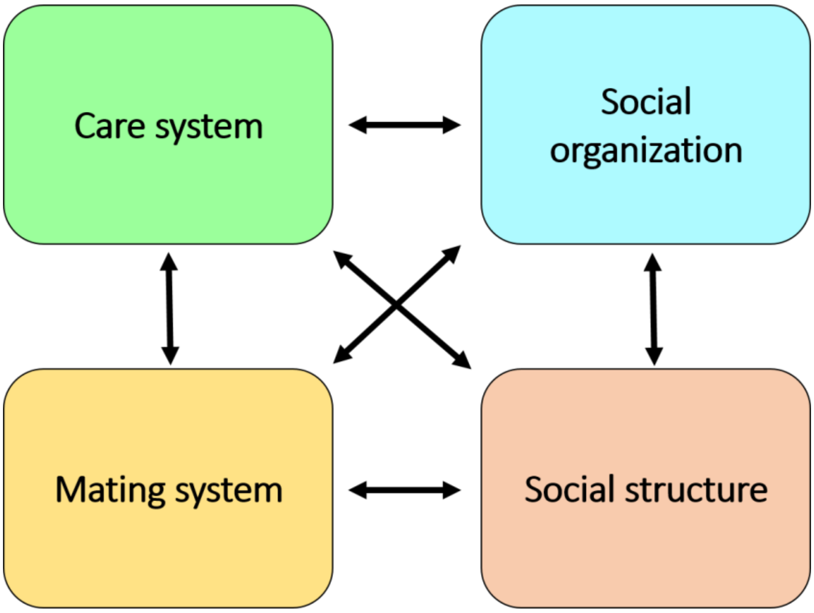


Figure I-2: *The four inter-related components of social system from Kappeler's classification in 2019.*

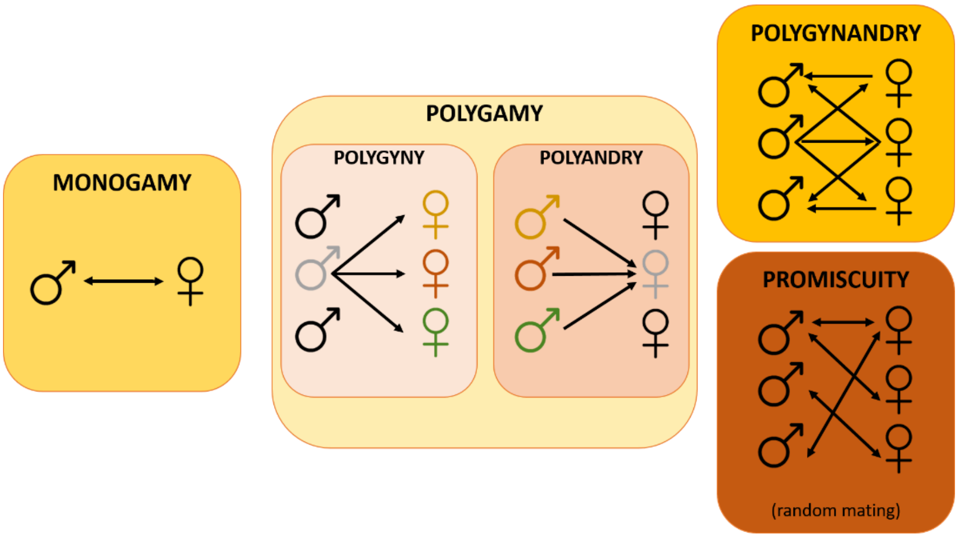
I.1.2 Social structure

Different interactions between members of the same group and the resulting relationships emerging from repeated interactions are described by the social structure (Kappeler 2019). There are different types of social interactions, caused by differences in the nature, frequency and intensity of interactions (Hinde 1976; de Waal 1986; de Waal 1989), resulting in passive or aggressive-aimed interactions. Social interactions can be sort in two main categories: dominance hierarchies and social bonding. In species that live socially, agonistic behavior leads to dominance hierarchies (rank order, social hierarchy). Dominance between two individuals in a relationship describes which individual wins most social interactions and thus has better access to resources. Dominance is a key aspect in the social system because it contributes to regulate resource access such as food or mates.

Social bonds represent a subset of differentiated relationships with particular characteristics (high affiliation and low agonism) and often have functional importance (Silk et al. 2012, 2013; Seyfarth and Cheney 2015). Therefore, social bondings are characterised by social preference or by males and females remaining together after mating and often even during non-reproductive periods (Carter et al. 1995). It also occurs between parents and offsprings, in matrilines or in male coalitions.

I.1.3 Mating system

The mating system describes who mates with whom and the reproductive consequences (paternity, timing of mating). There are several types of mating system, depending on the number of mating partners of males and females (Clutton-Brock 1989; Loue 2007). Here, I distinguish five types of mating system: monogamous, polygynous, polyandrous, polygynandrous and promiscuous (**Figure I-3**) based on the definitions by Clutton-Brock (1989). It is one of the most difficult components to study as it is highly challenging to observe mating, which often occurs hidden. As a result, genetic studies are needed to ensure the presumed paternity of the offspring. Mating system includes different forms of mate guarding adapted to the spatial and temporal distribution of receptive females which, in turn, depends on variation in resource distribution, predation pressure, costs of social living and activities of other males (Bradbury and Vehrencamp 1977; Emlen and Oring 1977). The five types of mating system are associated with four main forms of mate guarding : the defence of individual females during part or all of their period of receptivity; the defence (usually intrasexual) of feeding territories that overlap the ranges of individual females or groups of females partly or completely; the defence of particular groups of females either during the mating season or throughout the year without the defence of any fixed area; and the defence of dispersed or clustered mating territories within a portion of the female range. In most species of mammals, single males defend females but in a few cases several males cooperate to defend access to female groups or their ranges (Bradbury and Vehrencamp 1977; Emlen and Oring 1977).



<u>Figure I-3:</u> Description of the five different types of animal mating system based on Clutton-Brock's (1989) definitions.

Monogamy, which means one male and one female reproducing exclusively together, has been regarded as a hallmark of social evolution (Kleiman 1977; Lukas and Clutton-Brock 2013; Garber et al. 2016; Tecot et al. 2016). In contrast to birds, monogamy is a rare phenomenon in mammalian species and is found in less than 8% of species (Kleiman 1977). In some species, monogamy will only last for one breeding season (*e.g.* red foxes, penguins), while in other species pairs remain together until one partner dies (*e.g.* wolves, gibbons, lovebirsds). The term "monogamy," however, has been used unconsciously in the literature to refer to: a type of social organization (pair-living), social relationship (close social bonding between two adults of opposite sex), and/or mating system (exclusive and consistent monogamous mating; Fuentes 1998; Reichard and Boesch 2003; Wickler and Seibt 1983). The term 'social monogamy' is even employed in some literature (Lukas and Clutton-Brock 2013) referring to a mix between social organization (pair-living) and mating system (monogamy). In this thesis, monogamy refers only to the mating system.

Polygyny is the most common mating system in mammals (Emlen and Oring 1977; Kleiman 1977; Rutberg 1983; Clutton-Brock 1989), and implies a male to reproduce with several females. In mammals, the most common mechanisms leading to polygyny are the defence of a group of females or harem, defence of a territory with resources required by females, or defence of an area within leks (Clutton-Brock 1989).

In polyandrous mating system, a female will mate with multiple partners and each male mates only with her during a single reproductive event (Hrdy 1979), thus reducing the risk of infanticide (Tardif and Garber 1994; Garber 1997). Polyandrous females give several males a reproductive contribution, which creates paternity confusion that prevents these males from killing what could be their own offspring (Schaik and Janson 2000; Wolff and Macdonald 2004; Auclair et al. 2014).

Polygynandry is a mating system in which both males and females have multiple mating partners during a breeding season. This mating system exist in a wide variety of taxa: from carnivores to primates (Szala and Shackelford 2019).

Finally, in a promiscuous mating system, males and females will mate randomly (*e.g.* leporids; Cowan and Bell 1986). In contrast to polygynandry, this means mating with multiple partners, without any selection-based process or quality-based discrimination of mating partners (Garcia-Gonzalez 2017).

I.1.4 Care system

By caring for offspring, individuals can increase their offspring`s probability of survival and as a consequence increase their own fitness. The care system is about who cares of the dependent offspring (Kappeler 2019) and consists of feeding, protecting or cleaning them. There are five types of care system: no care, maternal care only, paternal care only, biparental care and alloparental care. Alloparental care when done by other breeders is called communal breeding in contrast to alloparental care done by non-breeders (helpers), called cooperative breeding. While most animal species (especially arthropods) show no care, in all mammals the female shows maternal care (Tallamy 2001).

I.1.5 Social organization

Finally, the social organization describes the size, the sexual composition and spatio-temporal cohesion of a group (Kappeler and van Schaik 2002). Three major categories of social organization occur: solitary living (males and females live solitary with or without dependent offspring), pair-living (a male and a female living together), or group-living (a male and several females, a female with several males, a group of males, a group of females or a group of multiple males and females living together; **Figure I-4**).

In this thesis, solitary species are defined by adult males and females foraging independently and only meeting for mating (*i.e.* they do not stay together for periods longer than courtship and mating) and are otherwise alone (Sandell 1989). Pair-living social organization is defined by two adults of opposite sex living together within a home range with or without their non-reproducing offspring (Fuentes 2000; Tecot et al. 2016). Groups consist of at least three individuals and the number of males and females will determine the additional distinction between groups (Kappeler 2000). Hence, different forms of group-living can be distinguished: groups composed of one male and several females, groups of one female and several males and groups with several males and several females. All these groups share the same home range. Finally, there exists sex-specific groups, *i.e.* groups composed only of males (bachelor groups) or only female groups. Nevertheless, it is important to note that the number of individuals in a group is not taken into account while classifying the social organization. For instance, a group with one male and two females will have the same status as a group with one male and 20 females.

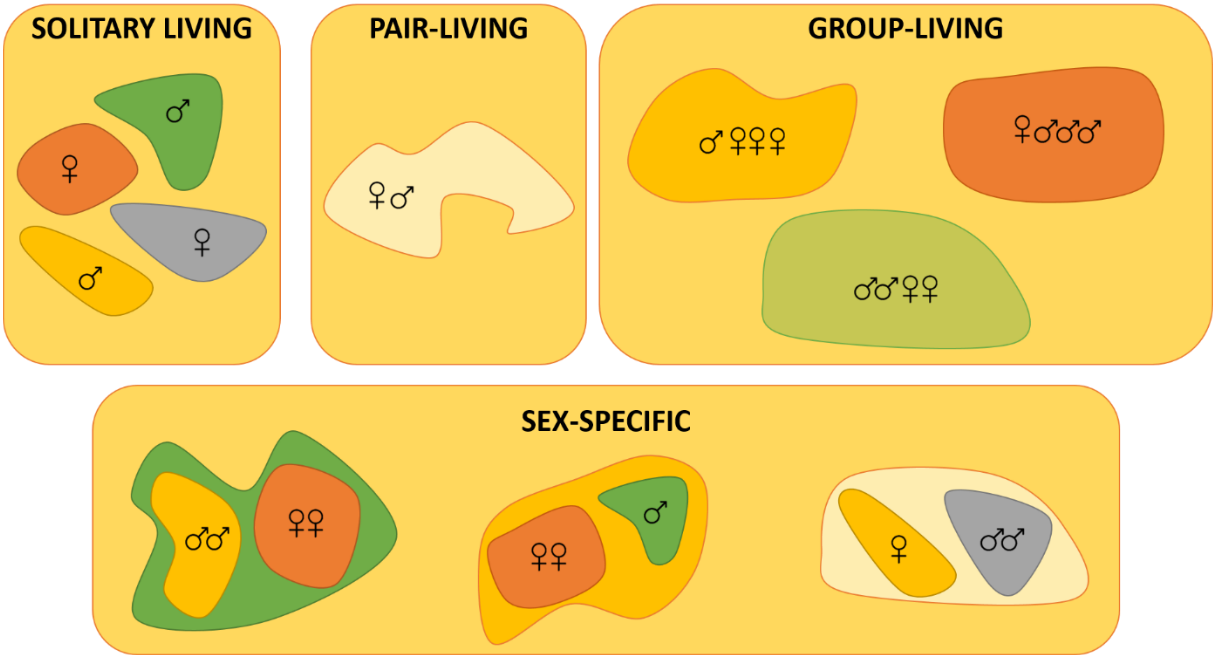


__Figure I-4:__ The different categories of social organization. Solitary species are defined by adult males and females foraging independently and only meeting for mating. Pair-living social organization is defined by two adults of opposite sex living together within a home range with or without their non-reproducing offspring. Groups consist of at least three individuals and the number of males and females will determine the additional distinction between groups, they share the same home range. Species can be composed of sex-specific groups meaning that either each sexes live in different groups or groups can be composed of groups of females and solitary males or groups of bachelor and solitary females.

All four components of social systems influence each other (Kappeler 2019). For example, monogamous species have often been characterized to be pair-living (social organization), to mate exclusively with each other (mating system) because they have strong pair bonds (social structure) also explaining biparental care (care system; Kleiman 1977). However, such classifications can be problematic as this is not necessarily the case in all species. For example, rarely any pair-living species has a strict monogamous mating system and extra-pair paternity is common in both birds and mammals (Westneat and Stewart 2003; Cohas and Allainé 2009; Brouwer and Griffith 2019), highlighting the importance of studying the different components of social systems separately from each other (Kappeler 2019; Huck et al. 2020; Fernandez-Duque et al. 2020).

The social organization of a species is easier to measure than the social structure, the mating system, or the care system and is thus, more commonly reported from field studies providing us the most data for comparative studies on social evolution.

I.2 Social evolution

I.2.1 Fitness and social evolution

Social systems and social organization in particular is a product of individual evolved behavior. To understand the evolution of behavior and consequently the social evolution, natural selection must be investigated. Natural selection is the differential survival and reproduction of individuals due to differences in their phenotype. For evolution to take place this differences must at least be partly due to genetic differences. It is a key mechanism of evolution, i.e. the modification of the hereditary traits characteristic of a population over generations. Within populations, variation between individuals exists. This variation is partly due to random sexually transmitted mutations in the genome of an individual organism. As a result, some individuals will survive and reproduce more than individuals without the mutation creating an evolution of the population since these mutations are heritable and thus transmitted to the offspring.

In a given environment, a phenotypic trait like behavior, e.g. whether to associate with conspecifics or not, may influence the survival and reproduction of an individual i.e. Visser and Gienapp 2019; Iler et al. 2021. Social organization is the result of the sum of individual social behaviors and therefore of their evolution. Thus, the evolution of the social organization also represents the evolution of individual social behaviors. Ultimately, the evolution of social organization corresponds to the variation in the frequencies of genes associated with individual social behaviors in a population over generations (Wade and Kalisz, 1990). Another key point in the evolution of social organization is the sex difference in how social behavior may maximize individual fitness. In order to maximize individual fitness, males should breed with as many females as possible and invest as minimum energy as possible in caring for the offspring. Females, on the other hand, should breed and invest as little as possible in maternal care to acquire more food and produce more eggs. Due to the sexual differences in potential reproductive rates (Clutton-Brock and Parker 1992), male and female fitness are limited by different factors resulting in a conflict between sexes. The outcome of this conflict determines individual social and reproductive tactics and as such the evolution of: mating system, social structure, care system and social organization of the population.

However, a part of the trait (*e.g.* behavior) variation within and between generations may be explained by phenotypic plasticity. Indeed, phenotypic plasticity is the capability to produce different phenotypes in response to contrasted environmental conditions, is a trait itself, and thus subject to selection (Nussey et al. 2007; Lane et al. 2019). When phenotypic plasticity occurs, the variation of the trait is visible within an individual's generation. Genes expression may change according to variations in the environment (*e.g.* a behavior that will vary during the life of an individual) and modify the phenotype accordingly. It should also be noted that the ability to transcribe genes according to the environment, and thus the ability to have phenotypic plasticity, is itself expressed by genes. These genes are then subjected to selection and thus the selection of phenotypic plasticity can be applied over several generations.

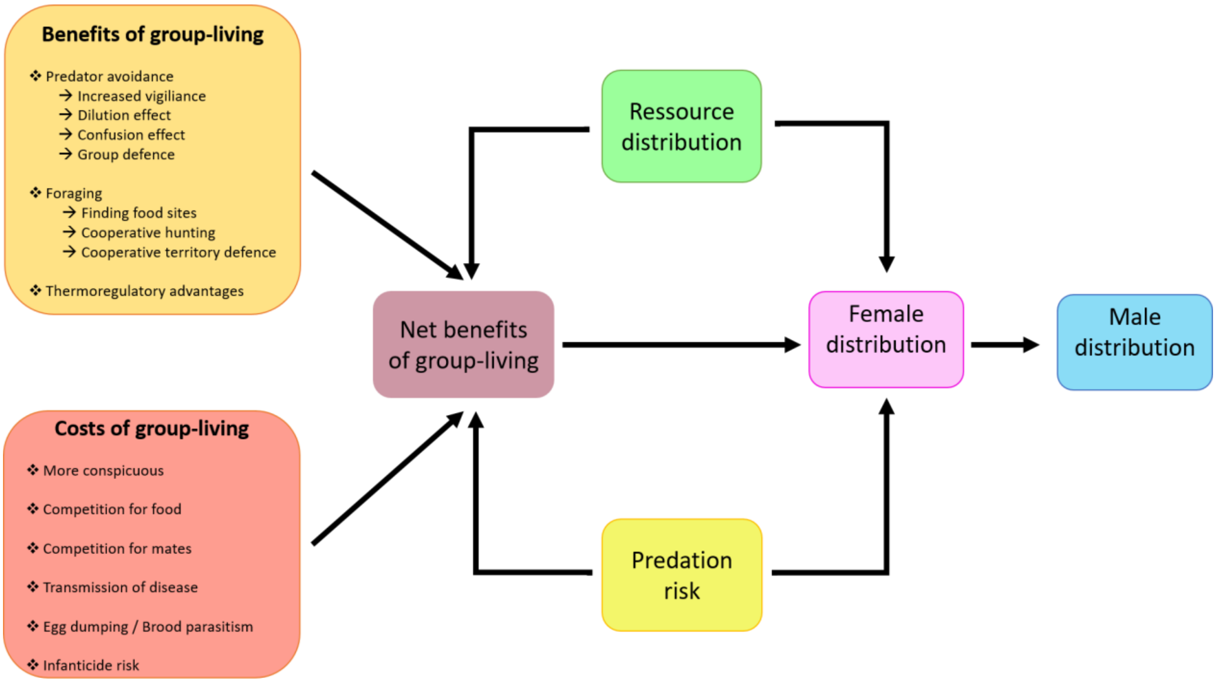
To conclude, natural selection acts on the phenotype, the characteristics of the organism which actually interact with the environment. The genetic (heritable) basis of any phenotype that gives a reproductive advantage may become more common in a population. Over time, natural selection can result in populations that specialise for particular ecological niches (microevolution) and may eventually result in speciation (the emergence of new species, macroevolution; Paradis 2014). Macroevolution can also be studied from comparative phylogeny method, by comparing its variation with the distribution of the phenotypic trait among species.

I.2.2 Socio-ecological model

The question that can be asked when studying social organizations is: why do some species live alone, while others live in pairs and even others live in groups? Social behaviors is favoured by natural selection in response to several environmental factors. According to van Schaik (1989), there are two main factors that would lead individuals to have a certain social organization: resource distribution and predation risk (see also Crook and Gartlan 1966). These two factors constitute the main elements of the socio-ecological model.

The socio-ecological model (SEM; Crook and Gartlan 1966; Emlen and Oring 1977; Terborgh and Janson 1986) relates “ecological factors such as resource distribution, type of competition, predation risks with characteristics of social systems (social organization and social structure) and allows predictions” (van Schaik 1989). As mentioned in the previous section "Fitness and social evolution", the evolution of social organization is related to different evolutionary constraints between males and females. Accordingly, the SEM assumes that female distribution in space and time is mainly determined by the distribution of risks and resources. The males will be distributed according to the distribution of females (Clutton-Brock 1989). The model is driven by female distribution and is therefore related to their social organization. Do females form groups? Do they live alone? The distribution of resources, especially food, influences reproductive success. If food is present in abundance then egg/offspring production will be higher and females could live in groups. This is especially true if food is clumped or shareable.

Predation risk is a second key factor to consider in the distribution of females. If the risk of predation is high, then living in groups can be beneficial, especially if the distribution of resources is abundant and not limited. However, it may be costly for females to be group-living despite a high risk of predation when the risk of infanticide by other females in the group is greater than the risk of death by predation for example (**Figure I-5**). In which case, if there is a high cost for female reproductive success, they will live alone. The distribution of males is driven by the distribution of females. Thus, if there is not a large distribution of females, males will tend to have a solitary or pair-living social organization. In contrast, if the females are distributed in groups, males will try to defend such groups against other males to monopolise reproduction (harem groups). If female groups are very large, then one male might not be able to defend them alone against all other males, and several males will join the group, leading to a social organization of multi-male multi-female. Therefore, the determinants of social organization are mostly related to the cost-benefit balance of living in groups.



<u>Figure I-5:</u> Diagram showing the socio-ecological model of group-living social organization which links female associations and relationships to ecological factors and male associations and relationships to the spatio-temporal distribution of females and mating opportunities.

I.2.3 Costs and benefits of group-living

I.2.3.1 Costs of group-living

There are various costs associated with living in a group. First of all, a group of individuals can be more easily detected than single individuals. This might explain why some group-living species forage solitarily, as is the case with striped mice where groups share a nest to sleep (Schradin 2004). Competition for food and mates as well as the transmission of diseases (bacteria, viruses or external parasites) can also have a negative impact on individuals living in groups. For example, Hoogland in 1979 showed that in prairie dogs, ectoparasites were significantly more present in large colonies than in smaller ones. This discovery is further supported with studies done by Sadoughi in primate species. Finally, brood parasitism and infanticide also represents costs to group-living.

I.2.3.2 Benefits of group-living

While the costs associated with group-living can be numerous, there are also many benefits. One main beneficial effect of living in a group is predator avoidance. Individual vigilance declines with increasing group size while overall vigilance still increases. Indeed, the more individuals there are in a group, the faster danger can be perceived. Already Kenward in 1978 demonstrated that in the goshawk, attacks on single pigeons or small flocks were more successful than attacks on larger ones. A similar finding was reported in dark-eyed juncos, where scan durations for predators decrease with group size (Lima et al. 1999). This shared vigilance in groups allows individuals to allocate more time and energy foraging, increasing their fitness. The life in group may also participate to the dilution effect. Indeed, the more individuals are in a group, the lower the chance that they are predated and the greater predator will have to cope with the confusion effect (Schradin 2000). To conclude on the beneficial effects of predator avoidance, when prey are in large numbers, they can associate and cooperate to avoid predators (Treherne and Foster 1982).

The second major beneficial effect of living in a group concerns food searching (foraging). For species feeding on clumped food sources, such as fruit, it may be easier to find good sites where food is abundant when several individuals of the group are seeking simultaneously. More experienced individuals usually know where resources are (e.g primates and elephants). For predators, living in a group can help them to cooperate in hunting (Packer and Ruttan 1988; Boesch 1994). The same applies to territory defence, where a group of individuals will be more able to defend a territory than one single individual (Farabaugh et al. 1992). Moreover, one of the other assets of group-living include thermoregulation which is improved when individuals share the same nesting site.

Individuals will live in groups when, in a given environment, the costs of this social organization are lower than its benefits (**Figure I-5**). That being so, to estimate which factors influenced the evolution of social organization of a species or population, identifying the environmental factors affecting cost and benefits of group-living is essential.

I.2.4 Ancestral social organization

Understanding the ancestral social organization is mandatory for understanding the evolution of social organization. Comparative analyses of social organization have aimed to estimate the social organization of species` ancestors and how different forms of social organization evolved thereafter (Dalerum 2007; Lukas and Clutton-Brock 2013; Kappeler and Fichtel 2016). The results of this investigation led Kappeler and Fichtel to reveal that pair-living evolved at least once from group-living ancestors in the genus *Eulemur*. Lukas and Clutton-Brock in 2013 defined the ancestor of all mammals as solitary living while Dalerum in 2007, did not found clear results regarding the ancestor of carnivores.

From these studies, the most general hypothesis is that the social organization of mammals evolved from a solitary ancestor to more complex social organizations such as group-living and pair-living (Packer and Knerer 1986; Gittleman 1989; Ewer 1998; Shultz et al. 2011; Lukas and Clutton-Brock 2013). Interestingly, for carnivores (mammals) it has been suggested that the ancestor was flexible (with the possibility of having several different social organizations) and that the currently known social organizations evolved in parallel into more specialized ones through ecological constraints (Dalerum et al. 2006, 2007). In contrast to mammals, Wcislo and Danforth 1997 studying phylogenies in bees suggested that solitary living bees may have evolved from a non-solitary ancestor.

The reasons for such discrepancies in mammals (Lukas and Clutton-Brock 2014; Opie et al. 2014) can be explained by the notable differences in their classification of social organization (Kappeler 2014; Tecot et al. 2015) associated with different databases or different conceptual analysis frameworks (Kappeler and van Schaik 2002). Moreover, to account for the largest number of species possible, some authors have used information from secondary literature and taxonomic inferences: their database contains data on species for which no information on their social organization are available, but for which it has been assumed that they have the same form of social organization as closely related species that have been studied. Some studies have misclassified social organization mixing social organization and mating system (Lukas and Clutton-Brock 2013). To resolve these different outcomes, comparative studies should be based on primary literature using the correct social organization classification without considering assumptions.

I.3 Factors linked to social organization

The predation pressure or resource distribution are factors that are not available for the ancestor. To reliably estimate the social organization of the common ancestor, the use of proxies *i.e.* factors related to predation pressure and resource distribution is necessary. Environmental factors (resource distribution and predation risk) may induce selection pressures, which will act on other biological traits than social organization, while some phenotypic traits (such as body mass or activity pattern) may have co-evolve with social organization. Phylogeny is an evolutionary constraint that should also be considered when estimating the ancestral social organization and factors associated.

I.3.1 Ecology and life history influencing sociality

Ecological and life history factors can be closely related to sociality. According to Van Schaik (1983), larger primates tend to be less vulnerable to predation than smaller ones and are thus expected to live in smaller groups (at equivalent habitat). Moreover, Clutton-Brock stated in 1977 that small body size was an important determinant of solitary-living. Small group size has been observed in nocturnal primate species while large groups are associated in savannah dwelling species, maybe because food supplies are clumped, widely dispersed and because it could be an anti-predator adaptation. Both for primates and for ungulates, group size is positively correlated with body weight (Jarman 1974). Body size and activity pattern have also been discussed to be related to canine sociality, where social species are large and diurnal, while solitary species are small and nocturnal (Bekoff et al. 1981). Kappeler and Van Schaik stated in 2002 that nocturnal activity is strongly correlated with a solitary life style in primates because group cohesion and coordination would be more difficult at night and might ease predators' attacks. However, not all nocturnal primates are solitary (Wright 1989; Gursky 2000). Concerning locomotion, Van Schaik (1983) and Janson and Goldsmith (1995) suggested that terrestrial primates live more in groups than arboreal species.

Altmann (1974) and Clutton-Brock (1974) suggested the existence of a relationship between food and sociality. Indeed, primates that live and forage in groups are able to exploit food more easily than solitary individuals because they can regulate the return times to food patches and are able to maintain exclusive territories, whereas those foraging alone cannot. For Van Schaik (1983), this argument is more likely appropriate for species needing large territories to support their needs. For example, specialist species such as frugivores, which feed on several trees that produce seasonal fruit, are more likely group-living species. Furthermore, when it is not possible to predict the presence of food at a certain location, group-living may be favoured if individuals within a group share foraging grounds and information about them. This occurs in some bird species and promotes coloniality (Ward and Zahavi 1973; Krebs and Dames 1981). This implies that information between members of the same group is exchanged, forming cohesion. This is what happens when certain species of highly frugivorous forest primates that inhabit large home ranges live in fission-fusion groups, with animals gathering around large food sources.

I.3.2 Environmental factors

As seen previously, environmental factors such as predation risk or resource competition can shape social organization by determining grouping patterns of individuals (Wrangham 1980; van Schaik and van Noordwijk 1989). In open habitats, species are more vulnerable to predation (Crook and Gartlan 1966; Janson and Goldsmith 1995), which means that individuals benefit more from living in groups. Indeed, terrestrial species in open habitats are more at risk than forest-living species because there are few refuges and they are far from each other (Crook and Gartlan, 1966). Predators have to be detected at larger distances to allow for safe retreat or organization of cooperative defence.

In addition, the climate, which is linked to habitat, is also a very important environmental factor. Cooperative groups occur more often in arid environments than in mesic ones (Brashares and Arcese 2002; Jetz and Rubenstein 2011; Ebensperger et al. 2012a, b; Firman et al. 2020), whereas humid and temperate habitats often support solitary species (Firman et al. 2020). Many studies have linked climate-related environmental harshness to sociality (Lukas and Clutton-Brock 2017; Cornwallis et al. 2017; Firman et al. 2020). Arid environments with low and unpredictable rainfall are positively correlated with the care system, *i.e.* the occurrence of non-breeding helpers in birds (Cornwallis et al. 2017) and mammals (Lukas and Clutton-Brock 2017).

I.3.3 Phylogeny

Finally, phylogeny may have an important influence on the social organization of a species. Social systems, and in particular the social organization of a species, directly relate to the species phylogenetic history. Closely related species tend to show more similar social organization than more distantly related ones do (Di Fiore and Rendall 1994; Shultz 2017). Quantitative phylogenetic analysis of social systems in primates reveals that social organization can be highly conserved in some lineages, even in the face of considerable ecological variability (Di Fiore and Rendall 1994). It has also been observed in macaques, where a strong phylogenetic effect has been observed on their social behavior (Thierry et al. 2000). This has also been shown in other taxa: parental care and social organization were influenced by phylogeny in birds (Rhijn 1990). Thus, to understand the evolution of social organization, considering the phylogenetic relationships between species is essential.

I.4 Intra-specific variation in social organization

I.4.1 Definition

Previously, it was widely believed that each species has a specific form of social organization, which varied between species. However, it has recently been recognised that social organization can also vary within species (Lott 1984; Schradin et al. 2018). Indeed, Schradin discovered in 2018 that striped mouse could change their social organization between solitary, pair-living and group-living according to ecological and life history factors. Intraspecific variation in social organization (IVSO) has also been reported in many other taxa such as shrews and their relatives (order Eulipothyphla; Valomy et al. 2015), even-toed ungulates (Artiodactyla; Miles et al. 2019), strepsirrhines (Agnani et al. 2018), and New World monkeys (Platyrrhines; Agnani 2016), suggesting that variable social organization in mammals may be more common than previously thought. However, while IVSO has been reported in some mammalian orders, detailed studies are still missing for most orders. Considering IVSO might transform our understanding of mammalian social evolution (Schradin et al. 2018; Jaeggi et al. 2020) as it describes more accurately the social organization than a simple categorization. In 2013, Schradin proposed four different mechanisms that can lead to IVSO. Those four mechanisms are dependent on environmental factors.

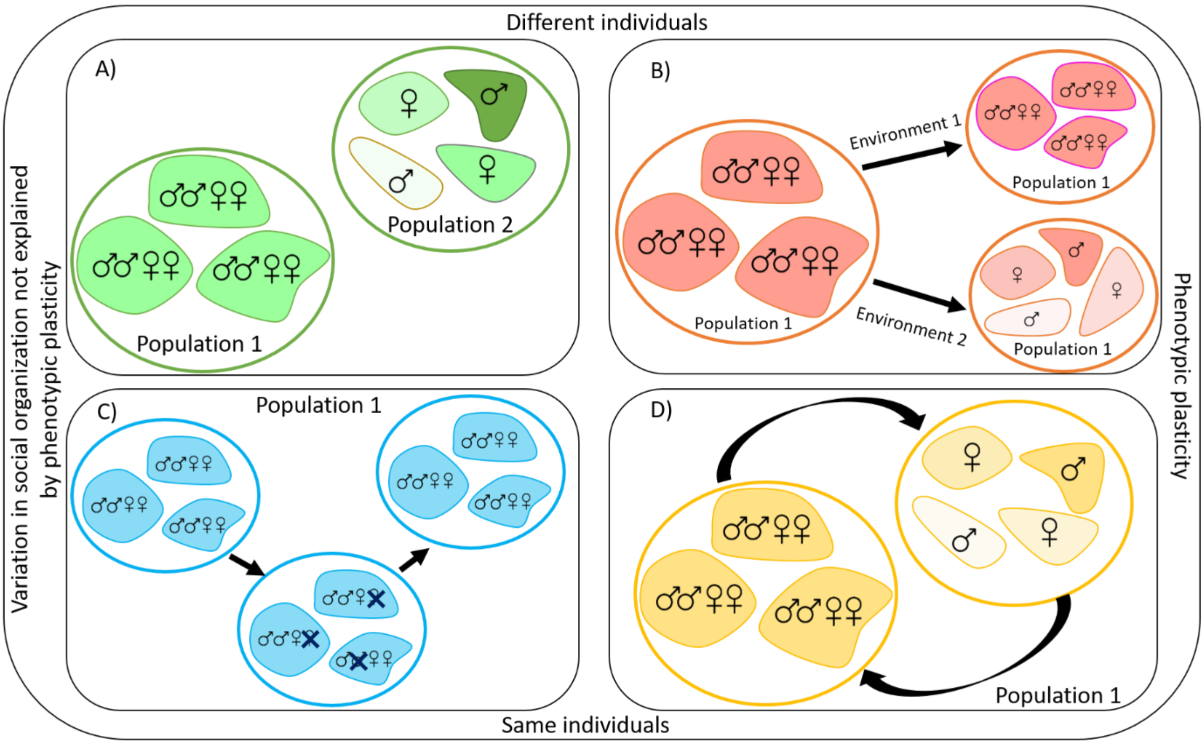
I.4.2 Mechanisms leading to IVSO

First, environmental differences between populations can lead to local adaptation through genetic differentiation (Stirling et al. 2002). Within a species, there is genetic variability. This genetic variability could result in variability in behaviors contributing to IVSO between and within populations. Genetic variation is then not related to individual plasticity and can occur between different individuals (**Figure I-6A**).

Second, different forms of social organization can appear due to developmental plasticity according to varying environmental condition within a same population (Champagne and Curley 2005). Indeed, when the environment between two generations of the same population changes, the development of individuals at early stage (pre and or post-natal) can be different than the last generation, affecting the phenotype of the new generation. Therefore, developmental plasticity is not reversible as it is a response to the early environment inducing different developmental pathways, leading to intraspecific variation in social organization (**Figure I-6B**).

Third, social flexibility, which corresponds to individuals of both sexes expressing alternative social tactics depending on the prevailing environmental or individual conditions, can occur as a reversible response of individuals to short-term environmental variation (Schradin et al. 2012; **Figure I-6D**). This is reversible phenotypic plasticity, as the same individuals can switch their tactic again depending on environmental changes. Ecological constraints are one of the most important factors for the evolution of social flexibility (Koenig et al. 1992; Schradin et al. 2012). These constraints can vary from year to year due to changes in population density for example. Depending on this, some years group-living will be favoured while other years it will be solitary living. Social flexibility is predicted to occur in less predictable environments than in the developmental plasticity case (Schradin et al. 2012). Consequently, social flexibility is adaptive when the environment in which an individual grows up does not provide significant information about the environment in which an individual will reproduce as an adult.

Finally, intraspecific variation in social organization can also result solely from extrinsic factors (stochastic processes) leading to non-adaptive changes in social organization. In this case the observed intraspecific variation in social organization is a direct consequence of a demographic interruption, and this variation is not due to an adaptive response of individuals to environmental change. Instead, the individuals will be forced to show flexibility in their behavior to respond adaptively to the change (such as starting mate searching, dispersal), but this flexibility is not the reason for the observed intraspecific variation in social organization (IVSO) that we want to explain but its consequence (**Figure I-6C**). For that reason, extrinsic factors such as the death of an individual can lead to variation in the social organization without adaptive value (Clutton-Brock and Janson 2012).



<u>Figure I-6:</u> *Figure adapted from Schradin et al. 2013. The four processes that can lead to intraspecific variation in social organization. In A) and B) different individuals differ in social organization.* ***A)*** *Genetic variation: individuals of the same species but of two different populations differ genetically, leading to differences in social organization.* ***B)*** *Developmental plasticity: depending on the environment in which individuals grow up, environmental cues will activate developmental pathways for social behavior that either leads to the same social organization as observed in their parent generation (environment 2) or to a different kind of social organization (environment 1). In C) and D), the same individuals occur in different forms of social organization.* ***C)*** *Entirely extrinsic factors: the unpredictable death/ disappearance of some breeding individuals is the only cause of changes in social organization.* ***D)*** *Social flexibility: if the environment changes, social tactics of individuals change, which as a consequence will change the social organization of the population. B) and D) represent phenotypic plasticity.*

I.4.3 Evolution of IVSO and social organization

So far, the ancestor of all mammals is believed to be solitary living. However, taking IVSO into consideration may challenge this statement. For now, only one study considered IVSO in mammals, in the carnivore (Dalerum 2007), which then found support for a socially flexible ancestor in most families of this order. This shows the importance of accounting for IVSO when studying social evolution, as not every species can be assigned to one single form of social organization (Lott 1984).

I.5 Objective of study and organizational layout

My introduction tried to show that the evolution of social organization remains a controversial study subject with many open and unresolved questions. The search for ancestral social organization in mammals is essential to understand our own ancestry. However, with the discovery of IVSO and a proper classification of social systems, the evolution of social organization can be better understood.

In my thesis I am interested in the evolution of social organization in mammals. Mammals are a great class to study as they occur in all terrestrial and marine habitats and some of them can even fly. They have been extensively studied, count more than 5500 species and are present on all continents (Kleiman and Malcolm 1981; Thierry et al. 2000; Lukas and Clutton-Brock 2013). The study of this class can be extrapolated to other clades. Recent discoveries concerning fossils of early mammals and their ancestors have shown that the ancestor of mammals might have been more social than previously thought. During the Triassic period, the cynodonts (mammalia forms living between 260 and 230 million years ago) that gave rise to the mammals spent most of their time in burrows. Fossils of cynodonts have been found in these burrows grouping juveniles with adults as well as several adults fossilised together indicating a social lifestyle (Jasinoski and Abdala 2017). Moreover, the absence of sexual dimorphism associated with the small number of adults found together indicates that this could be a pair-living organization. These results corroborate with Groenewald in 2001 where bones of about 20 individuals *Trirachodon* from the lower Triassic (250 million years ago) were found together indicating a group-living social organization for this cynodont. In Bolivia, the remains of 35 skeletons of mammals have been collected that are from the early Palaeocene, 60 million years ago. These individuals were probably belonging to the same group as they were buried in a single catastrophic event. The preservation of multiple adult, sub-adult and juvenile individuals in close proximity (<1m^2) supports this theory and indicates either a gregarious social lifestyle or at least a high degree of social tolerance. This study shows that sociality occurred early in marsupials and that solitary behavior may not be plesiomorphic (Ladevèze et al. 2011).

Hence, there is palaeontological evidence against a solitary mammalian ancestor. Previous studies of ancestral social organization had the shortcomings of not taking variation into account, and of making assumptions of the social organization of many no studied species. My thesis is written in this context and is aimed to better **understand the evolution of the social organization in mammals**, by asking:

1) How much variation in social organization exists in mammals at the species and population level?

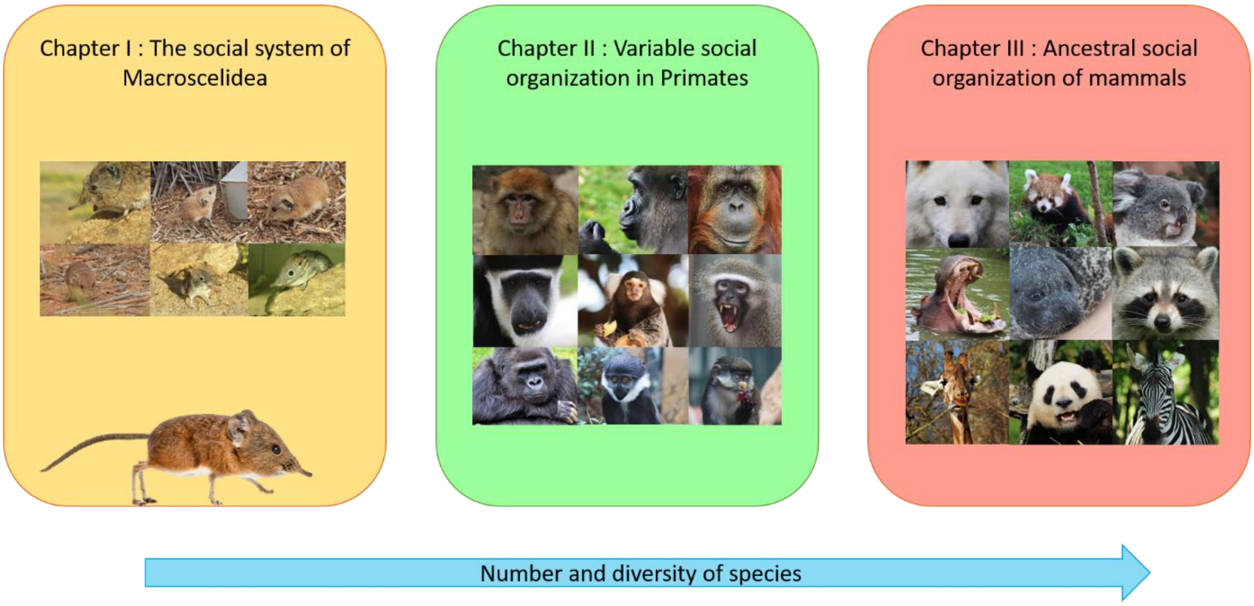
2) Does our understanding of the ancestral social organization change when we take variation into account?

3) Which ecological and life history factors are associated to the different forms of social organization (including variation)?

4) What was the ancestral social organization of all mammals?

To achieve my aims, I created a database of all current mammalian species considering only on primary literature on social organization observed during field studies. In this database I recorded any variation of social organization. Then, using modern Bayesian statistics and considering for the first time IVSO as a continuous variable, I studied the ancestral state of mammals.

My thesis contains one review and three research chapters in which I studied different taxa of mammals, starting with an order with few species and ending with a study of all extant mammalian species (**Figure I-7**).



<u>Figure I-7:</u> Schematic representation of the structural framework developed in this thesis. *Chapter 1 covers questions on social systems of Macroscelidea, chapter 2 on the social organization of Primates and chapter 3 is about the ancestral social organization of all mammals*.

Chapter 1 - Revisiting the components of Macroscelidea social systems: Evidence for variable social organization, including pair-living, but not for a monogamous mating system.

In the first chapter, I studied elephant-shrews (Macroscelidea), an order of mammals comprising of only 19 species. They have been considered to be the only mammalian order where all species were believed to be monogamous (mating system) because of observations of them living in pairs (social organization). To identify gaps in our knowledge of their social system, I reviewed evidence for a pair-living social organization, mate fidelity (mating system), pair bonds (social structure), and biparental care (care system). I created a database reporting all these aspects and analyzed the ancestral social organization of Macroscelidea. I reconstructed the ancestral social organization of Macroscelidea using Bayesian phylogenetic mixed-effects models based on the main social organization of the different Macroscelidea populations or by considering variation in a categorical way. I also wanted to investigate if factors such as body mass, population density or habitat were related to certain types of social organization.

Chapter 2 - Primate Social Organization Evolved from a Flexible Pair-Living Ancestor.

Next I studied the most studied mammalian order and our closest relatives, the primates. The first objective of this study was to review what we know about their social organization and investigate how often IVSO has been reported within and between species through an intensive primary literature search of all 445 primates species. The second aim was to determine the ancestral social organization of all primates using modern Bayesian phylogenetic mixed effect model. It has often been suggested that the ancestor of all primates was solitary and that other forms of social organization evolved later (Shultz et al. 2011; Lukas and Clutton-Brock 2013; Kappeler and Pozzi 2019). In contrast to chapter 1, in which variation was considered as a categorical variable, here we used more advanced statistics in order to take into account IVSO as a continuous variable. Finally, the effect of several life history (body mass, diet, locomotion, activity pattern, foraging pattern) and environmental factors (habitats) on sociality at the population and the species level was also tested.

Chapter 3 – Was the ancestral placental mammal really solitary living?

To finish with the levels of complexity, I have studied all extant mammals. The aim of this study was to create a database on the social organization of mammalian species and to determine the ancestral social organization of all mammals by taking IVSO into account. Finally, I investigated which life-history or environmental factors were related to certain social organization.

Chapter 4– Global Change and Conservation of Solitary Mammals

Lastly, in this final chapter, I have written an opinion piece aimed at highlighting the importance of knowing the behavior of species and more precisely their social organization to conserve them in a context of global change.

The main aim of my thesis was to provide a new perspective on the evolution of mammalian social organization by 1. Focusing only on species studied in their natural environment, 2. for the first time taking IVSO into account, and 3. by using for the first time IVSO as a continuous variable in a Bayesian statistical framework.

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CHAPTER 1

II. Chapter 1: Revisiting the components of Macroscelidea social systems: Evidence for variable social organization, including pair-living, but not for a monogamous mating system

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II.1 Résumé

Les musaraignes-éléphants (Macroscelidea) ont longtemps été considérées comme le seul ordre de mammifères entièrement monogame (système d’accouplement) sur la base d’observations de la vie en paire (organisation sociale). Nous avons passé en revue les études concernant les quatre composantes des systèmes sociaux (organisation sociale, système d'accouplement, structure sociale et système de soins) chez les musaraignes-éléphants afin d'évaluer si elles sont réellement monogames. Afin d’identifier nos connaissances sur leurs systèmes sociaux, nous avons examiné les indicateurs de fidélité (système d'accouplement), d’organisation sociale en couple, de liens entre les couples (structure sociale) et de soins biparentaux (système de soins). Concernant l'organisation sociale, sept des huit espèces de musaraignes-éléphants étudiées sur le terrain présentaient une vie en couple, c'est-à-dire qu'un mâle et une femelle partageaient un même domaine vital. Cependant, ces sept espèces présentaient des variations intra-spécifiques dans l'organisation sociale : deux des sept espèces vivaient également en solitaire, deux autres également en groupe, et les trois dernières en solitaire et en groupe ; la huitième espèce étant exclusivement solitaire. Nous avons reconstitué l'organisation sociale ancestrale des Macroscelidea en utilisant des modèles phylogénétiques bayésiens à effets mixtes. Nous avons constaté que l’état ancestral le plus probable était variable, plutôt qu’exclusivement en couple, bien qu'il y ait une grande incertitude. Aucun facteur socio-écologique (masse corporelle, densité de population et habitat) ne permettait de prédire la variation de l'organisation sociale. Les observations d'accouplements ont été extrêmement rares, de sorte qu’aucune certitude ne peut être établie sur le système d'accouplement. De plus, une étude non publiée a indiqué des niveaux élevés de paternité hors-couple. En ce qui concerne la structure sociale, aucune preuve de lien entre

les couples n’a été établie mais il y a des preuves de protection du partenaire existent. Pour le système de soins, seuls les soins maternels ont été observés. En effet, les femelles ont une stratégie d'absentéisme, c'est-à-dire qu'elles visitent leur progéniture uniquement pour de courtes périodes d'allaitement. Il n'existe aucune preuve empirique que les Macroscelidea représentent un ordre de mammifères monogames (système d'accouplement). Les variations intra-spécifiques dans l’organisation sociale sont courantes. Nous suggérons donc d’éviter l’affirmation selon laquelle les musaraignes-éléphants constituent un ordre monogame et nous invitons à réaliser davantage d’études de terrain sur l’organisation sociale et le système d’accouplement des Macroscelidea.

II.2 Abstract

Elephant-shrews (Macroscelidea) have long been considered the only mammalian order to be completely monogamous, based on observations of their pair-living social organization. We reviewed primary studies on the four components of social systems (social organization, mating system, social structure and care system) in elephant-shrews to evaluate whether they truly are monogamous. To identify gaps in our knowledge of their social system, we reviewed evidence for a pair-living social organization, mate fidelity (mating system), pair bonds (social structure), and biparental care (care system). Field data were available for eight species, and seven were often pair-living. However, these seven species exhibited intra-specific variation in social organization; two of these species were also solitary living, two species were also group-living, and the remaining three species were both solitary and group-living. The eighth species was exclusively solitary. We reconstructed the ancestral social organization of Macroscelidea using Bayesian phylogenetic mixed-effects models and found that variable social organization, rather than exclusive pair-living, was the most likely ancestral state, though there was high uncertainty. No socio-ecological factors (body size, population density and habitat) predicted a specific social organization. Observations of mating have been rare, such that no firm statements can be made. However, one unpublished study indicated high levels of extra-pair paternity. Regarding social structure, there was no evidence of pair-bonding, but there was evidence of mate guarding. Only maternal care has been observed, with females having very short nursing bouts. Evidence suggests that despite having often a pair-living form of social organization, Macroscelidea should not be described as a monogamous order, as little or no evidence supports that designation, nor are they exclusively pair-living (social organization) and we urge further field studies on Macroscelidea social systems.

Key words: sengi, intra-specific variation, social flexibility, *Elephantulus*, *Macroscelides, Petrodromus, Rhynchocyon*

Running title: elephant-shrew social systems

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Conflict of interest statement and ethical considerations

The authors and co-authors have no conflict of interest to declare. Ethics approval was not required for this research.

II.3 Introduction

Kappeler (2019) suggested that animal social systems are composed of four inter-related components: social organization, social structure, mating system, and care system. The social organization describes the size, sexual composition and spatiotemporal cohesion of a group (Kappeler & van Schaik, 2002). Three major categories of social organization occur: solitary living, pair-living, or group-living. The social structure describes the different interactions between members of the same group and the resulting relationships. The mating system describes who mates with whom and the reproductive consequences (e.g. paternity). There are four types of mating system, depending on the number of mating partners for males and females (Clutton-Brock, 1989; Loue, 2007): monogamy, polygyny, polyandry or polygynandry. Finally, the care system is about who cares for the dependent offspring (Kappeler, 2019).

Over the last decades, the study of animal social systems has undergone significant progress due to long-term studies and advances in technology (e.g genotyping ; Clutton-Brock 2021). Often the focus has been on specific social systems such as monogamy (Kleiman 1977; Mock & Fujioka, 1990; Lukas & Clutton-Brock 2013). Initially, pair-living (a form of social organization) was often regarded to be indicative of a monogamous social system in mammals (Kleiman 1977, 1981). However, genetic fingerprinting revealed that extra-pair paternity is common in many pair-living species (Cohas & Allainé, 2009), leading to the realization that seemingly monogamous relationships do not necessary predict genetic outcomes (i.e., genetic monogamy). As a result, some researchers introduced the term “social monogamy” (Dobson, Way & Baudoin 2010; Gowaty & Buschhaust 1998) to distinguish social behavior within pairs from genetic monogamy. Recent reviews from multiple research groups advocate abandoning the term "social monogamy", and using the term "monogamy" only in the context of mating systems (Fernandez-Duque et al. 2020; Garber et al. 2016; Huck, Di Fiore & Fernandez-Duque 2020; Kappeler & Pozzi 2019; Kvarnemo 2018; Tecot, Singletary & Eadie 2016). Arguments against the use of the term "social monogamy" are centered on the importance of distinguishing between the different components of social systems for understanding their evolution. For example, if one wants to understand why animals live in pairs, it is not necessary to assume that they mate monogamously, only, that pair-living adds to a higher fitness than alternative forms of social organization. It is therefore necessary when describing the social system of a species, that social organization, mating system, social structure and care system are considered (Kappeler 2019).

Describing all four components of a social systems is a challenge, for a number of reasons. For example, it was previously assumed that "socially monogamous" species are pair-living (social organization), have pair bonds (social structure), and engage in biparental care (Kleiman, 1977; Mock & Fujioka, 1990). However, it is well known that several pair-living taxa do not fit this syndrome (Kleiman, 1977), such as dwarf antelopes (Bovidae) that do not exhibit biparental care (Komers, 1996), elephant-shrews (Macroscelididae) that do not have pair bonds (*i.e.* individuals showing a preference for a specific opposite sex-individual, which can be tested experimentally: Carter et al., 1995; Garnier and Schradin 2019) or exhibit biparental care (Rathbun & Rathbun, 2006). Most confusion, however, arises from the inconsistent use of the term "monogamy" (see above and Kappeler, 2019; Solomon & Ophir, 2020), which should be restricted to describe the mating system where reproduction occurs mainly within pairs (Kappeler, 2019; Kappeler & van Schaik, 2002; Mock & Fujioka, 1990). For understanding the evolution of pair-living, the different components of social systems should be studied separately from each other (Fernandez-Duque et al., 2020; Huck et al., 2020; Kappeler, 2019).

A species' social organization is typically characterized by the most frequent form, an approach that ignores intra-specific variation (Schradin et al., 2018). For example, the greater white-toothed shrew (*Crocidura russula*) has a variable social organization including solitary, pair and group-living (Cantoni & Vogel, 1989; Ricci & Vogel, 1984). Intra-specific variation in social organization (IVSO) has now been reported in many mammalian taxa, including Artiodactyla (Jaeggi et al., 2020), Carnivora (Dalerum, 2007), Eulipotyphla (Valomy et al., 2015), and Strepsirrhini (Agnani et al., 2018). IVSO may be more common in other mammalian taxa as well, where variation has been possibly ignored to emphasize the most frequent or the most interesting form of social organization (Schradin et al., 2018). A consideration of IVSO, and variation within the three other components of social systems can transform our understanding of social evolution (Jaeggi et al., 2020; Schradin et al., 2018).

The mammalian order Macroscelidea (elephant-shrews or sengis) includes 19 extant species in four genera, all occurring in Africa, ranging in body mass from 27g to 700g (Rathbun & Dumbacher, 2015; Rovero et al., 2008) and occupying a diversity of habitats including deserts, semi-deserts, savannahs, rocky mountains, lowland forests and tropical rain forests (Kingdon et al., 2013 ; Rathbun, 1979). Macroscelidea is the only mammalian order for which all extant species are believed to be monogamous (Lukas & Clutton-Brock, 2013; Rathbun & Rathbun, 2006; Ribble & Perrin, 2005), though this typically refers to a pair-living social organization (Schubert et al., 2009). Theory predicts that the ability of males to monopolize access to females, which depends on ecological factors and population density, will greatly influence mating systems (Emlen & Oring, 1977). The main hypothesis for monogamy in Macroscelidea is that low population density, possibly due to their insectivorous diet, makes it unfeasible for males to defend more than one female (Ribble & Perrin, 2005; Schubert et al., 2009). Males generally mate-guard a single female, leading to pair-living and potentially monogamous mating (Fitzgibbon, 1997; Ribble & Perrin, 2005; Schubert et al., 2009). Thus, their small body size combined with low population density is believed to have favored the evolution of monogamy.

The long-held assumption that all elephant-shrews are monogamous might have led to an underappreciation of variation in their social systems. The last detailed review on monogamy in elephant-shrews was published more than 40 years ago (Rathbun, 1979), and was updated within the discussion of a more recent case study (Rathbun & Rathbun, 2006). Therein, the importance of considering intra-specific variation for understanding the social systems of elephant-shrews, which were still considered to be all monogamous, was emphasized (Rathbun & Rathbun, 2006). To date, no review has differentiated between the four different components of social systems in elephant-shrews or summarized the observed intra-specific variation.

The overall aim was to describe all four components of the social system of elephant-shrews, taking intra-specific variation into account. First, we conducted a systematic review of the primary literature on elephant-shrew social organization, mating systems, social structure and parental care. This approach allowed us to evaluate the empirical evidence suggesting that elephant-shrews are pair-living and monogamous. Second, we compared our dataset on elephant-shrew social organization – the component of the social system with the most data – with other available datasets that also used secondary sources to summarize their social systems (Heritage, 2018; Lukas and Clutton-Brock, 2013; Nowak & Wilson, 1999). Third, we report the results of phylogenetic comparative analyses to estimate the ancestral state of all elephant-shrews. Social organization was the only component for which sufficient data were available to conduct such an analysis. Based on previous reports, we expected the ancestral social organization to be pair-living. Body mass and habitat diversity differ widely between species and could influence their social organization. For example, living in variable habitats can affect density or grouping pattern of a population, through food availability or predation pressure (Geist 1974). We therefore expected that variability in social organization will increase with variability in habitats (Schradin et al., 2018). Population density is the factor most emphasized to have influenced the evolution of pair-living in elephant-shrews (Rathbun & Rathbun, 2006) and mammals more broadly (Lukas & Clutton-Brock, 2013 but see Dobson et al. 2010), such that we predicted pair-living to be associated with low population density, making it difficult for a male to associate with more than one female.

II.4 Materials and Methods

II.4.1 Literature searches

The 19 species of elephant-shrews were identified using the IUCN (International Union for Conservation of Nature) database (2019). Literature searches on the four social system components were conducted in Web of Science (Thomson Reuters) and in Google Scholar between November 2019 and March 2020 using specific key words (see the different sections below). This search yielded 166 articles that were scanned for information on social systems. Additional papers cited in those 166 articles were also studied. Data were recorded at the population-level.

II.4.2 Social organization

For each species, the current and previously used Latin name of the species and the term “social” was searched. If no literature on social organization was found, the search was repeated in Web of Science and Google Scholar, only with the Latin name (for 10 species). To obtain information on social organization, only peer-reviewed literature from studies conducted in the field about elephant-shrews were taken into account, and reviews and studies in captivity were ignored. For each study, the following keywords were searched throughout the PDF’s: "social", “solitary”, “group”, “pair”. All figures and tables were examined. Data on social organization were found in 11 papers on 8 species.

Seven categories of social organization including solitary living, pair-living, and different forms of group-living (one male with multiple females, multiple males with multiple females, one female with multiple males, multiple females and multiple males) were defined, of which only three were reported in the elephant-shrew studies (Table II- 1).

Table II-1: *Types of social organization reported in field studies on elephant-shrews.*

Social organization	Definition
Solitary living	Both resident adult solitary males and solitary females occur in the population (excluding dispersing individuals)
Pair	One adult female and one adult male share a home range, with or without dependant offspring
One male multi female groups	Multiple breeding females and one breeding male share a home range

For our study, we only considered adult and mature individuals. For each paper, we recorded the number of social units reported as solitary, pair-living, or group-living. Individuals of a species were considered as solitary only if both sexes have been observed to be solitary, as single individuals of one sex could represent dispersers. Identified dispersers were always ignored. For solitary living, we used the smaller number of the two sexes to have a number comparable to pairs (*e.g.* when four solitary males and three solitary females were observed, we recorded “3” solitary social units). Individuals of a species were considered as being pair-living when a male and a female have a significant overlap of their home ranges with each other but not with other individuals. Populations in which two or more forms of social organization were recorded were categorized as variable resulting in four possible social organizations within populations: solitary, pair-living, group-living, and “variable” (solitary/pair; pair/group; solitary/pair/group). In addition, we recorded whether the study took place during the breeding season, during the non-breeding season or throughout the year.

II.4.3 Mating system

For the mating system, peer-reviewed literature from studies conducted in the field and in captivity were taken into account. Searches included the following key words: “monogamy”, “polygamy”, “polyandry”, “polygyandry” and “promiscuity”. In addition, we report data presented on a poster available on researchgate (Peffley et al. 2009).

II.4.4 Social structure

For the social structure, peer-reviewed literature from studies conducted in the field and in captivity were taken into account. Searches were made using the following key words: “solitary foragers”, “pair bond”, “aggression”, “mate guarding”. This resulted in five suitable studies on social structure. Information on pair-bonds, aggression toward offspring, foraging, time spent between individuals, chasing, mate guarding and aggression between females or between males was recorded as present or absent.

II.4.5 Care system

For the care system, peer-reviewed literature from studies conducted in the field and in captivity were used. Searches were made using the following key words: “maternal care”, “paternal care”, “offspring”, “direct paternal care”, “indirect paternal care” and “absentee strategy” which are common terms for Macroscelidea (Rathbun, 1979). Indirect paternal care represents behaviors shown by the fathers independent of the presence of offspring which are beneficial for the offspring (while direct paternal care is a direct response to the presence of offspring; Kleiman, 1977). This resulted in six suitable studies of care systems. We reported whether maternal and paternal care was observed.

II.4.6 Dataset comparison

We compared our data with the database from Lukas and Clutton-Brock (Lukas & Clutton-Brock, 2013). Additionally, we compared our database with information in secondary literature, specifically in Walker’s Mammals of the World Volume II (Nowak & Wilson, 1999) and the Handbook Mammals of the World (Heritage, 2018), compiled by taxon-specific experts. This comparison was only made for social organization, the only category for which sufficient data from peer-reviewed literature were available.

II.4.7 Predictors for social organization

We included the following predictors in our Bayesian model described below: body mass, population density, number of studies per population and habitat heterogeneity (see

Supplementary Material SII-1, SII-2 and SII-3). Habitat heterogeneity represents the maximum number of habitats per population. Habitat type was reported from the primary literature and categorized on IUCN classification as shrubland, rocky areas, bushlands, desert or forest. Habitat heterogeneity and whenever possible, body mass and population density, were extracted from the same study in which data on social organization had been reported. If no information was available in that same study, we searched for other studies of the same population (two species). Finally, if no information was available, we searched the primary literature for data on the same species in other populations (one species).

II.4.8 Phylogenetic comparative analysis

All statistical analyses were conducted in R v.3.6.1 (The R foundation for statistical computing). To analyze social organization, Bayesian phylogenetic mixed-effects models were used in order to account for the multilevel structure of the dataset (populations nested within species) and the phylogenetic relationships among species (de Villemereuil, 2014). To represent the phylogenetic relationships and their uncertainty a sample of 100 phylogenetic trees was downloaded from the online database VertLife (http://vertlife.org/data/). The parameter used to create the tree was "Mammals birth death node dated completed tree". We used the R package *brms* (Bürkner) to fit multinomial models to the response variable social organization, wherein each population could occupy one of several mutually exclusive states. We created three models. In model 1, the social organization (solitary, pair-living, group-living and variable) was the response variable. In model 2, the response variable was separated into all possible combinations (solitary+pair-living, pair+group-living and solitary+pair-living+group-living) to estimate the most likely ancestral social organization. In model 3, we used the main (*i.e.* the modal or most common) form of social organization, defined as the social organization for which the most social units were observed (solitary, pair-living and group-living) as the response variable. In this model, variability was not included except for one species, *Macroscelides flavicaudatus*, where an equal number of social units were solitary and pair-living.

For each model, we also calculated the percentage of the difference between the probability of two different social organization using the posterior samples (*e.g.* all samples for the probability of variable social organization minus all samples for the probability of pair-living) and whether the probability of that difference was greater than zero (*i.e.* the proportion of the resulting samples >0); the ability to compute such contrasts between model parameters is a notable strength of Bayesian inference (McElreath 2019), whereas frequentist models are limited to comparing estimated parameters to 0. Hence we can directly express the model's greater confidence that a given social organization had a higher probability than others, which cannot be learned by merely comparing each social organization's mean probability and confident intervals. Thus, even if the exact probability of each social organization is estimated with high uncertainty (large 95% CIs), we can have more confidence in the probability of differences between the probabilities of two social organizations.

We included the following predictors in our models: body mass, population density, number of studies per population and habitat heterogeneity (number of habitat per population; see Supplementary Material SII-1, SII-2 and SII-3). The number of studies per population (one or two) was added to control for research effort. The number of studies per population and habitat heterogeneity were centered on one. Body mass and population density were centered on their mean.

Our model converged well with Rhat values (potential scale reduction factor) ≤ 1.01. The likelihood of each social organization being the ancestral state was inferred from the intercepts of the model, *i.e.* the probability of each social organization when predictors were at their means. Pair-living was the reference category in our two models.

The phylogenetic signal (ʎ) was calculated as the proportion of variance captured by the phylogenetic random effects (Nakagawa & Schielzeth, 2013):

$$ʎ = \frac{\boldsymbol{\sigma_p^2}}{\boldsymbol{\sigma_p^2 + \sigma_r^2 + \sigma_d^2}}$$

$\sigma^2{}_p$ represents the variance of the phylogeny random effect, $\sigma^2{}_r$ is the variance of the species-level random effect and $\sigma^2{}_d$ is the distribution-specific variance equal to $\pi^2/3$ (Nakagawa and Schielzeth, 2013).

II.5 Results

II.5.1 Social organization

Data on social organization were reported for twelve populations of eight species (**Table II-2**). One species (*Macroscelides micus*) was only reported to be solitary living whereas the other seven species had variable social organizations. Two species were solitary and pair-living, three species were solitary, pair- and group-living and two species pair- and group-living (**Table II-2**). Of the twelve studied populations, one population was solitary (*Macroscelides micus)* and two populations of *Petrodromus tetradactylus* were pair-living. The other 10 populations (75%) had a variable social organization (**Table II-2**).

Table II-2: The different forms of social organization reported in the primary literature*. Numbers refer to the numbers of social units observed. BS: breeding season; NBS: non-breeding season; BOTH: breeding and non-breeding season; ALL: non-seasonal breeding throughout the year. No data could be found on social organization of the remaining species (Elephantulus brachyrhynchus, Elephantulus edwardii, Elephantulus fuscipes, Elephantulus fuscus, Elephantulus pilicaudus, Elephantulus rozeti, Elephantulus rupestris, Rhynchocyon cirnei, Rhynchocyon petersi and Rhynchocyon udzungwensis).*

Species	Population	Solitary	Pair-living	One male several females	References
Elephantulus intufi	Erongo Wilderness Lodge Okapekaha Farm, Namibia	-	6 (BOTH)	1[‡] (BOTH)	Rathbun & Rathbun, 2006
Elephantulus myurus		5 (BOTH)	18 (BOTH)	-	-
	Weenen Nature Reserve, South Africa	1 (BS)	12 (BS)	-	Ribble & Perrin, 2005
	Goro Game Reserve, South Africa	2 (BS) 2 (NBS)	4 (BS) 2 (NBS)	-	Hoffmann et al., 2019
Elephantulus rufescens	Bushwacker, Kenya	2 (ALL)	7 (ALL)	1[‡] (ALL)	Rathbun, 1979
Macroscelides flavicaudatus	Namib Desert, Namibia	2 (BS)	2 (BS)	-	Sauer, 1973
Macroscelides micus	Eastern Goboboseb Mountains, Namibia	2 (BS)	-	-	Rathbun & Dumbacher, 2015
Macroscelides proboscideus	Goegap Nature Reserve, South Africa	1 (BOTH)	32 (BOTH)	1[‡] (BOTH)	Schubert et al., 2009
Petrodromus tetradactylus		-	5 (BOTH)	1 (BS)	-
	Tembe Elephant Park, South Africa	-	4 (NBS)	-	Oxenham & Perrin, 2009
	Arabuko Sokoke Forest, Kenya	-	1 (BOTH)	-	Fitzgibbon, 1995
	Sodwana Bay National Park, South Africa	-	-	1 (BS)	Linn et al., 2007
Rhynchocyon chrysopygus		1 (ALL)	12 (ALL)	3 (ALL)	-
	Arabuko Sokoke Forest, Kenya	-	5 (ALL)	2[‡] (ALL)	Fitzgibbon, 1997
	Gedi Forest	1 (ALL)	7 (ALL)	1[‡] (ALL)	Rathbun, 1979

[‡] *One male and several female association (group-living) lasted two weeks for Elephantulus intufi, 42 days for Elephantulus rufescens, five to six weeks for Macroscelides proboscideus, six weeks, two and three months for Rhynchocyon chrysopygus.*

II.5.2 Mating system

Our search generated only one paper that reported observations of mating in the field (Rathbun, 1979). A male *Rhynchocyon chrysopygus* chased the female and then copulated with her during two seconds with five rapid copulations. Schubert et al. (2012) found in captive experiments that female *Macroscelides proboscideus* showed as many sexual interactions with a neighboring male as with her pair partner, and that males actively aimed to mate with non-pair neighboring females. In an unpublished poster on a study using micro-satellites to determine paternity in *Macroscelides proboscideus*, Peffley et al. (2009) found for the population studied by Schubert et al. (2009) that only two out of six mother-offspring families resulted from serially monogamous mating. From a sample of 19 offspring, the male of the pair was the sire of only seven. At least six offspring were sired by another male than the female's social mating partner.

II.5.3 Social structure

Our search generated six studies reporting information about social interactions (Table II-3). Individuals living together had little social interaction, there were no pair-bonds, and they were solitary foragers (Rathbun, 1979). Mate guarding was said to occur in five species (Table II-3). In *Elephantulus myurus* (Ribble & Perrin, 2005) and in *Rhynchocyon chrysopygus* (Fitzgibbon, 1997), males defended territories containing females, and these territories were quickly taken over by other males after the pair male disappeared (resulting in a change of the adult sex ratio). This was regarded as evidence of male mate guarding. The same association pattern has been interpreted as mate guarding in several other species, where males followed their females when in estrus, though mate guarding was not measured directly (Rathbun, 1979). The only study that directly measured mate guarding was in *Macroscelides probiscideus*, where males reduced the distance to their female in the periods they were receptive (Schubert et al., 2009). Similarly, in the solitary species *Macroscelides flavicaudatus*, males associated with females when these were receptive, but then male left, searching for other females (Sauer, 1973). Moreover, both sexes defend a territory and are very aggressive towards conspecifics of the same sex (FitzGibbon, 1997; Rathbun, 1979). Schubert et al. (2012) found in captive experiments no evidence for pair-bonding, but individuals of both sexes readily interacted with opposite sex conspecifics with which they were not paired.

In several species, aggression towards young was observed around weaning. Some species tolerated their weaned offspring for periods ranging from 21 to 40 days old (Rathbun, 1979; Schubert et al., 2012) while in *Elephantulus rufescens*, parents tolerated one of their young for the entire period of 193 days. In *Elephantulus rufescens*, some offspring can remain in their parents' territory long after reaching adulthood (Rathbun, 1979).

Table II-3: *The different components of social structure identified in our primary literature research. Pair-bond (PB); aggression toward their offspring (ATO); solitary foragers (SF) ; Male and female spend considerable time together (Time MF); chase conspecific that entered their territory (Chase); mate guarding (MG); aggression between neighboring females (Ag FF); aggression between neighboring males (Ag MM).*

Species	PB	ATO	SF	Time MF	Chase	MG	Ag FF	Ag MM	References
Elphantulus myurus	-	-	-	-	-	yes	-	-	Ribble & Perrin, 2005
Elephantulus rufescens	no	yes (40 days old)	yes	-	-	yes	yes	yes	Rathbun, 1979
Macroscelides flavicaudatus	no	-	yes	no	-	yes	-	-	Sauer, 1973
Macroscelides proboscideus	no	yes (21 days old)	-	-	yes	yes	-	yes	Schubert et al., 2012; Schubert et al., 2009

Petrodromus tetradactylus	no	-	yes	-	-	-	yes	yes	Rathbun, 1979
Rhynchocyon chrysopygus	-	no (193 days old)	yes	no	yes	yes	yes	yes	Rathbun, 1979; FitzGibbon, 1997

II.5.4 Care system

We found information on the care system for six of the 19 species (Table II-4). The precocial young were visited and nursed by the mother for very short periods of 10-60 seconds, which has been called an absentee strategy (Rathbun, 1979). During this period, the female was not engaged in other care activities, such as cleaning or huddling the offspring. Maintenance of pathways by males to allow offspring to move quickly and escape from a predator was reported for five species (Table II-4) and interpreted as indirect paternal care while no direct paternal care was observed.

Table II-4: *Care system identified in literature for Macroscelidea.*

Species	Direct maternal care	Direct paternal care	Indirect paternal care	References
Elephantulus intufi	yes	no	yes	Rathbun & Rathbun, 2006
Elephantulus myurus	-	no	yes	Ribble & Perrin, 2005
Elephantulus rufescens	yes	no	yes	Rathbun, 1979
Macroscelides flavicaudatus	yes	-	-	Sauer, 1973
Rhynchocyon chrysopygus	yes	no	yes	Rathbun, 1979 ; FitzGibbon, 1997
Rhynchocyon petersi	-	no	yes	Baker et al., 2005

II.5.5 Dataset comparison

In our database, the most frequent form of social organization observed of six of the eight species of Macroscelidea was pair-living (**Table II-5**), while one species had a solitary main social organization (*M. micus*) and another had an equal number of solitary and pair-living social units, hence a variable main social organization (*M. flavicaudatus*). Thus, our results of main social organization were similar to what was reported by Lukas and Clutton-Brock (2013). Seven (87.5%) of the species with information available showed IVSO and the only species (12.5%) with a single form of social organization was solitary. This high prevalence of IVSO was not represented in the database of Lukas and Clutton-Brock (2013), in which 15 (93.3%) of the elephant-shrew species were reported to be pair-living and one (6.7%) to be solitary (Table 5 and Supplementary Material SII-4). They reported *Petrodromus tetradactylus* to be solitary, which we found to be variable with pair and group-living, while the species we reported to be solitary, *Macroscelides micus*, was studied after the paper from Lukas & Clutton-Brock (2013) by Rathbun & Dumbacher (2015) (see Supplementary Material SII-4).

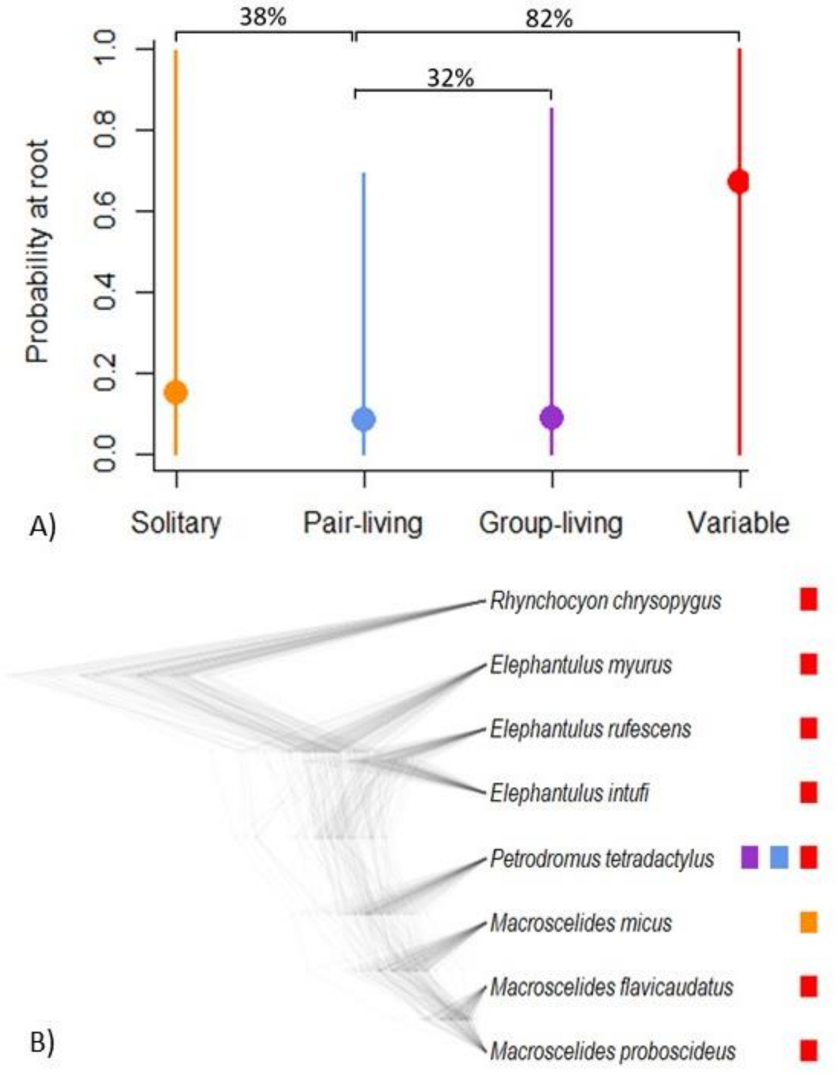
The Handbook Mammals of the World (Heritage, 2018) reported all elephant-shrew species to be pair-living. Walker's Mammals of the World (Nowak & Wilson, 1999) reports data on eight species, with five (62.5%) of them showing IVSO, two (25%) being pair-living and one (12.5%) being solitary living (**Table II-5**).

Table II-5: *Social organization of Macroscelidea reported in primary literature and compared to three published databases (Lukas and Clutton-Brock 2013, the book Mammals of the World by Nowak and Wilson, 1999, and the Handbook Mammals of the World by Heritage 2018). Note that Lukas and Clutton-Brock as well as Handbook Mammals of the World only report the most frequently observed form of social organization and did not consider IVSO. WMW=Walker's Mammals of the World; HMW=Handbook of the Mammals of the World.*

	Our study	Our study (main social organization)	Lukas and Clutton-Brock 2013	WMW 1999	HMW 2018
Number of species with information on social organization	8	8	15	8	10
Number of species showing IVSO	7 (87.5%)	1 (12.5%)	0	5 (62.5%)	0
Number of exclusively solitary species	1 (12.5%)	1 (12.5%)	1 (6.66%)	1 (12.5%)	0
Number of exclusively pair-living species	0	6 (75%)	14 (93.33%)	2 (25%)	10 (100%)
Number of exclusively group-living species	0	0	0	0	0

II.5.6 Phylogenetic comparative analysis

The phylogenetic mixed effects models showed no significant effects of habitat heterogeneity, population density, body mass and number of studies on social organization (see Supplementary Material SII-5, SII-6 and SII-7). The phylogenetic signal for model 1 was moderate (mean=0.35, 95% CI= 0.008- 0.75). Variable social organization had the highest probability as ancestral state (mean probability = 0.67, 95% CI = 0-1) compared to solitary living (mean = 0.15, 95% CI = 0 – 1.0), group-living (mean = 0.09, 95% CI = 0 - 0.85), and pair-living (mean = 0.08, 95% CI = 0 - 0.69). Despite the large confident intervals surrounding the exact probability of each social organization, we can express greater confidence about the differences between these probabilities; namely, we are 82% confident that variable was more likely than pair-living, 32% confident that group-living was more likely than pair-living and 38% confident that solitary was more likely than pair-living (**Figure II-1**; Supplementary Material SII-8).



<u>Figure II-1:</u> ***A)*** *The likelihood of each social organization (solitary, pair-living, group-living and variable) being the ancestral state ("probability at root"). Percentages represent the probability that the difference between the estimated probabilities of different social organizations compared to pair-living was greater than 0 (e.g. variable is 82% more likely than pair-living).* ***B)*** *Phylogeny of the eight Macroscelidea species with data on social organization from 12 populations. Colored boxes at the tip of phylogenetic tree correspond to social organization(s) observed within species (orange = solitary; blue = pair-living; violet = group-living and red = variable), and if two populations of the same species had different social organization, then two boxes are shown.*

In order to understand which kind of variable social organization was the most likely ancestral state, a second analysis was conducted using all different categories of variable social organization (model 2; **Figure II-2**; Supplementary Material SII-9). The phylogenetic signal of this analysis was moderate (*mean* = 0.32, *95% CI* = 0.0027 – 0.74). Solitary+pair-living+group-living was the most likely ancestral state (*mean* = 0.29, *95% CI* = 0 – 1), followed by pair+group-living ((*mean* = 0.28, *95% CI* = 0 – 1) and solitary+pair-living (*mean* = 0.19, *95% CI* = 0 – 1)). Those three social organizations were part of the category "variable" in our first analysis (**Figure II-1**) and were respectively 60%, 67% and 45% more likely than pair-living (**Figure II-2**; Supplementary Material II-9). The probability that the ancestral social organization was solitary was relatively low (*mean* = 0.12, *95% CI* = 0 – 0.99). Group-living (*mean* = 0.06, *95% CI* = 0 – 0.52) and pair-living (*mean* = 0.05, *95% CI* = 0 – 0.32) were the least likely ancestral social organization.

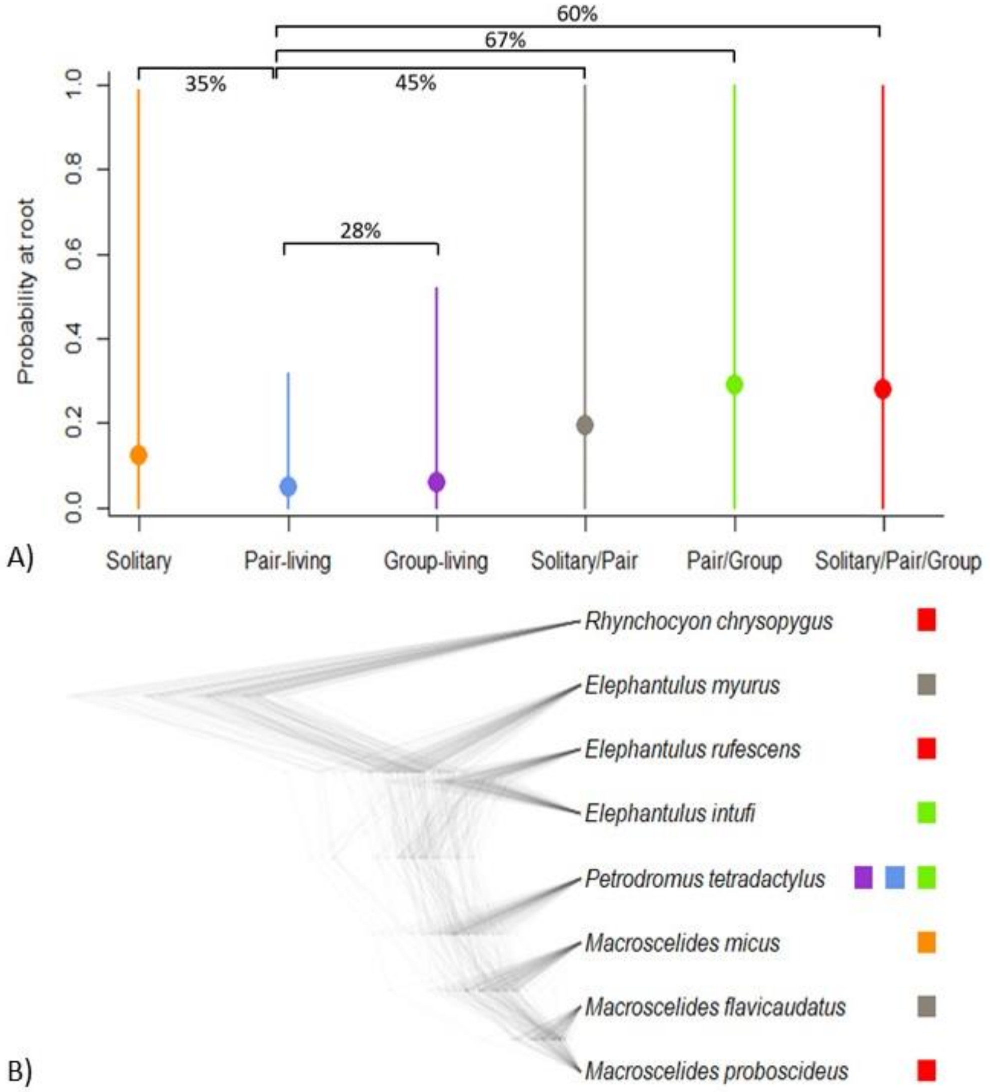


__Figure II-2:__ ***A)*** *The likelihood of each social organization (solitary, pair-living, group-living, solitary+pair-living, pair+group-living and solitary+pair-living+group-living) being the ancestral state ("probability at root"). Percentages represent the probability that the difference between the estimated probabilities of different social organizations compared to pair-living was greater than 0.* ***B)*** *Phylogeny of the eight Macroscelidea species with data on social organization from 12 populations. Colored boxes at the tip of phylogenetic tree correspond to social organization(s) observed within species (orange = solitary; blue = pair-living; violet = group-living; grey = solitary+pair-living; green = pair+group-living; red = solitary+pair-living+group-living), and if two populations of the same species had different social organization, then two boxes are shown.*

In model 3, we calculated what the ancestral state would be if we only took the main social organization into account, neglecting variability (**Figure II-3**). The phylogenetic signal was again moderate (*mean* = 0.36, *95% CI* = 0.00008 – 0.8). Pair-living was the most likely ancestral state (*mean probability* = 0.58, *95% CI* = 0 – 1), but again with large uncertainty. Group-living (*mean* = 0.08, *95% CI* = 0 – 0.74), solitary (*mean* = 0.20, *95% CI* = 0 – 1) and solitary/pair-living (*mean* = 0.14, *95% CI* = 0 – 1) had lower mean probabilities and similar uncertainties (**Figure II-3** ; Supplementary Material SII-10).

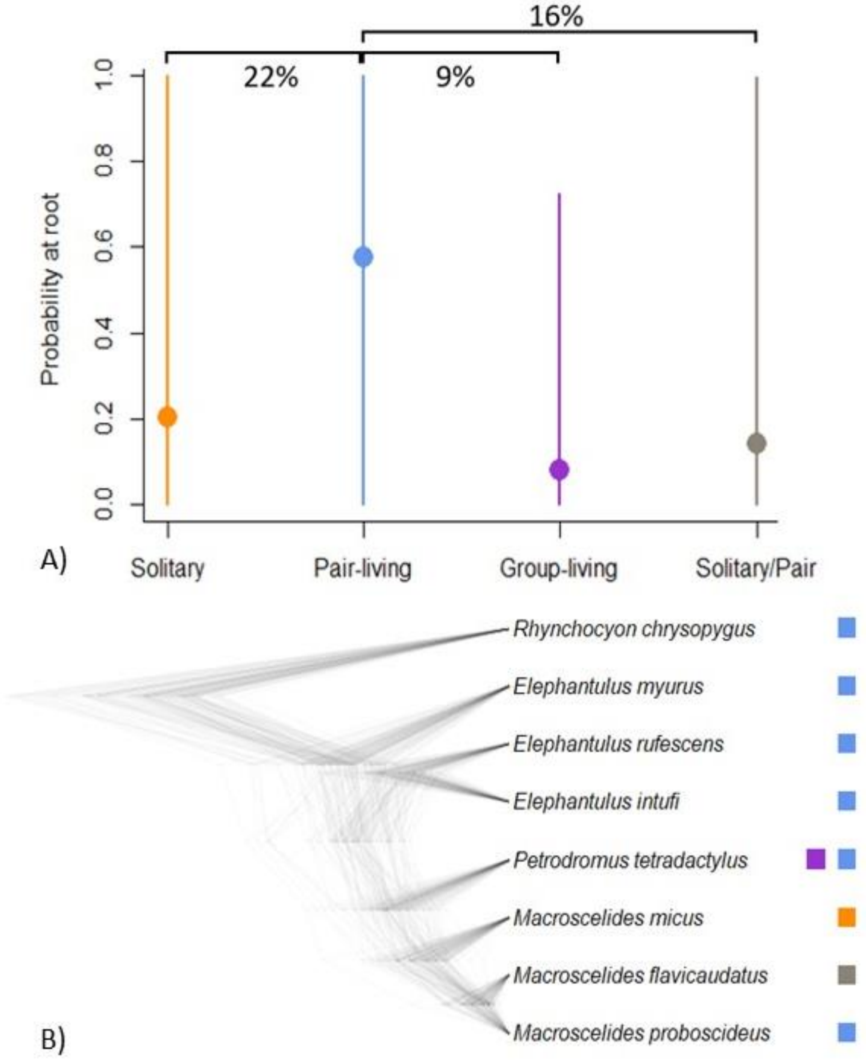


__Figure II-3:__ ***A)*** *The likelihood of each main form of social organization (solitary, pair-living, group-living, and solitary with pair-living) being the ancestral state ("probability at root"), ignoring the observed variation. Percentages represent the probability that the difference between the estimated probabilities of different social organizations compared to pair-living was greater than 0.* ***B)*** *Phylogeny of the eight Macroscelidea species with data on social organization for 12 populations. Colored boxes at the tip of phylogenetic tree correspond to social organization(s) observed within species (orange = solitary; blue = pair-living; violet = group-living; grey = solitary and pair-living), and if two populations of the same species had different social organization, then two boxes are shown.*

II.6 Discussion

Our comprehensive review of the literature on Macroscelidea indicated that their best studied social system component is social organization. The most frequent form of social organization was pair-living, though all pair-living species exhibited a variable social organization, including either solitary and/or group-living. Our approached revealed that (1) elephant-shrew social organization is best characterized as variable, (2) the ancestral form of social organization could not be reliably determined, but pair-living had the lowest probabilities when IVSO was taken into account, and (3) there is no empirical evidence that any of the species typically exhibit a monogamous mating system.

II.6.1 Social system

Consistent with a previous report (Rathbun & Rathbun, 2006), our literature review indicates Macroscelidea have a variable form of social organization, with pair-living occurring in 87.5% of the species, solitary living occurring in 75% of the species and group-living occurring in 62.5% of the species. While pair-living is common in many species of Macroscelidea, it is neither the only form of social organization nor the main form of social organization in all species. Solitary living occurred in most species and was as common as pair-living in one species and the only form of social organization for another species. Importantly, pair-living was mainly derived from the extensive home range overlap of one male and one female with each other but not with other individuals. Thus, even though spatial organization indicated pair-living, individuals spent most of their time alone, and other researchers might categorize these individuals as solitary rather than pair-living. In some cases, the home ranges of two females and one male overlapped heavily such that the social units were categorized as single male / multi-female groups. These associations lasted for a few weeks up to several months (Fitzgibbon, 1997; Rathbun, 1979; Schubert et al., 2009), which is long for species that lives between two and four years (Rathbun, 1979). Typically, such groups occurred because of the death / disappearance of the male of a neighboring pair (Rathbun, 1979; Schubert et al., 2009). However, pairs were more stable than groups in *Elephantulus rufescens* (pairs=one year, groups=2 months; Rathbun, 1979), *Rhynchocyon chrysopygus* (pairs=up to 16 months, groups=up to 3 months; Fitzgibbon, 1997), and *Macroscelides proboscideus* (pair=2 years, groups=5-6 weeks; Schubert et al., 2009).

Our study suggests that the long-held assertion that Macroscelidea is the only monogamous mammalian order (Lukas & Clutton-Brock, 2013; Rathbun, 1979; Rathbun & Rathbun, 2006; Ribble & Perrin, 2005; Handbook Mammals of the World 2018) is an over-simplication of elephant-shrew mating systems. The only available information regarding the mating system is from an unpublished study that was presented as a poster, representing data from the study population of Schubert et al. 2009 (samples had been collected by Schradin & Schubert). These non-peer-reviewed data indicate that *M. proboscideus* are not genetically monogamous and that females tend to reproduce with more than one male (Peffley et al., 2009). Many pair-living mammal species do not have a monogamous mating system but show extra-pair paternity, varying between 0 and 92% (Cohas & Allainé, 2009). Future studies will have to investigate how common extra-pair paternity is in the different Macroscelidea species.

II.6.2 Dataset comparison

We found that 75% of the species had pair-living as their most frequent form of social organization. In comparison, the Handbook Mammals of the World (Heritage, 2018) considers all species of elephant-shrews to be pair-living and Lukas & Clutton-Brock (2013) reported 93% of species as pair-living. There are several explanations for these differences. We relied only on information from field studies, whereas Lukas & Clutton-Brock (2013) also included data from captivity and assumed that species without data have the same form of social organization as closely related species. Thus, their database comprised of 15 species while we only found field data for eight species. The references in their database include one paper making the general statement that Macroscelidea are monogamous (Rathbun & Rathbun, 2006), one paper reporting data from captivity (Lawes & Perrin, 1995), one paper that cannot resolve the social organization of the studied species (*Petrodromus tetradactylus*; Jennings & Rathbun, 2001), as well as one paper that does not provide data on social organization (Koontz & Roeper, 1983). Interestingly, the only species which they do not regard to be monogamous but solitary, *Petrodromus tetradactylus*, was reported by us to be group or pair-living. Our results compare well with the expert opinions published in the book Walker's Mammals of the World (Nowak & Wilson, 1999). Like us, they report data for only eight species, 12.5% of which were believed to be solitary, 25% to be pair-living and 62.5% to be variable. Based on these differences, we argue that our database based on primary field studies is the most robust of these datasets.

II.6.3 Phylogenetic comparative analysis

We could not reliably identify the ancestral form of social organization, but found in all analyses a moderate phylogenetic signal indicating that social organization is influenced by phylogenetic history. Considering a posteriori the small sample size and the high variation between species and populations, this is not surprising. Nevertheless, the phylogenetic analyses revealed that variable social organization was 82% more likely to be the ancestral state than pair-living.

Most Macroscelidea had a variable type of social organization which was also the most likely ancestral form of social organization. More precisely, it was solitary+pair-living+group-living followed by pair+group-living that were the most likely ancestral forms of social organization. The uncertainty surrounding these inferences was large. Of note is that the previous assumption, of a pair-living ancestral social organization was the least supported. Importantly, when considering the variation reported from the field, pair-living always received very little support as the ancestral form. In contrast, when we considered only the main social organization (and ignored variation), pair-living became the most likely ancestral form of social organization, but with a lower mean probability than the variable ancestral state in the first analysis. What we can hypothesize is that the ancestor of all Macroscelidea was able to be pair-living, but with significant variation in its social organization that also allowed for solitary and group-living.

Low population density has been considered as the main factor leading to pair-living in animals (Emlen & Oring, 1977) and specifically in Macroscelidea, since it makes it difficult for males to defend more than one female (Rathbun & Dumbacher, 2015; Rathbun & Rathbun, 2006). However, we found no indication that social organization was related to population density. This might be because the lowest population densities (reported for two species of the genus *Macroscelides*) were associated with solitary living, which is in contrast to Rathbun & Rathbun's (2006) prediction of an increased incidence of pair-living with decreasing population density. Body mass and habitat type, two factors varying widely between populations and species, also had no influence on social organizations. Thus, even though we found important variation in social organization within and between populations, we could not explain this variation by the ecological and life history factors included in our analysis. To gain a better understanding of the evolution and diversity of Macroscelidea social organization, more field studies would be needed, especially on the 11 species for which we could not find any data.

II.6.4 Social monogamy vs. sengi syndrome

Aspects of the care system and of the social structure have been discussed in the literature to be associated with monogamy. Social monogamy has been characterised by pair-living, monogamous mating, biparental care, pair bonding and mate guarding (Lukas & Clutton-Brock, 2013; Mock & Fujioka, 1990). Direct paternal care is absent in Macroscelidea, though indirect paternal care, i.e. behaviors of the male which benefit the offspring but which are shown to be independent to the presence of offspring, has been reported for several species (Rathbun, 1979). However, indirect paternal care did not evolve because of its benefits for the offspring, but because it has direct survival benefits for the males, such as improved ability to escape predators (Rathbun, 1979; Ribble & Perrin, 2005). Macroscelidea is the only taxon where indirect paternal care has been discussed in detail, possibly to fit the proposed social monogamy. There is also general consensus that pair-bonding (i.e. individuals showing an attachment to a specific opposite-sex individual, Carter et al.,1995) does not exist in Macroscelidea (Rathbun & Rathbun, 2006).

In Macroscelidea, individuals of a pair spend little time together (Fitzgibbon, 1997; Koontz & Roeper, 1983; Rathbun, 1979) apart from the period when the female is receptive (Fitzgibbon, 1997; Schubert et al., 2012). This represents the behavioral pattern of many solitary living species (Schülke & Kappeler, 2003). Females defend territories against other females and males against other males (Rathbun, 1979). Mate guarding has been observed in several elephant-shrew species (FitzGibbon, 1997; Rathbun, 1979; Sauer, 1973; Schubert et al., 2012). This tactic consists of a male keeping within a short distance to a female as long as she is receptive, possibly to prevent male competitors to have access to that female (Huck et al., 2004). For example, in M. probscideus, a male and female sharing a home range were much closer to each other in the period during which the female was sexually receptive than when she was not (Schubert et al., 2009). Our evaluation of the four components of social systems independently in Macroscelidea shows that this taxon is in general neither pair-living nor monogamous, and thus not “socially monogamous”.

It was recognized early on that Macroscelidea did not fit the typical description of social monogamy (Kleiman, 1977; Rathbun & Rathbun, 2006). Instead, Rathbun & Rathbun 2006 discussed a “sengi syndrome” for small mammals with the sengi typic morphology: compact body, large head and long and narrow snout. Species falling under this syndrome have a relatively long life expectancy, produce few precocial young and have an insectivorous diet, which can explain a conserved social organization of pair-living even though the different species inhabit diverse habitats. The sengi syndrome has been discussed in relation to their phylogenetic ancestry (Rathbun & Rathbun, 2006). We found that phylogeny has a moderate effect on social organization, suggesting that social organization is somewhat constrained by phylogenetic history, but can also adapt to local ecology. Indeed, the phylogenetic signal in all of our three models had a much higher mean probability compared to other studies (*e.g.* 0.05 in Jaeggi et al., 2020 on Artiodactyla social organization). Thus, our study is not in contrast to the suggested sengi syndrome but indicates that instead of fixed pair-living, a flexible social organization including solitary and pair-living is likely part of this syndrome.

II.6.5 Conclusions

The Macroscelidea (elephant-shrews or sengis) have been regarded for decades as the only mammalian order in which all extant species are monogamous. Reviewing field studies of the last 5 decades we found that the social organization of elephant-shrews is much more flexible than previously recognized and not all species are pair-living. More species must be studied in the field to reliably infer the ancestral form of social organization and the ecological and life history factors related to Macroscelidea social evolution. Our analysis predicts a socially variable ancestor that had pair-living as one of several possible forms of social organization. Paternity studies are needed to determine the genetic mating system, but the flexible social organization predict that extra-pair paternity is common and that Macroscelidea are not a monogamous order. In sum, elephant-shrews are not exclusively pair-living, do not fit the definition of socially monogamous (Kleiman 1977; Rathbun 2006), and there is no evidence for a genetically monogamous mating system.

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II.7 Supplementary Material

Supplementary Material SII-1: *Table of social organization of Macroscelidea used for the Bayesian analysis. Habitat Type (HT); Habitat Heterogeneity (HTT); Number of habitat per species (NHS); Number of studies (NS); Pair-living (MF); One male several female (MFF).*

Genus species	Population	HT	HTT	NHS	Solitary	Pair-living	One male several females	Social Units	NS	Social state	Social state class	Main social organization	Population density	Body mass
Elephantulus intufi	Erongo Wilderness Lodge Okapekaha Farm Namibia	Shrubland	1	1		6	1	8	1	MF_MFF	Variable	Pair-living	NA	45.8
Elephantulus myurus		RockyAreas Bushlands	1	2	5	18		33	2	Solitary_MF	Variable	Pair-living	NA	60.5
Elephantulus myurus	Weenen Nature Reserve South Africa	RockyAreas	1	1	1	12		16	1	Solitary_MF	Variable	Pair-living	1.2	60.5
Elephantulus myurus	Goro Game Reserve South Africa	Bushlands	1	1	4	6		17	1	Solitary_MF	Variable	Pair-living	1.2	60.5
Elephantulus rufescens	Bushwackers kenya	Bushlands	1	1	2	7	1	13	1	Solitary_MF_MFF	Variable	Pair-living	2.0	58.0
Macroscelides flavicaudatus	Namib desert	Desert	1	1	2	2		7	1	Solitary_MF	Variable	Solitary and Pair-living	0.007	26.43
Macroscelides micus	Eastern Goboboseb Mountains Namibia	Rocky Areas	1	1	2			5	1	Solitary	Solitary	Solitary	0.12	26.9
Macroscelides proboscideus	Goegap Nature Reserve South Africa	Desert	1	1	1	39	1	50	1	Solitary_MF_MFF	Variable	Pair-living	0.74	42.95
Petrodromus tetradactylus		Forest	1	1		5	1	9	3	MF_MFF	Variable	Pair-living	1.43	201.54
Petrodromus tetradactylus	Tembe Elephant Park South Africa	Forest	1	1		4		6	1	MF	Variable	Pair-living	0.2	195.5
Petrodromus tetradactylus	Arabuko Sokoke Forest Kenya	Forest	1	1		1		1	1	MF	Pair-living	Pair-living	2.1	203
Petrodromus tetradactylus	Sodwana Bay National Park South Africa	Forest	1	1			1	2	1	MFF	Variable	Group-living	1.17	206.11

<u>Supplementary Material SII-2</u>: Population density (number of individuals per hectare) for Macroscelidea species.

Species Macroscelidea	Population	Population density (ind/ha)	References
Elephantulus intufi	ErongoWilderness Lodge Okapekaha Farm, Namibia	NA	NA
Elephantulus myurus	Weenen Nature Reserve, South Africa	1.2	Ribble and Perrin 2005
Elephantulus myurus	Goro Game Reserve, South Africa	NA	NA
Elephantulus rufescens	Bushwacker, Kenya	2.0	Rathbun 1979 ;
Macroscelides flavicaudatus	Namib desert, Namibia	0.007	Sauer 1973
Macroscelides micus	Eastern Goboboseb Mountains, Namibia	0.12	Rathbun and Dumbacher 2015
Macroscelides proboscideus	Goegap Nature Reserve, South Africa	0.74 [‡]	Schubert et al. 2009
Petrodromus tetradactylus	Tembe Elephant Park, South Africa	0.2	Oxenham and Perrin 2009
Petrodromus tetradactylus	Arabuko Sokoke Forest, Kenya	2.1	FitzGibbon 1995
Petrodromus tetradactylus	Sodwana Bay National Park, South Africa	1.17	Linn et al. 2007
Rhynchocyon chrysopygus	Arabuko Sokoke Forest, Kenya	0.74	FitzGibbon 1995
Rhynchocyon chrysopygus	Gedi Forest	1.6	Rathbun 1979

[‡] Population density was averaged across different study periods

__Supplementary Material SII-3:__ Body mass (in grams) for Macroscelidea species. We did not find information for the Elephantulus myurus population in Goro and thus used the mean value from the same species in Weenen.

Species Macroscelidea	Population	Body mass (g)	References
Elephantulus intufi	ErongoWilderness Lodge Okapekaha Farm, Namibia	45.8	Mammals of Africa, 2013 (Kingdon et al.)
Elephantulus myurus	Weenen Nature Reserve, South Africa	60.5	Ribble and Perrin 2005
Elephantulus myurus	Goro Game Reserve, South Africa	60.5	Ribble and Perrin 2005
Elephantulus rufescens	Bushwacker, Kenya	58.0	Rathbun 1979
Macroscelides flavicaudatus	Namib desert, Namibia	26.43	Dumbacher et al. 2014
Macroscelides micus	Eastern Goboboseb Mountains, Namibia	26.9	Rathbun and Dumbacher 2015
Macroscelides proboscideus	Goegap Nature Reserve, South Africa	42.95‡	Schubert et al. 2009
Petrodromus tetradactylus	Tembe Elephant Park, South Africa	195.5 ‡	Oxenham and Perrin 2009
Petrodromus tetradactylus	Arabuko Sokoke Forest, Kenya	203 ‡	FitzGibbon 1995
Petrodromus tetradactylus	Sodwana Bay National Park, South Africa	206.11	Downs and Perrin 1995
Rhynchocyon chrysopygus	Arabuko Sokoke Forest, Kenya	535	Fitzgibbon 1997
Rhynchocyon chrysopygus	Gedi Forest	540.3	Rathbun 1979

‡ Body mass was averaged across different seasons

<u>Supplementary Material SII-4</u>: *The different forms of social organization identified in our primary literature research, compared to the social organization provided by Lukas and Clutton-Brock (2013), Mammals of the World (Nowak and Wilson, 1999) and the Handbook Mammals of the World (HMoW; Heritage, 2018).*

Species	Lukas and Clutton-Brock 2013	Mammals of the World	HMoW	Our database	Our references	References cited by Lukas and Clutton-Brock 2013
Elephantulus brachyrhynchus	Social monogamy		Pair	-	-	Rathbun and Rathbun 2006
Elephantulus edwardii	Social monogamy	Solitary/ pairs/ small groups	NA (pair assumed)	-	-	Rathbun and Rathbun 2006
Elephantulus fuscipes	Social monogamy		-	-	-	Rathbun and Rathbun 2006
Elephantulus fuscus	Social monogamy		-	-	-	Rathbun and Rathbun 2006
Elephantulus intufi	Social monogamy	Solitary/ pairs/ small groups	Pair	pairs/one male several females	Rathbun and Rathbun 2006	Rathbun and Rathbun 2006
Elephantulus myurus	Social monogamy	Solitary/ pairs/ small groups	Pair	Solitary/ pairs	Ribble and Perrin 2005; Hoffmann et al. 2019	Rathbun and Rathbun 2006
Elephantulus pilicaudus	-		-	-	-	-
Elephantulus revoili	Social monogamy		-	-	-	Rathbun and Rathbun 2006
Elephantulus rozeti	Social monogamy		-	-	-	Rathbun and Rathbun 2006
Elephantulus rufescens	Social monogamy	pairs	Pair	Solitary/ pairs/one male several females	Rathbun 1979	Koontz and Roeper 1983
Elephantulus rupestris	Social monogamy	Solitary/ pairs/ small groups	Pair	-	-	Rathbun and Rathbun 2006
Macroscelides flavicaudatus	-	solitary	Pair	Solitary/ pairs	Sauer 1973	-
Macroscelides micus	-		Pair	Solitary	Rathbun and Dumbacher 2015	-
Macroscelides proboscideus	Social monogamy		Pair	Solitary/ pairs/one male several females	Schubert et al. 2009	Lawes and Perrin 1995
Petrodromus tetradactylus	Solitary	-	Pair	pairs/one male several females	Fitzgibbon 1995; Linn et al. 2007; Oxenham and Perrin 2009	Jennings and Rathbun 2001
Rhynchocyon chrysopygus	Social monogamy	pairs	Pair	Solitary/ pairs/one male several females	Fitzgibbon 1997; Rathbun 1979	Rathbun 1979

Rhynchocyon cirnei	Social monogamy	Alone and groups (foraging)	-	-	-	Rathbun and Rathbun 2006
Rhynchocyon petersi	Social monogamy		-	-	-	Rathbun and Rathbun 2006
Rhynchocyon udzungwensis	-		-	-	-	-

Supplementary Material SII-5: *Outputs of the phylogenetic mixed effects model when including variable social organization as an outcome category. Lwr95 and upr95 represent the lower and upper 95% credible interval.*

			Estimate	Estimate error	Lwr 95	Upr 95
Group-level effects	Genus species (Number of levels: 24)	Interecept of group-living	2.74	3.65	0.10	13.68
		Intercept of solitary living	8.86	26.08	0.10	49.25
		Intercept of variable	6.13	21.82	0.07	30.92
	Phylogeny (Number of levels : 24)	Interecept of group-living	1.12	1.49	0.03	3.77
		Intercept of solitary living	5.90	14.66	0.11	35.32
		Intercept of variable	3.18	4.31	0.24	13.51
Population-level effects		Intercept of group-living	-2.86	5.69	-16.35	7.37
		Intercept of solitary living	-3.09	8.55	-18.68	14.02
		Intercept of variable	5.80	7.88	-9.61	22.77
		Intercept of population density	0.02	0.30	-0.56	0.60
		Intercept of body mass	0.01	0.27	-0.49	0.55
		Relation between group-living and habitat heterogeneity	0.12	1.04	-1.78	2.18
		Relation between group-living and number of studies	-0.26	0.91	-2.21	1.42
		Relation between solitary and habitat heterogeneity	0.08	1.02	-1.94	2.08
		Relation between solitary and number of studies	0.05	0.97	-1.87	1.74
		Relation between variable and habitat heterogeneity	0.00	0.95	-1.77	2.09
		Relation between variable and number of studies	1.04	0.83	-0.61	2.66
		Relation between group-living and population density	0.16	0.94	-1.60	2.14
		Relation between group-living and body mass	0.09	0.98	-1.84	1.96
		Relation between solitary and population density	-0.13	1.05	-2.28	1.81
		Relation between solitary and body mass	-0.22	0.97	-2.24	1.74
		Relation between variable and population density	0.17	0.90	-1.43	1.92
		Relation between variable and body mass	-0.15	0.97	-2.12	1.67

<u>Supplementary Material SII-6:</u> Outputs of the phylogenetic mixed effects model when including each social organization as an outcome category. Lwr95 and upr95 represent the lower and upper 95% credible interval.

			Estimate	Estimate error	Lwr 95	Upr 95
Group-level effects	Genus species (Number of levels: 24)	Interecept of group-living	2.5	3.95	0.05	9.94
		Interecept of pair and group-living	3.28	4.38	0.13	16.45
		Interecept of solitary	8.28	21.91	0.08	44.13
		Interecept of solitary and pair-living	25.53	138.26	0.12	96.10
		Intercept of solitary, pair and group-living	12.48	28.60	0.11	68.97
	Phylogeny (Number of levels : 24)	Interecept of group-living	1.02	1.11	0.03	4.14
		Interecept of pair and group-living	1.58	1.73	0.06	6.09
		Interecept of solitary	7.07	23.54	0.08	43.31
		Interecept of solitary and pair-living	7.86	23.01	0.10	52.59
		Intercept of solitary, pair and group-living	2.76	4.36	0.12	10.90
Population-level effects		Interecept of group-living	-3.26	5.42	-15.25	5.57
		Interecept of pair and group-living	2.24	6.11	-12.12	14.47
		Interecept of solitary	-3.35	7.88	-19.41	12.79
		Interecept of solitary and pair-living	-0.78	8.18	-17.36	14.65
		Intercept of solitary, pair and group-living	1.36	7.42	-13.58	16.59
		Intercept of population density	0.00	0.33	-0.60	0.62
		Intercept of body mass	-0.01	0.27	-0.59	0.50
		Relation between group-living and habitat heterogeneity	0.08	1.02	-1.79	2.10
		Relation between group-living and number of studies	-0.41	0.87	-2.21	1.11
		Relation between pair, group-living and habitat heterogeneity	0.03	1.01	-1.85	1.95
		Relation between pair, group-living and number of studies	0.72	0.81	-0.85	2.34
		Relation between solitary and habitat heterogeneity	0.01	1.03	-2.00	2.08
		Relation between solitary and number of studies	-0.12	0.97	-1.97	1.77
		Relation between solitary, pair-living and habitat heterogeneity	-0.08	1.04	-2.12	1.90

		Relation between solitary, pair-living and number of studies	0.03	1.02	-1.87	2.23
		Relation between solitary, pair-living, group-living and habitat heterogeneity	-0.06	0.96	-1.98	1.86
		Relation between solitary, pair-living, group-living and number of studies	0.23	0.95	-1.43	2.07
		Relation between group-living and population density	0.28	0.99	-1.64	1.94
		Relation between group-living and body mass	0.10	1.01	-1.90	2.08
		Relation between pair, group-living and population density	0.02	0.89	-1.69	1.90
		Relation between pair, group-living and body mass	0.03	0.96	-1.94	1.86
		Relation between solitary and population density	-0.16	0.99	-2.13	1.61
		Relation between solitary and body mass	-0.27	1.00	-2.21	1.66
		Relation between solitary, pair-living and population density	-0.26	0.95	-1.98	1.51
		Relation between solitary, pair-living and body mass	-0.14	0.94	-2.05	1.51
		Relation between solitary, pair-living, group-living and population density	0.45	1.03	-1.62	2.64
		Relation between solitary, pair-living, group-living and body mass	-0.02	1.02	-1.98	2.00

Supplementary Material SII-7: *Outputs of the phylogenetic mixed effects model when using only the main social organization as outcome categories. Lwr95 and upr95 represents the lower and upper 95% credible interval.*

			Estimate	Estimate error	Lwr 95	Upr 95
Group-level effects	Genus species (Number of levels: 24)	Intercept of group-living	2.75	4.48	0.08	11.46
		Intercept of solitary	8.20	24.94	0.10	57.56
		Intercept of solitary/pair-living	7.13	29.72	0.15	33.48
	Phylogeny (Number of levels : 24)	Intercept of group-living	1.31	1.86	0.04	5.05
		Intercept of solitary	6.83	19.57	0.11	48.91
		Intercept of solitary/pair-living	5.33	36.97	0.03	23.90
Population-level effects		Intercept of group-living	-6.51	5.09	-17.57	3.33
		Intercept of solitary	-5.24	8.29	-21.44	13.02
		Intercept of solitary/pair-living	-6.54	6.80	-20.31	7.77
		Intercept of population density	0.01	0.32	-0.63	0.59
		Intercept of body mass	-0.00	0.31	-0.64	0.64
		Relation between group-living and habitat heterogeneity	-0.05	1.02	-1.97	1.87
		Relation between group-living and number of studies	-0.40	0.89	-2.18	1.40
		Relation between solitary and habitat heterogeneity	0.01	1.02	-1.81	2.18
		Relation between solitary and number of studies	-0.02	0.96	-1.81	1.89
		Relation between solitary/pair-living and habitat heterogeneity	0.05	1.01	-1.99	2.14
		Relation between solitary/pair-living and number of studies	-0.12	1.03	-2.02	1.91
		Relation between group-living and population density	0.23	0.90	-1.49	2.05
		Relation between group-living and body mass	0.09	0.91	-1.62	1.80
		Relation between solitary and population density	-0.10	0.99	-2.12	1.80
		Relation between solitary and body mass	-0.25	1.02	-2.32	1.75
		Relation between solitary/pair-living and population density	-0.75	1.05	-2.68	1.40
		Relation between solitary/pair-living and body mass	-0.28	1.03	-2.22	1.77

***<u>Supplementary Material SII-8</u>*:** *Table of the percentages representing the probability that the difference between the estimated probabilities of different social organizations compared to pair-living was greater than 0 in model 1 (e.g. variable is 82% more likely than pair-living).*

Social organization	Pair-living
Solitary	38%
Group-living	32%
Variable	82%

Supplementary Material SII-9: *Table of the percentages representing the probability that the difference between the estimated probabilities of different social organizations compared to pair-living was greater than 0 in model 2 (e.g. Pair/Group is 67% more likely than pair-living).*

Social organization	Pair-living
Solitary	35%
Group-living	28%
Solitary/Pair	45%
Pair/Group	67%
Solitary/Pair/Group	60%

<u>Supplementary Material SII-10:</u> *Table of the percentages representing the probability that the difference between the estimated probabilities of different social organizations compared to pair-living was greater than 0 in model 3 (e.g. Solitary is 22% more likely than pair-living).*

Social organization	Pair-living
Solitary	22%
Group-living	9%
Solitary/Pair-living	16%

Chapter 2

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III. Chapter 2: Primate Social Organization Evolved from a Flexible Pair-Living Ancestor

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CAO, JSM, AVJ and CS wrote the original draft; CAO, CP, PA, CK and CS collected the data; JSM, AVJ, CAO, CS and CP analyzed data; CAO, JSM, AVJ, CS, LH, and PA reviewed and edited the draft.

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Keywords: social system, social structure, monogamy, prosimian, simian

Note: This chapter is currently under revision and thus different from the preprint version.

III.1 Résumé

L'explication de l'évolution de l'organisation sociale des primates est fondamentale pour comprendre la socialité humaine et l'évolution sociale en général. Il a souvent été suggéré que l'ancêtre de tous les primates était solitaire et que d'autres formes d'organisation sociale ont évolué par la suite. Cependant, les recherches antérieures partaient de l'hypothèse que de nombreuses espèces de primates peu étudiées étaient solitaires, puis ont constaté que les transitions vers des systèmes sociaux plus complexes étaient déterminées par divers traits d'histoire de vie et facteurs écologiques. Nous montrons ici que lorsque la variation intra-spécifique est prise en compte, l'organisation sociale ancestrale des primates était variable; l'organisation sociale la plus courante étant la vie en couple, mais environ 15 à 20 % des unités sociales de la population ancestrale s'écartent de ce schéma en vivant en solitaire. Nous avons construit une base de données détaillée à partir d'études primaires de terrain quantifiant le nombre d'individus (unités sociales) exprimant différentes organisations sociales dans chaque population. Nous avons utilisé des modèles phylogénétiques bayésiens pour déduire la probabilité de chaque organisation sociale, conditionnée par plusieurs prédicteurs socio-écologiques, dans les populations ancestrales. La taille du corps et les modèles d'activité ont eu des effets importants sur les transitions entre les types d'organisations sociales. Nos résultats remettent en question l'hypothèse selon laquelle les primates ancestraux étaient solitaires et que la vie en couple a évolué par la suite. De plus, nos résultats soulignent l'importance de se concentrer sur les données de terrain et de tenir compte de la variation intra-spécifique. La vie en couple est ancienne du point de vue de l'évolution (probablement en raison d'avantages reproductifs tels que l'accès à des partenaires et la réduction de la compétition intra-sexuelle)

avec une structure sociale plus complexe (liens entre paires) et des systèmes de soins (soins biparentaux et allo-parentaux) apparus plus tard.

III.2 Abstract

Explaining the evolution of primate social organization has been fundamental to understand human sociality and social evolution more broadly. It has often been suggested that the ancestor of all primates was solitary and that other forms of social organization evolved later. However, previous research included the assumption that many understudied primate species were solitary, then finding transitions to more complex social systems being driven by various life history traits and ecological factors. Here we show that when intra-specific variation is accounted for, the ancestral social organization of primates was variable, with the most common social organization being pair-living but with approximatively 15-20% of social units of the ancestral population deviating from this pattern by being solitary living. We built a detailed database from primary field studies quantifying the number of individuals (social units) expressing different social organizations in each population. We used Bayesian phylogenetic models to infer the probability of each social organization, conditional on several socio-ecological predictors, in ancestral populations. Body size and activity patterns had large effects on transitions between types of social organizations. Our results challenge the assumption that ancestral primates were solitary and that pair-living evolved afterwards. Moreover, our results emphasize the importance of focusing on field data and accounting for intra-specific variation. Pair-living is evolutionary ancient, likely caused by reproductive benefits such as access to

partners and reduced intra-sexual competition, with more complex social structure (pair-bonding) and care systems (biparental and allo-parental care) evolving later.

Significance Statement

Was the ancestor of all primates a solitary-living species? Did more social forms of primate societies evolve from this basic and simple society? The dogmatic answer is yes. We used a modern statistical analysis, including variations within species, to show that the ancestral primate social organization was most likely variable. Most lived in pairs, and only 15-20% of individuals were solitary. Living in pairs was likely ancient and caused by reproductive benefits, like access to partners and reduced competition with the sexes. More complex social elaborations like pair-bonds, and biparental and allo-parental care, probably evolved later.

III.3 Introduction

Understanding primate social evolution is central to understand our own social ancestry. Numerous comparative studies have inferred that the ancestor of all primates was nocturnal, small, arboreal and solitary (1-3). Previous research explained transitions from solitary living to more complex social systems by various ecological factors and life history traits (1-5). The inferred ancestral solitary stage hinged largely on strepsirrhines, which are basal to the primate phylogeny but understudied and previously often assumed to be solitary living (6). However, several field studies over the last decades indicate strepsirrhines to be more social (1, 6) and often pair-living (7).

Social systems are composed of different components including the social organization (composition of social units), social structure (interactions between individuals), care system (who cares for infants), and mating system (who mates with who) (8, 9). It has been argued that these components should be studied independently from each other to understand social evolution, especially in primates (1, 10, 11). For example, pair-living as a form of social organization has often been equated with monogamy, even though monogamy refers to a mating system (1, 11-14). Importantly, pair-living species can vary significantly in their mating system, *i.e.* the degree of extra-pair paternity (15, 16). Similarly, primate social organization varies greatly between (1, 3) but also within species (6, 17). Previous studies were statistically limited by assigning a single type of social organization to each species, such that the analysis could only consider between but not within species variation (1-3, 18).

Here we examined whether taking intra-specific variation in social organization (IVSO) into account and focusing on data from field studies, including many recent studies on nocturnal strepsirrhines, but excluding assumptions about non-studied species, changes our estimate of the ancestral primate social organization. Primate social evolution is assumed to largely depend on ecology and life history (19, 20). For example, small species are generally assumed to be solitary and large species to be group-living, with group composition depending on diet (3, 8, 19). Species living in heterogeneous habitats are predicted to have a more variable social organization (21). Therefore, we tested in how far multiple ecological and life history factors influenced primate social organization.

We assembled a database on the social organization of 499 populations of 216 primate species observed in the field, as published in the primary peer-reviewed literature. Rather than selecting a single social organization per species we treated each study population as the unit of analysis. Furthermore, within each population we counted the number of social units exhibiting different social organizations, allowing us to quantify within population variation (**Figure III-1**). Therefore, our statistical approach allowed us to consider variation in social organization (i) between species, (ii) between populations of species and, (iii) between social units within populations. We developed a flexible Bayesian phylogenetic GLMM framework to partition this extensive variation in social organization across populations, species, and superfamilies, as well as to infer its phylogenetic and socio-ecological determinants. Using a multinomial likelihood, we modelled the relative frequency of each social organization being observed within each population, adjusting for phylogeny and research effort. We defined the ‘main social organization’ as the social organization with the greatest probability of being observed within a population. As a second response variable in the same model, we used a binomial likelihood to directly account for the degree of intrapopulation variation in social organization (IVSO) observed in each population, calculated as the proportion of social units deviating from the most frequent social organization (**Figure III-1**). This allowed us to estimate effects of socio-ecology and phylogeny on IVSO per se, irrespective of the relative probabilities of specific social organizations within a population.

III.4 Materials and Methods

III.4.1 Materials

Definition of social organization.—Animal social systems can be characterized by variation in four inter-related components (9): social organization (composition and size of groups), social structure (social interactions), mating system (who mates and who reproduces with whom), and care system (who takes care of the offspring). Previous research has often used heterogenous terminology to describe social systems across taxa, resulting in ambiguous definitions and confounding of distinct selection pressures (29). Here we strictly focused on the composition of groups, a central aspect of social organization. Data for group composition were taken from the methods and results section of peer-reviewed primary literature, avoiding any interpretations from the authors in the discussion. We defined social organization as solitary, pairs (MF), single male + multi-female (MFF), multi-male + single female (FMM), multi-male + multi-female (FFMM), and sex specific, where groups consisted of one sex only.

Database on social organization.—We identified 450 species of primates using the IUCN (International Union for Conservation of Nature) database (2019). We then conducted literature searches on social organization in Web of Science (Thomson Reuters) and in Google Scholar between January 2016 and September 2019. For each species, we initially search the Latin name of the species and the term “social” (*e.g.* “*Alouatta caraya* AND social”; “*Gorilla*

gorilla AND social”). If no literature on social organization was found, only the Latin name was searched. For several species the Latin name changed over the years, in which case we repeated the search with the previous versions of their names.

Searches on Web of Science were restricted to articles within one of the following three categories: “behavioral science”, “zoology” and “environmental science/ecology”. Only peer-reviewed literature from field studies was considered while reviews, laboratory-based studies and captive studies were ignored, to ensure that the social organization observed by a given species also occurred in their natural habitat (*e.g.* many species can be kept in captivity in pairs, but this does not mean that pairs occur in nature). For each study, we read the abstract, examined all figures and tables, and searched the following keywords throughout the papers: "social", “solitary”, “group”, and “pair”. As such, our literature search focused on the data reported in methods and results sections of the peer-reviewed studies, not on the interpretation of the authors regarding the social organization in the introduction or discussion. This search yielded more than 2000 articles that were scanned for information on social organization. Of these, a total of 946 papers contained useable data (83 for Strepsirrhines, 247 for New World monkeys, and 636 for Old World monkeys). Overall, data on social organization were found for 499 populations from 223 species. To determine the forms of social organization present in each population, we recorded the adult sex composition of all social units in a population using the classical definitions from Kappeler and van Schaik (8) and adding “sex specific group” as an additional category (Table III-1). Studies that did not report the sex of individuals were not taken into account, following (30).

<u>Table III-1:</u> The different forms of social organization recorded in our study.

Social organization	Definition
Solitary	Adult males and females forage independently and only meet for mating (do not stay together for periods longer than courtship and mating) and are otherwise alone. All identified dispersers were excluded. Cases where only one sex occurred alone were considered as potential dispersal or alternative reproductive tactics and were not accounted as a solitary social organization.
Pair-living (MF)	Repeated observations of one adult male and one adult female with or without dependent offspring. The home ranges of a pair overlap with each other to a great extent (>>80%) but not with others.
Groups of multiple males and one female (MMF)	Observations of stable groups with multiple adult males and one adult female with or without dependent offspring.
Groups of one male and multiple females (MFF)	Observations of stable groups with one adult male and multiple adult females with or without dependent offspring.
Groups of multiple males and multiple females (MMFF)	Observations of stable groups with multiple adult males and multiple adult females with or without dependent offspring.
Sex-specific group	Both multiple adult female groups and multiple adult male groups occur in the population. Cases where only one sex-group occurred alone were considered as potential dispersal or alternative reproductive tactics and were not considered as a sex-specific social organization.

From each paper, we recorded how often each category of social units was observed *e.g.* how many solitary individuals, pairs or different groups were recorded. We only recorded solitary living as a form of social organization when both sexes had been observed to be solitary, as single individuals of one sex may often represent dispersers. Whenever individuals were explicitly reported to be dispersers, they were not considered in the recording of social organization. Therefore, to record one social unit of solitary living, at least one solitary male and one solitary female were needed, to make the classification comparable to the criterion used for pair-living (one pair also consists of one male and one female). For example, when 5 solitary males and 4 solitary females were reported, we recorded 4 solitary social units. The same procedure was done with sex-specific groups. We only recorded sex specific groups as a form of social organization when both sexes had been observed to live in unisex groups. To record one social unit of sex-specific groups, at least one group of males and one group of females were needed. For example, when 10 groups of males and 4 groups of females were reported, we recorded 4 sex-specific groups social units. Overall, we only observed sex-specific groups in nine species, indicating that intersex units are the dominant form of social organization in group-living primates. This low count prevented us from drawing meaningful inferences about phylogenetic and ecological effects on the probability of sex-specific units occurring, and we therefore excluded these units from our analyses.

Data were collected at the population level by recording the total number of papers reporting a given social organization in a population. When the same observed individuals and their social units were included in more than one published paper, we considered only the most precise paper, *e.g.* papers where the precise number of social organizations and/or the sex of individuals was described, to avoid considering the social units of a social organization several times. The total number of studies reporting social organization per population was then recorded in the database to account for any effects of research effort. For example, populations with multiple studies over decades might be more likely to show variation in social organization than populations with only one single study. Similarly, taxa exhibiting greater (or lesser) variation in social organization may be more or less likely to be investigated by researchers.

The database records for each population whether multi-level societies or fission-fusion societies occurred. When multilevel societies (31) occurred within a population, indicating hierarchically structured social organization, we only recorded the composition of the core group defined in the study. We did this because the different core groups within primates' multilevel societies tend to maintain their social organization across interactions, such as the maintenance of the one male multiple female groups composing large multilevel hamadryas baboon (*Papio hamadryas*) societies (32). In contrast, when fission-fusion societies (33) occurred in the population, suggesting a more fluid social organization, we recorded all forms of group composition observed, as this indicated that individuals of this population could exhibit multiple forms of social organization within their society over time.

Intrapopulation variation in social organization (IVSO).— IVSO was identified when different forms of social organization occurred within a population, indicating some degree of behavioral plasticity in a species' social organization. However, the following cases were not regarded as IVSO: when only one sex had two or more forms of social organization or cases of dispersing individuals (solitary individuals of one sex only) or of alternative reproductive tactics (for example male followers during the breeding season). Environmental disruption such as the death of a dominant breeder or predation of group-members can also change the social organization of a unit (Schradin 2013), but these changes do not reflect the evolved behavioral plasticity we want to explain. Thus, such environmental disruption events were not considered in our database but were recorded separately.

Previous studies have treated IVSO as a distinct category of social organization (26, 28). However, given the wealth of data available for primate social organization, we were able to continuously measure IVSO at the population level as the proportion of social units deviating from the most frequently observed (‘main) social organization within a population. In the present study, we therefore conceptualized and measured IVSO as a distinct trait capturing the overall degree of variation in social organization, which may coevolve with the composition and frequency of specific social organizations within a population. This avoided the use of arbitrary thresholds for categorizing the presence or absence of IVSO, retaining the continuous information provided by previous literature, and allowed us to consider how the evolution of specific forms of social organization and the overall degree of IVSO are related across species and populations.

Predictors of social organization.— We included the following predictors in our Bayesian model to account for potential social, ecological, life-history and methodological causes of variation in social organization: habitat heterogeneity, habitat type, body mass, diet, activity pattern, locomotion, number of studies per population, and foraging strategy (**Table III-2**). Habitat type was recorded from the primary literature and categorized on IUCN classification and used to calculate habitat heterogeneity (total number of habitats per population). Further, we classified the different types of habitat as open, closed or open and closed. Populations were also categorized as having group- or solitary foraging individual or both, depending on information in the primary literature use to categories social organization.

Table III-2: Predictors and from which database the information was used.

Predictors	Definition	Database
Habitat heterogeneity	Total number of habitats per species.	Based on our own primary literature search.
Habitat type	The type of habitat depending on whether it is open, closed or both. Open: grassland, shrubland, rocky areas, savanna, desert. Closed: forest, wetland, cave, woodland. Both: artificial.	Based on our own primary literature search.
Body mass	Mean from the body mass of male and female; the standard deviation was used to account for measurement error.	*(30, 31*)
Diet	Percentage of the diet consisting of fruits and foliage throughout the entire year.	*(30, 31*)
Activity Pattern	Diurnal, nocturnal or cathemeral.	*(30, 31*)
Locomotion	Terrestrial, arboreal or both.	*(30, 31*)
Foraging strategy	Species that forage solitarily, in groups or both (solitarily and in groups).	Based on our own primary literature search.

We used two published databases (34, 35) for the predictors body mass, diet, activity pattern and locomotion. First, we compared the two databases to see if their information was very similar. This was the case for locomotion (terrestrial, arboreal and both) and activity pattern (diurnal, nocturnal and cathemeral). However, for body mass and diet we found differences between the two databases, which could undesirably influence our statistical inferences. Body mass was recorded for males and females, with some studies only reporting average body mass across sexes. If for one species more than one measurement for body mass was available for either sex, then we calculated the mean value and the standard deviation. For food, information was available at the species level for average diet composition, including percentage of fruits and foliage (addition of mature leaves, undefined leaves and young leaves) as well as the percentage of seed and animal protein consumed. We took multiple steps to ensure that estimated effects for these variables were robust to variation in diet and body size results between the databases. Whenever there was a difference between the two databases, we checked whether their information was based on the same or on different published studies. If both databases reported the same primary study, we checked the publication ourselves and only utilized the data reported directly in the paper. If the two databases were not based on the same study, we then entered the average result across databases to account for potential heterogeneity and/or measurement error within taxa. We also conducted analyses of body size separately within each database to ensure that aggregated estimates were robust across datasets. No meaningful differences were observed between the databases in the main effects of body size on social organization and IVSO (all $\Delta\beta$ 90% CIs included zero), so we used the average species body size between databases for all reported analyses. Information on diet was also combined between the databases when possible to increase sample size, due to heterogeneous patterns of missing data across species.

III.4.2 Methods

Statistical analyses.— We developed multilevel phylogenetic models to investigate the evolution of social organization and IVSO across primates, and we conducted all analyses within a flexible Bayesian framework to account for non-Gaussian outcome measures, measurement error in social and ecological data within taxa, as well as uncertainty in phylogenetic relationships across taxa (36-38). Our analyses relied on one of the most recent and up-to-date mammalian phylogenies from the VertLife project (39), ensuring that evolutionary relationships were accurately represented between all species in our dataset. Main social organization was modelled as a multinomial response variable, appropriate for repeatedly measured categorical data (40), while IVSO was treated as a binomial response, representing the number of groups deviating from the main social organization out of the total number of groups observed (*i.e.* each social group observed in a population was coded as either being 'main' = 0 or 'non-main' = 1 in organization). Multi-response models were estimated to simultaneously assess phylogenetic and ecological effects on these measures, as well as to conduct robust ancestral state reconstruction of the main social organization and magnitude of IVSO expected in an ancestral primate populations. We took multiple steps to integrate uncertainty in our phylogeny and empirical measures during these analyses, which were supported by robustness checks to ensure appropriate inferential stability among models. Conservative, weakly regularizing priors were also used to introduce more realistic assumptions into the estimators, as well as to reduce the risks of inferential bias caused by multiple testing and measurement and sampling error (38, 41). Code for all analyses described in the text can be found at https://github.com/Jordan-Scott-Martin/primate-SO-analysis along with the original database at https://github.com/CharlotteAnaisOLIVIER/Social-organization-of-primates.

For all analyses, we estimated two generalized multilevel phylogenetic models, one for describing the probability of each social organization with a multinomial distribution and the other for describing overall IVSO with a binomial distribution. For population p for species s, the multinomial model predicted the number of units observed in category i as a function of the total number of units observed n_{ps} and a vector of parameters θ_{ps} for the relative probabilities of each category compared to the base category, which in this case is solitary social organization.

$$\text{Social organization}_{ps} \sim \text{Multinomial}_{\text{K}}\left(n_{\text{ps}}, \boldsymbol{\theta}_{\boldsymbol{ps}}\right)$$

$$\text{logit}\left(\theta_{ps}^{(i)}\right) = \mu_0^{(i)} + \boldsymbol{x}'_{ps}\boldsymbol{\beta}^{(\boldsymbol{i})} + \alpha_{\text{phylo(s)}} + \alpha_{\text{species(s)}} + \alpha_{\text{superfamily(s)}} + \alpha_{\text{population(p)}}$$

$$\text{for } i, \dots, K-1$$

The parameters $\theta_{ps}^{(i)}$ for each category *i* (MF, MFF, FMM, FFMM) as compared to *K* (Solitary) were predicted on the transformed logit scale by a category-specific intercept $\mu_0^{(i)}$, fixed effects $\boldsymbol{\beta}^{(\boldsymbol{i})}$ (research effort and ecological predictors), where $\boldsymbol{x}'_{ps}$ is the transposed vector of population- and/or species-specific predictors, and by the random effects α, which capture Brownian Motion phylogenetic effects $\alpha_{\text{phylo(s)}}$ as well as any deviations from these phylogenetic predictions at the superfamily, species, and population level. Note that $\alpha_{\text{population(p)}}$ is as an observation-level random effect capturing overdispersion from the expected variance.

By adjusting for any species-level effects, the *K*-1 intercepts $\boldsymbol{\theta}_{\boldsymbol{ps}}$ provide appropriate relative probabilities of non-solitary compared to solitary social organization for an average ancestral population. These values can be transformed to the absolute scale using the logistic function, which facilitates calculating the probability of social units in an average ancestral population showing each of the *K* social organizations. In particular, for solitary and any other social organization *i*

$$\Pr(\text{Solitary}) = \frac{1}{1 + \sum_i^{K-1} \exp\left(\text{logit}\left(\theta_0^{(i)}\right)\right)} \qquad \Pr(i) = \frac{\exp\left(\text{logit}\left(\theta_0^{(i)}\right)\right)}{1 + \sum_i^{K-1} \exp\left(\text{logit}\left(\theta_0^{(i)}\right)\right)}$$

Note that this standard parameterization of the multinomial model can be equivalently specified with *K* intercepts, where $\theta_0^{Solitary} = -\sum_{i \neq Solitary}^{K-1} \theta_0^{(i)}$. This approach allows for modelling predictors directly on the probability of each category, as shown in **Figure III-2A**, and can be implemented manually in Stan.

The variance explained in social organization by each set of effects can be calculated on the transformed scale using model predictions for the fitted data. Specifically, the total latent variance for social organization *i* is given by

$$V_{T^{(i)}} = V_{\boldsymbol{\beta}^{(i)}} + V_{\alpha^{(i)}_{\text{phylo}}} + V_{\alpha^{(i)}_{\text{species}}} + V_{\alpha^{(i)}_{\text{superfamily}}} + V_{\alpha^{(i)}_{\text{population}}} + \left(\frac{\pi}{\sqrt{3}}\right)^2$$

where $\left(\frac{\pi}{\sqrt{3}}\right)^2$ is the theoretical variance of the logit scale. The latent variance explained (R^2), also known as the repeatability or phylogenetic signal λ) can then be estimated by

$$R^2_{\boldsymbol{\beta}^{(i)}} = V_{\boldsymbol{\beta}^{(i)}} \,/\, V_{T^{(i)}}$$

$$R^2_{\boldsymbol{\alpha}^{(i)}} = V_{\boldsymbol{\alpha}^{(i)}} \,/\, V_{T^{(i)}}$$

$$\boldsymbol{\lambda}_{\,(i)} = V_{{\alpha_{phylo}}^{(i)}} \,/\, V_{T^{(i)}}$$

The same approach is taken for predicting the total probability τ_{ps} of IVSO given the number of social units n_{ps} for population *p* of species *s* using a Binomial distribution

$$\text{Overall IVSO}_{ps} \sim \text{Binomial}\left(n_{ps}, \tau_{ps}\right)$$

$$\text{logit}\left(\tau_{ps}\right) = \mu_0 + \boldsymbol{x}'_{ps}\boldsymbol{\beta} + \alpha_{\text{phylo(s)}} + \alpha_{\text{species(s)}} + \alpha_{\text{superfamily(s)}} + \alpha_{\text{population(p)}}$$

The probability τ_{ps} predicts the proportion of social units expected to deviate from the main social organization observed in the population or, equivalently, the probability of deviating for a randomly selected social unit.

Heterogeneous patterns of missing data were present for our ecological and life-history measures across species. As a consequence, a few populations lacked data for foraging style

(1%), primary locomotion (2%), body size (2%), while many lacked data on the proportion of dietary reliance on fruits (18%), foliage (28%), seeds (60%), and animal protein (51%). Best practice for statistical estimation from a non-experimental dataset such as ours is to use some form of multiple imputation to account for non-random missingness across observations (38). Therefore, when seeking to assess the aggregate average effects of ecological predictors across species (Figure III-2A), we used the mice R package (42) to impute missing ecological and life-history values across predictors and obtain more reliable population statistics in our full model. However, for biological inferences about the effects of specific predictors (Figure III-2B) and the overall ancestral state (Figure III-3), we relied only on observed values taken from primary literature, excluding any rows containing missing data. Table SIII-1 provides sample sizes and posterior estimates for all predictors in the full model with and without imputation, as well as in univariate models capturing the total effect of each predictor.

Ancestral state reconstructions are commonly carried out with intercept-only random effects models, in which the global model intercept is interpreted as the expected ancestral state after marginalizing over any species-level phylogenetic or stochastic effects; multiple regression models are then used separately to identify relevant selection pressures across the sample (36, 43). However, as the size and depth of the sampled phylogenetic tree grows, so too does the potential bias introduced into a reconstruction by unmeasured temporal trends and processes of non-random convergent evolution. These concerns are particularly acute for our dataset, which contains unbalanced samples across all major clades within the primate order and covers a span of approximately 51 million years. Therefore, we conducted our reconstruction of primate social organization in the context of a broader multiple regression model accounting for the effects of key social and ecological factors thought to be relevant to understanding the adaptive niche of ancestral primates, and which may also be associated with directional change in social organization and IVSO across extant primates. In particular, we assumed that ancestral primates were of relatively small body size (~30 g or - 2 SD z-score log mean body size), largely arboreal in their locomotion, and nocturnal in their activity pattern. We also adjusted our reconstruction for any biased sampling caused by differential research effort within primate superfamilies.

Given that our analyses were conducted in a fully Bayesian framework, we avoided the limitations of null-hypothesis testing (44), and instead relied on multiple sources of information provided by posterior distributions of model parameters and predictions. Median posterior estimates and median absolute deviations (MADs) were used to characterize the central tendency and relative dispersion of estimated effects, while 90% Bayesian credible intervals (CIs) and posterior probabilities of positive or negative effects (*i.e.* $p+$ or $p-$) were used to gauge uncertainty in the magnitude and direction of these effects (Table SIII-2). Note that a 90% Bayesian CI excluding zero indicates greater than 0.95 posterior probability in support of a directional effect. These posterior probabilities $p+$ or $p-$ directly quantify support for substantive rather than null hypotheses, so that values closer to 1 indicate greater support for the directional effect (+,-) and values closer to 0 indicate greater support for the opposite directional effect (-,+). All models were estimated in the Stan statistical programming language (45) using R (R Core Team 2020) and the brms package(46).

III.5 Results

III.5.1 Distribution of social organization in extant primates

We observed relatively high rates of pair-living (main social organization in 26% of populations; MF) and low rates of solitary organization (main social organization in 3% of populations) in our database (**Figure III-1**). Previous studies (1, 3, 5) estimated many more species to be solitary living, as they were classified most solitary foragers as also having a solitary social organization. Our database challenges this assumption, showing that among 20 solitary foraging populations (from 15 species) only 8 had solitary living as main form of social organization, while in the remaining 12 populations pairs or groups shared one home range. The most common form of social organization in extant primates is multi-male multi female groups, followed by one male multiple female groups and pairs, while both one female multiple-male groups and solitary populations were rare (**Figure III-1**). Many species (47%) and populations (43%) exhibited more than one social organization, demonstrating that primate populations show substantial levels of variation in social organization (**Figure III-1**).

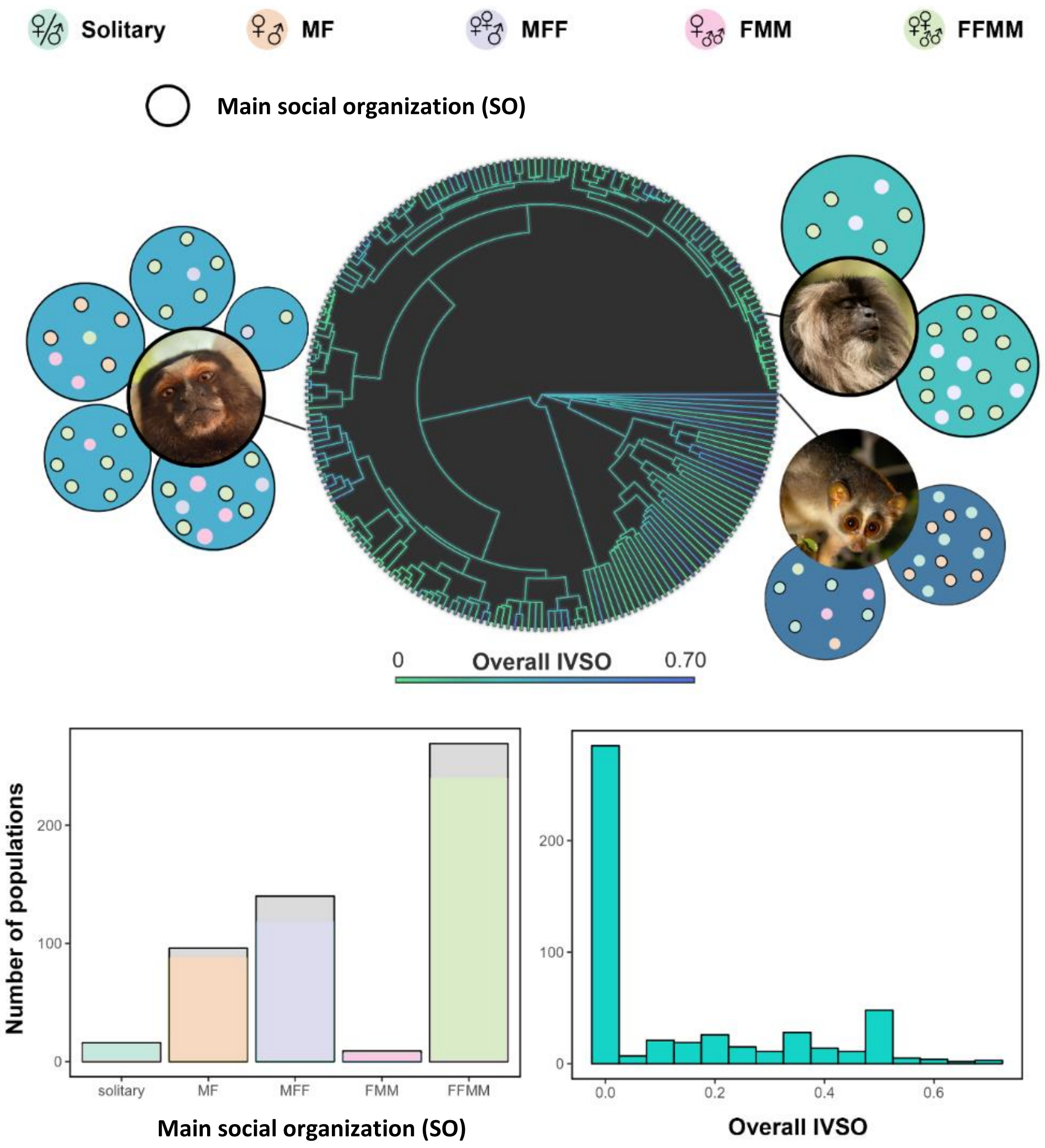
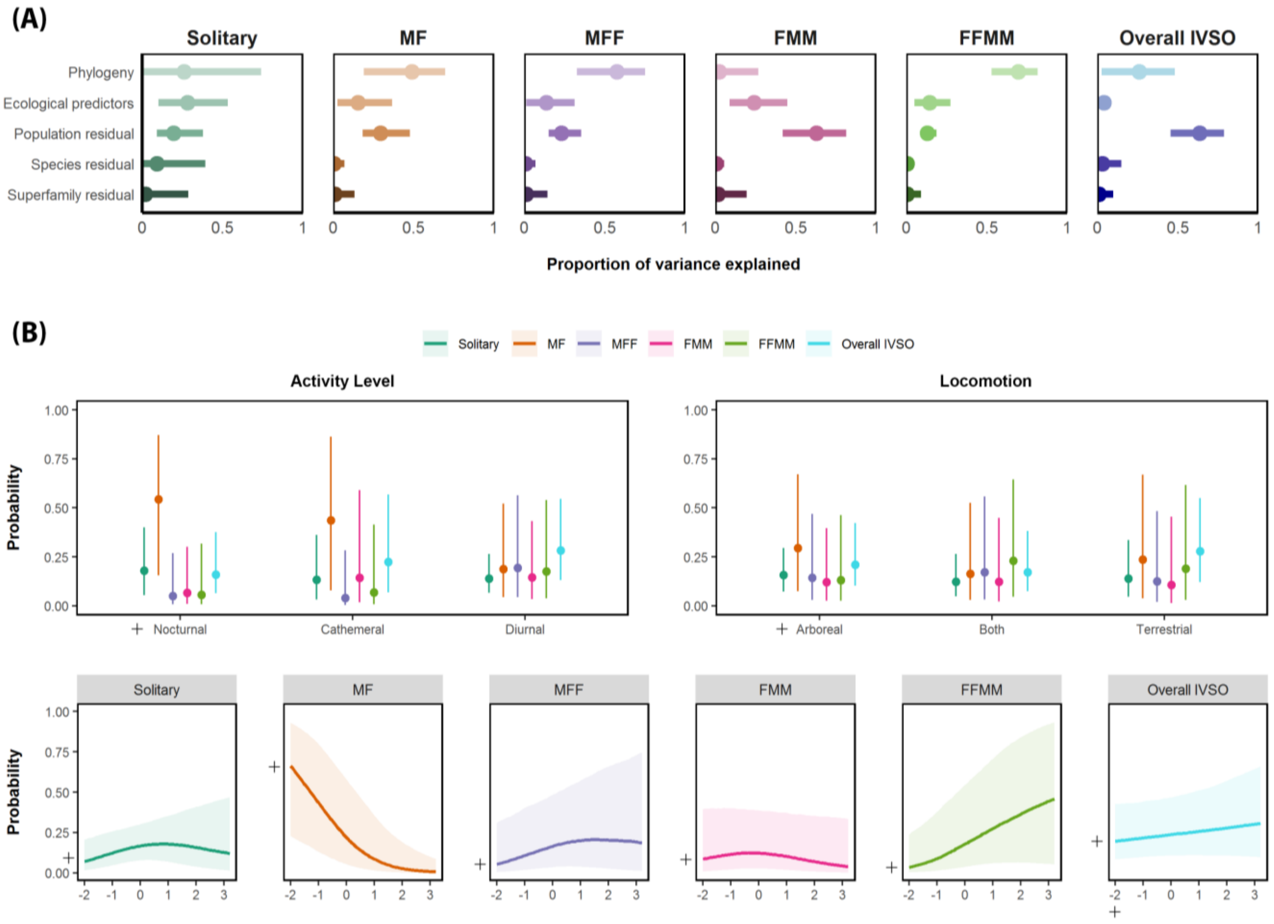


***Figure III-1:* The distribution of social organizations across extant primate populations.** *Three examples taken from field research on the slender loris (Loris lydekkerianus), common marmoset (Callithrix jacchus), and lion-tailed macaque (Macaca silenus) are shown. The top panel demonstrates how we coded social organization per population as solitary, male-female (MF) or pair-living, single male multi-female (MFF), single female multi-male (FMM), or multi-male and multi-female (MMFF). Large circles (middle) around pictures represent different populations of the species. Smaller circles within each large circle represents a single social unit within a population, with color correpsonding to the social organization observed. The phylogeny reflects a simple contour mapping of overall IVSO (# units deviating from main social organization / total # units) across taxa in our database. Note that the branch lengths have been arbitrarily modified for visual clarity and should not be directly interpreted. The low panel shows the total number of populations in our dataset exhibiting each form of main social organization, as well as overall IVSO (binwidth = 0.05). Gray bars represent uncertainty in the main social organization for populations exhibiting two social organization with equally high frequency.*

III.5.2 Variance due to phylogeny, ecology and life history

We first wanted to know how much variation in primate social organization and IVSO is explained by phylogenetic history, current ecological and life history conditions, or unmeasured effects at the levels of populations, species, and superfamilies. Ecological and life history conditions included habitat heterogeneity, open vs closed habitats, foraging strategy, locomotion, activity pattern, body size, and dietary reliance on fruit, foliage, seeds, or animal protein. Using multiple imputation to leverage all predictors despite missing data (see supplementary materials and supplementary data), we found that ecological and life history variables collectively explained only a small-to-moderate proportion of variation in social organization and IVSO (median R2 range: 0.04 – 0.30; **Figure III-2A**; see supplementary materials for details on the direct and total effects of each predictor with and without imputation). Phylogeny explained a moderate to large proportion of variation in social organization (median λ range: 0.26 – 0.69), although single-female multi-male social organization had much lower phylogenetic signal (median λ = 0.06). Species- or superfamily-level effects, independent of ecology and phylogeny, were weak (median R2 range: 0.01 – 0.13), suggesting against grade shifts. However, population-level heterogeneity was consistently larger (median R2 range: 0.13 – 0.63), indicating a sizable portion of unexplained variation among populations within the same species. These results suggest that while some forms of social organization are conserved within primate lineages, social organization often shows substantial variation among populations that remains unexplained by phylogeny, ecology or life history.



<u>Figure III-2 :</u> ***Variation in social organization among extant primates. A)*** *The proportion of variation in each social organization and overall IVSO accounted for by phylogenetic history, ecological and life-history factors ("ecological predictors": habitat type and heterogeneity, diet, foraging style, locomotion, activity pattern, and body size), research effort (number of published studies on a population, centered within superfamilies), as well as remaining residual (unexplained) variation among populations, species, and superfamilies. Dots indicate posterior medians and lines indicate 90% Bayesian credible intervals (CIs).* ***B)*** *Total effects of the ecological and life history factors (activity level, locomotion, and body size) used to predict ancestral social organization and IVSO. Cross lines (**+**) indicate assumed states used for ancestral state prediction (i.e. nocturnal activity, arboreal locomotion, and low [-2 SD] body size. Thick lines indicate posterior medians and ribbons indicate 90% Bayesian CIs.*

III.5.3 <u>Ecological predictors and reconstruction of the ancestral state</u>

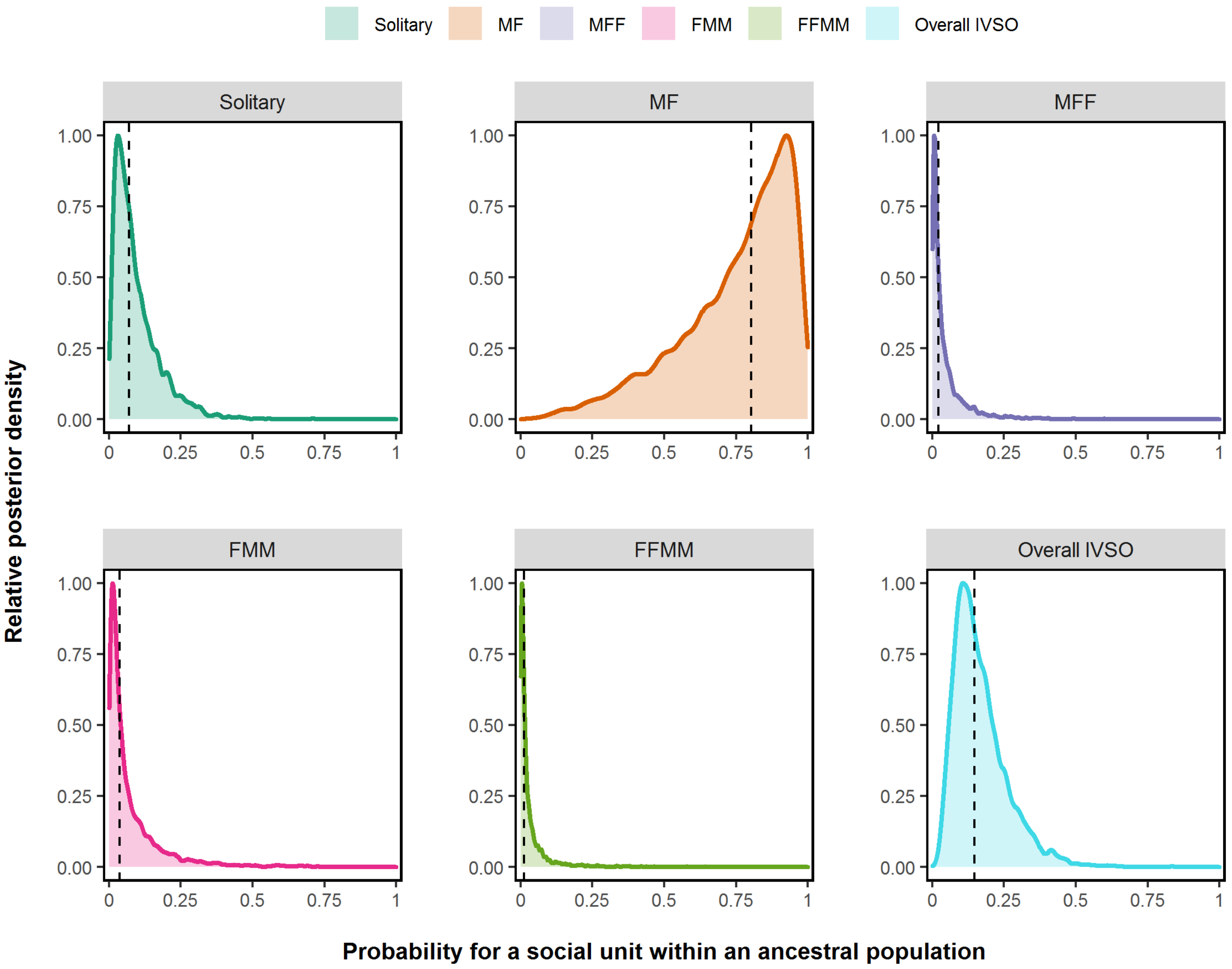
Next, we estimated the probability of each social organization and degree of IVSO for the last common ancestor of all primates, contingent on predictors. Specifically, current evidence strongly suggest that ancestral primates were small-bodied, arboreal, and nocturnal

(22, 23), hence body size, locomotion and activity pattern can be used to make more informed inferences about ancestral states. Conversely, since the literature does not offer strong a priori expectations about ancestral habitat types, foraging strategies, or specific dietary patterns we excluded these variables from this model, which had the added benefit of not requiring imputation.

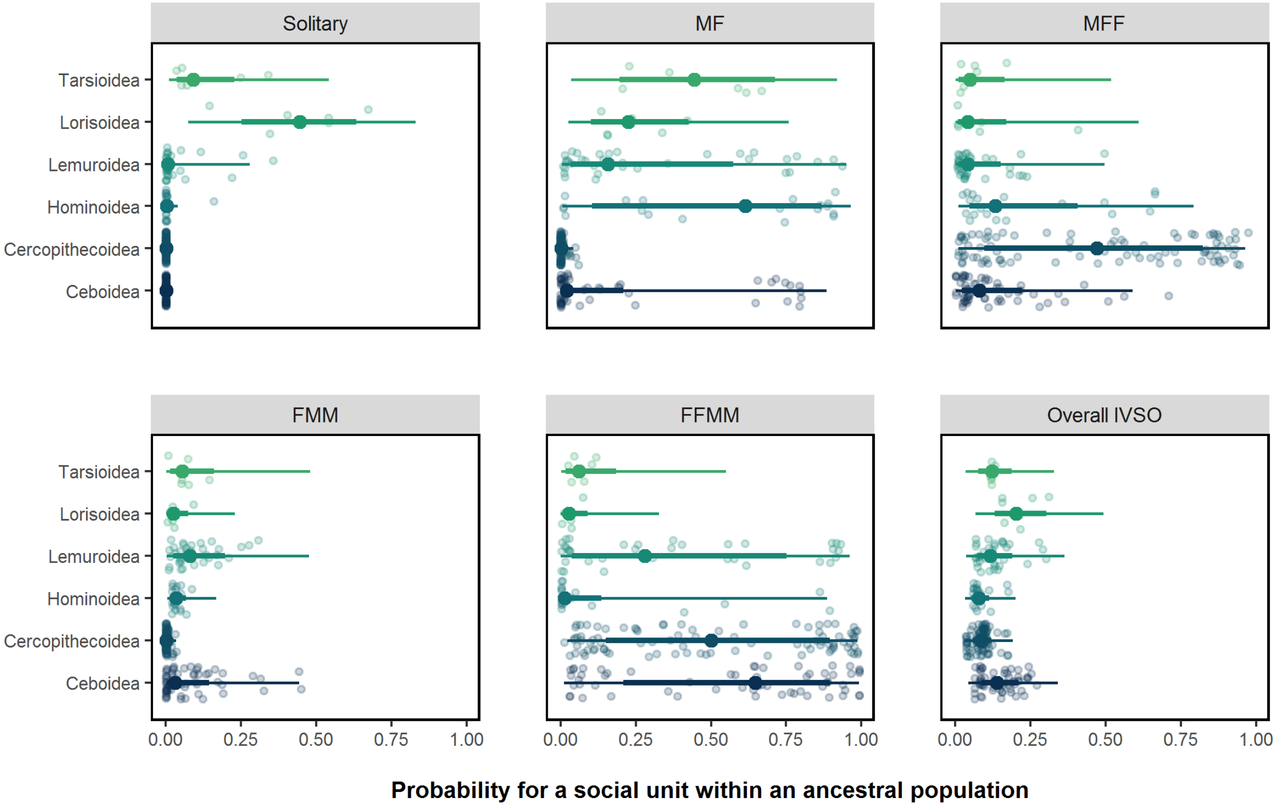
The total effects of body size, locomotion and activity pattern on social organization are shown in **Figure III-2B**. Overall, pair-living was more common with nocturnal than diurnal activity (median Δ probability = 0.30, 90% CI [0.04, 0.58]). Pair-living was also more likely among smaller bodied species (-1SD) compared to average-sized species (median Δ probability = 0.19, 90% CI [0.05, 0.35]) or larger species (+1 SD; median Δ probability = 0.32, 90% CI [0.09, 0.59]). Multi-male, multi-female groups were in turn more likely among larger-bodied species compared to average (median Δ probability = 0.08, 90% CI [-0.01, 0.26]) or small species (median Δ probability = 0.16, 90% CI [0.00, 0.47]). No clear effects were observed for differences in locomotion on the probability of social organization, and none of these ecological predictors consistently explained variation in the overall proportion of IVSO across populations.

The oldest known primates were very small (22, 24), and we therefore assumed an ancestral body size of 30g (-2 SD relative to extant species; **Figure III-2B**), which is an upper limit based on current fossil evidence (19). We also assumed nocturnal activity and arboreal locomotion. Under these assumptions, pair-living units are the most likely ancestral social organization (median probability = 0.80, 90% CI [0.33, 0.98]), compared to solitary (median Δ probability = 0.72, 90% CI = 0.16 – 0.95) and all forms of group-living (all median Δ probabilities ≥ 0.75 and 90% CIs exclude zero; **Figure III-3**). In addition, there is support for a small proportion of solitary social units occurring in ancestral populations (median probability = 0.07, 90% CI

[0.01, 0.26]), while little to no support is provided for the presence of group-living units (lower 90% CIs < 0.01). Put differently, if we could sample 10 social units in an ancestral population, we would expect ~80-90% of those units to be pair-living, but also ~10-20% to be solitary. This pattern is supported by the overall IVSO model, which estimates that approximately 10-20% of social units (median probability = 0.15, 90% CI [0.06, 0.35]) should deviate from the main social organization (pair-living). Thus, the last common ancestor of all primates most likely had a variable social organization, with most individuals living in pairs but some being solitary. Predicted ancestral IVSOs are also relatively constant across each of the six major primate superfamilies (**Figure III-4**), suggesting that specific clades do not differ in their propensity for intrapopulation variation. Despite pair-living likely being ancestral in early primates, support for pair-living is only found for ancestral strepsirrhines (lemurs and lorises) and tarsiers ('prosimians'). Ancestral cercopithecoids ('Old World' monkeys) and ceboids ('New World' monkeys) were instead more likely to be group-living, suggesting that pair-living is derived in Simiiformes and has evolved secondarily within these two superfamilies.



<u>Figure III-3:</u> Ecologically informed predictions of social organization in ancestral primate populations. *Predicted probabilities of a social unit exhibiting each social organization and some form of IVSO within ancestral populations, assuming the ecological conditions marked in Figure III-2B (nocturnal, arboreal and small), as well as average within-superfamily sampling effort. Scaled posterior densities are shown, with posterior medians indicated by the dotted line.*



<u>Figure III-4:</u> Predictions of ancestral social organization for the six primate superfamilies.
The dark dots and lines indicate median probabilities +/- 50% (thick line) and 90% CIs (thin line) for the expected probability of each SO and IVSO in an average population of each primate superfamily. Light circles in turn indicate median predictions for specific species within each superfamily. The root/basal predictions for each clade are the average of the posterior phylogenetically adjusted species predictions, assuming average within-superfamily sampling effort.

III.6 Discussion

Like previous analyses (1, 3, 5), our results suggest that group-living evolved late in primates' evolutionary history. However, our finding that pair-living was the ancestral primate social organization contrasts with previous studies which found solitary living to be ancestral (1, 3, 5). This difference is not likely a consequence of us having underestimated the occurrence of solitary living in extant primates. Instead, it is likely to be a consequence of our focus on well-studied species and the exclusion of non-studied nocturnal, cryptic species that have often been assumed to be solitary. Multiple field studies revealed that few nocturnal strepsirrhines exhibit solitary living, with instead pair-living being common in these species (7, 25). Accordingly, we found pair-living to be more common in nocturnal strepsirrhines than in diurnal simians, which contrasts previous beliefs. Further, we focused on the composition of social units (social organization), while most previous studies aimed at explaining "social monogamy", a concept combining the social organization of pair-living with the social structure of pair-bonding, biparental care and a primarily monogamous mating system (3, 5). This demonstrates how differences in classifying social systems can influence the interpretation of social evolution.

Here, we showed for the first time that the ancestral social organization of primates was variable, with approximately 15% of the individuals in the population deviating from pair-living. Our analysis differs from previous studies by taking IVSO into account. Both Shultz et al 2011 and Lukas and Clutton-Brock 2013 categorized each species as having one social system. Kappeler and Pozzi 2019 were the first to consider IVSO descriptively, but their statistical analysis relied on categorizing species into a single form of social organization. Variation is needed for evolutionary change, and it is therefore important to develop statistical tools that take this variation into account. Considering IVSO on the population level allowed us to come to a more realistic estimate of the ancestral social organization of primates.

Social monogamy has often been regarded as a derived form of social system needing specific explanation (1, 3, 5). Thus, it might seem surprising that we found pair-living to be the most likely ancestral social organization. However, pair-living has also been suggested to be the ancestral form in other mammalian orders when considering IVSO, including Artiodactyla (26), Eulipotyphla (27), and in Macroscelidea (28). Moreover, Kappeler and Pozzi 2019 suggested that pair-living is not a derived complex social organization in primates, but an ancestral form before the evolution of more complex social groups.

Our results indicate that pair-living is ancestral in primates, despite other components of “social monogamy” being derived traits present in only a few lineages, including a pair bonding social structure and biparental care system (**Figure III-5**). Pair-living without pair-bonding as observed in some extant strepsirrhines represents the ancestral primate state. However, our results also show that the direct ancestors of New World and Old World monkeys were most likely not pair-living (**Figure III-4**). In these taxa, pair-living might have evolved secondarily, and afterwards other components of the social system could have co-evolved. Pair-bonding evolved first, as observed in three of the four forms of pair-living social systems, while paternal care only evolved in some New World monkeys and siamangs (**Figure III-5**). Cooperative breeding with non-breeding helpers only evolved in the callitrichids. Thus, pair-living as in extant primate species can be part of four different social systems (**Figure III-5**), highlighting the importance to differentiate between different components of social systems (9-11).

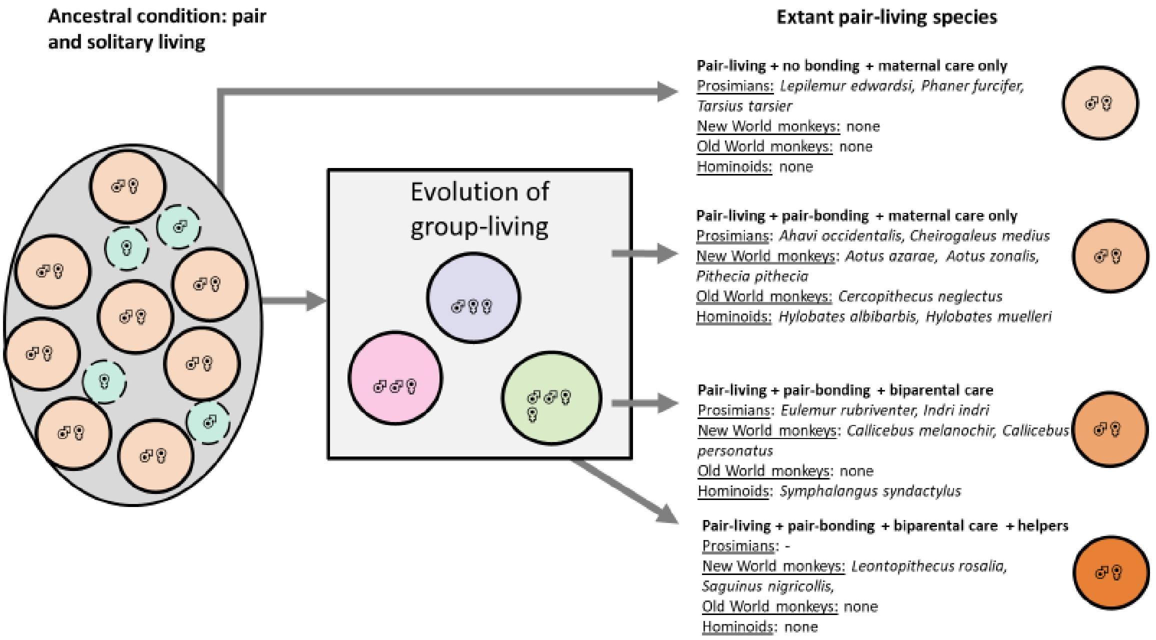


Figure III-5: Pair-living in extant primate species and other components of social monogamy.
While pair-living is an ancestral state in primates, pair-bonding and paternal care are considered to be independent traits that evolved later and not in all pair-living lineages. Ancestral pair-living seems to be maintained in Tarsioidea, Lorisoidea and Lemuroidea, but probably evolved secondarily in the other primate lineages. The large circle represents the ancestral population. Smaller circles represent social units with its outline corresponding to whether this social organization is the most frequently observed or is a form of intra-population variation in social organization (IVSO, dotted line). Colors and symbols represent the different types of social organization as in Figure III-1. Arrows indicate different possible evolutionary pathways. Far right: Pair-living (social organization) occurs in different combinations with the other factors of social systems (right: social structure and care-system), indicating that pair-living can be one component in four different types of social systems (different grades of orange). Examples of pair-living species in the different taxa are shown on the right.

Acknowledgments

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III.7 Supplementary Material

Robustness checks

Phylogenetic process— A model assuming multivariate Brownian Motion for the phylogenetic effects generated nearly identical predictions as compared to a Gaussian Process phylogenetic model, which used a more flexible, nonparametric model of the phylogenetic effects analogous to an Orstein-Uhlenbeck process. In particular, differences in median predictions for ancestral social organizations and IVSOs were all < 0.05 between these models, suggesting that findings were robust to this analytic choice. We therefore opted for the simpler and more computationally efficient BM model.

Accounting for phylogenetic uncertainty — We needed to account for uncertainty in the phylogenetic relationships among taxa while making inferences from our model. For Bayesian inference, a straightforward solution is to random sample multiple phylogenetic covariance matrices during model estimation, capturing the uncertainty in the phylogenetic tree, and to combine across their posterior distributions for statistical inference. However, due to the computational costs of running a complex Bayesian model multiple times, it is desirable to select a sufficiently small number of random phylogenetic trees for which results are relatively robust to the addition of further samples. We tested this for our model by comparing naïve ancestral state inferences between models using a single or multiple random trees (N = 1, 5, 10). At N = 5 samples, we found that further addition of random trees (N = 10) did not meaningfully change inferences (posterior median differences < 0.01). We therefore pooled uncertainty across 5 random trees for all reported analyses.

<u>Table SIII-I:</u> Effect sizes for ecological predictors across models. *Median posterior estimates are reported with posterior median absolute deviations (robust SDs) in parentheses. Estimates are taken from the full model including all ecological and life-history predictors with (N = 499 populations) or without imputation (N = 102 populations). Sample sizes are also reported in-line for total effect models with missing data, which only included fixed effects for research effort and the predictor of interest. Note that in a multinomial model, ecological effects on the total probability of each organization (e.g. as shown in Figure III-2) can be estimated using a predictor's effect on the difference in probability between solitary and the remaining social organizations (reported below).*

MF - Solitary			
Predictor	Effect size (β) and robust standard deviation (MAD)		
	Full model (imputation, N = 499 populations)	Full model (raw data, N = 102)	Total effect models (univariate)
Habitat heterogeneity	0.12 (0.41)	0.34 (0.56)	0.16 (0.39)
Habitat category			N = 494
-Closed v both	0.75 (0.69)	1.20 (0.88)	0.75 (0.70)
-Open v both	-0.37 (0.91)	-0.05 (0.96)	-0.35 (0.88)
Foraging style			N =496
-Groups v solitary	1.65 (0.76)	-0.12 (0.92)	1.50 (0.72)
-Both v solitary	-0.38 (0.70)	0.09 (0.91)	-0.30 (0.68)
Locomotion			N = 485
-Both v Arb.	-0.18 (0.67)	-0.03 (0.82)	-0.36 (0.70)
-Terrest. v Arb.	0.08 (0.90)	-0.43 (0.89)	-0.15 (0.80)
Activity pattern			
-Cathem. v Noct.	-0.42 (0.87)	0.16 (0.89)	0.03 (0.84)
-Diurn. v Noct.	-0.67 (0.77)	-0.15 (0.93)	-0.80 (0.76)
Diet			
-Fruit %	0.47 (0.80)	0.10 (0.93)	0.43 (0.79); N = 409
-Foliage %	0.01 (0.81)	0.31 (0.94)	1.20 (0.79); N = 361
-Seed %	-0.15 (0.89)	-0.12 (0.91)	-0.24 (0.92); N = 198
-Animal %	0.3 (0.87)	-0.38 (0.95)	0.10 (0.86); N = 244
Body size	-0.74 (0.35)	-1.70 (0.57)	-0.97 (0.36); N = 491

MFF - Solitary			
Predictor	Effect size (β) and robust standard deviation (MAD)		
	Full model (imputation, N = 499 populations)	Full model (raw data, N = 102)	Total effect models (univariate)
Habitat heterogeneity	-0.06 (0.32)	0.57 (0.48)	-0.07 (0.33)
Habitat category			N = 494
-Closed v both	-0.42 (0.56)	-0.51 (0.74)	-0.45 (0.58)
-Open v both	0.04 (0.71)	-0.59 (0.89)	0.08 (0.74)
Foraging style			N = 496
-Groups v solitary	1.99 (0.74)	0.19 (0.90)	2.11 (0.74)
-Both v solitary	-1.41 (0.77)	-0.19 (0.91)	-1.38 (0.77)
Locomotion			N = 485
-Both v Arb.	0.36 (0.57)	-1.28 (0.81)	0.41 (0.58)
-Terrest. v Arb.	-0.20 (0.70)	-0.56 (0.79)	-0.05 (0.71)
Activity pattern			
-Cathem. v Noct.	0.15 (0.86)	-0.20 (1.00)	0.10 (0.86)

-Diurn. v Noct.	1.22 (0.81)	0.21 (0.98)	1.52 (0.84)
Diet			
-Fruit %	0.03 (0.76)	0.04 (0.90)	-0.33 (0.75); N = 409
-Foliage %	0.02 (0.72)	0.20 (0.96)	0.22 (0.76); N = 361
-Seed %	0.82 (0.86)	0.00 (0.94)	-0.13 (0.88); N = 198
-Animal %	1.28 (0.82)	0.60 (0.95)	0.69 (0.86); N = 244
Body size	0.01 (0.36)	-0.23 (0.58)	0.12 (0.36); N = 491

FMM - solitary

Predictor	Effect size (β) and robust standard deviation (MAD)		
	Full model (imputation, N = 499 populations)	Full model (raw data, N = 102)	Total effect models (univariate)
Habitat heterogeneity	-0.34 (0.46)	0.11 (0.60)	-0.34 (0.47)
Habitat category			N = 494
-Closed v both	0.16 (0.65)	0.56 (0.86)	0.10 (0.66)
-Open v both	-0.34 (0.92)	-0.03 (1.00)	-0.29 (0.92)
Foraging style			N = 496
-Groups v solitary	2.62 (0.72)	0.33 (0.93)	2.81 (0.73)
-Both v solitary	-0.78 (0.70)	-0.33 (0.94)	-0.89 (0.71)
Locomotion			N = 485
-Both v Arb.	0.29 (0.62)	-0.08 (0.86)	0.27 (0.66)
-Terrest. v Arb.	0.08 (0.79)	-0.23 (0.97)	-0.02 (0.80)
Activity pattern			
-Cathem. v Noct.	0.89 (0.80)	-0.28 (0.95)	1.03 (0.83)
-Diurn. v Noct.	0.85 (0.77)	0.29 (0.92)	0.99 (0.76)
Diet			
-Fruit %	-0.05 (0.73)	-0.51 (0.90)	-0.28 (0.75); N = 409
-Foliage %	-0.12 (0.75)	0.08 (0.96)	0.25 (0.76); N = 361
-Seed %	0.91 (0.86)	0.63 (0.96)	0.58 (0.86); N = 198
-Animal %	0.06 (0.83)	-0.12 (1.00)	0.17 (0.83); N = 244
Body size	-0.33 (0.29)	-1.21 (0.59)	-0.23 (0.33); N = 491

FFMM - Solitary

Predictor	Effect size (β) and robust standard deviation (MAD)		
	Full model (imputation, N = 499 populations)	Full model (raw data, N = 102)	Total effect models (univariate)
Habitat heterogeneity	0.17 (0.36)	0.22 (0.59)	0.23 (0.36)
Habitat category			N = 494
-Closed v both	-0.29 (0.56)	-0.66 (0.73)	-0.36 (0.54)
-Open v both	0.65 (0.70)	0.60 (0.91)	0.61 (0.73)
Foraging style			N = 496
-Groups v solitary	2.19 (0.77)	1.10 (0.86)	2.23 (0.80)
-Both v solitary	-1.37 (0.76)	-1.11 (0.91)	-1.37 (0.79)
Locomotion			N = 485
-Both v Arb.	0.73 (0.59)	0.18 (0.78)	0.77 (0.59)
-Terrest. v Arb.	0.17 (0.71)	0.99 (0.79)	0.47 (0.71)
Activity pattern			
-Cathem. v Noct.	0.43 (0.85)	0.35 (0.96)	0.47 (0.88)
-Diurn. v Noct.	0.94 (0.80)	-0.40 (0.95)	1.23 (0.82)
Diet			
-Fruit %	-0.61 (0.74)	-0.15 (0.94)	-0.58 (0.75); N = 409
-Foliage %	-0.99 (0.71)	-0.30 (1.01)	-0.57 (0.79); N = 361
-Seed %	0.25 (0.78)	0.06 (0.94)	0.14 (0.91); N = 198
-Animal %	-0.34 (0.84)	-0.24 (0.96)	0.17 (0.87); N = 244
Body size	0.33 (0.38)	0.38 (0.59)	0.36 (0.40); N = 491

Total IVSO

Predictor	Effect size (β) and robust standard deviation (MAD)

	Full model (imputation, N = 499 populations)	Full model (raw data, N = 102)	Total effect models (univariate)
Habitat heterogeneity	-0.14 (0.18)	-0.10 (0.29)	-0.08 (0.18)
Habitat category			N = 494
-Closed v both	0.17 (0.35)	0.87 (0.57)	0.09 (0.33)
-Open v both	-0.20 (0.50)	-0.72 (0.86)	-0.01 (0.51)
Foraging style			N = 496
-Groups v solitary	-0.39 (0.56)	-0.73 (0.83)	-0.17 (0.50)
-Both v solitary	0.59 (0.55)	0.71 (0.85)	0.58 (0.57)
Locomotion			N = 485
-Both v Arb.	-0.37 (0.30)	-0.56 (0.59)	-0.26 (0.30)
-Terrest. v Arb.	0.44 (0.42)	0.37 (0.64)	0.37 (0.38)
Activity pattern			
-Cathem. v Noct.	0.81 (0.68)	-0.47 (0.94)	0.41 (0.65)
-Diurn. v Noct.	0.93 (0.55)	0.48 (0.94)	0.74 (0.52)
Diet			
-Fruit %	-0.83 (0.57)	-0.49 (0.84)	-1.16 (0.48); N = 409
-Foliage %	0.11 (0.55)	-0.22 (0.84)	0.70 (0.51); N = 361
-Seed %	0.39 (0.79)	-0.15 (0.83)	0.11 (0.73); N = 198
-Animal %	1.04 (0.70)	0.36 (0.94)	0.55 (0.67); N = 244
Body size	0.11 (0.16)	0.20 (0.35)	0.11 (0.16); N = 491

*<u>Table SIII-2</u>: **Correlation of social organization and IVSO across species.** Species-level correlations. Median posterior correlations are shown for the phylogenetic and species residual effects on the relative probability of pair and group-living in comparison to solitary social organization. Posterior probabilities in support of a positive correlation p+ shown in parentheses. Posterior probabilities lower than 0.95 and greater than 0.05 provide weak evidence of a positive or negative effect, respectively. Overall, little evidence was found for species-level correlations between specific forms of social organization and overall IVSO, with most posterior correlations centered near zero with relatively high uncertainty. No clear associations were observed for residual species differences in social organization or IVSO. Therefore, to enhance computational efficiency, we simplified our statistical models by assuming independent evolution of social organization and IVSO across the phylogenetic tree. However, specific forms of social organization did tend to coevolve within lineages, as indicated by moderate positive correlations between the relative probability of MF and MFF (median r = 0.52, $p_{+} = 0.99$) and FMM (median r = 0.67, $p_{+} = 1.00$) in comparison to solitary living. The relative probability of MFF was also positively correlated with FMM (median r = 0.67, $p_{+} = 1.00$) and FFMM (median r = 0.63, $p_{+} = 1.00$), as well as the relative probability of FMM and FFMM (median r = 0.58, $p_{+} = 0.99$). See Table SIII-2 for all results.*

Phylogenetic correlation

	Solitary/MF	Solitary/MFF	Solitary/FMM	Solitary/FFMM	Overall IVSO
Solitary/MF	1				
Solitary/MFF	0.52 (0.99)	1			
Solitary/FMM	0.67 (1.00)	0.67 (1.00)	1		
Solitary/FFMM	-0.00 (0.49)	0.63 (1.00)	0.58 (0.99)	1	
Overall IVSO	0.13 (0.73)	0.16 (0.80)	0.32 (0.94)	-0.17 (0.33)	1

Species residual correlation

	Solitary/MF	Solitary/MFF	Solitary/FMM	Solitary/FFMM	Overall IVSO
Solitary/MF	1				
Solitary/MFF	0.06 (0.56)	1			
Solitary/FMM	0.05 (0.55)	-0.00 (0.50)	1		
Solitary/FFMM	-0.03 (0.47)	0.01 (0.51)	0.07 (0.53)	1	
Overall IVSO	0.03 (0.53)	0.11 (0.53)	0.09 (0.59)	-0.17 (0.24)	1

Chapter 3

IV. Chapter 3: Was the ancestral mammal really solitary living?

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IV.1 Résumé

Il est généralement admis que l'ancêtre de tous les mammifères avait un mode de vie solitaire. Cependant, des preuves fossiles indiquent un mode de vie grégaire chez certains premiers mammifères et même chez les Cynodontes, ancêtres des mammifères. Nous avons créé une base de données basée uniquement sur la littérature primaire, évaluée par les pairs, sur l'organisation sociale des 5740 espèces de mammifères existantes et avons trouvé des informations sur 806 espèces et 1622 populations. Parmi celles-ci, 412 espèces (51%) et 631 populations (39%) avaient une organisation sociale variable avec plus d'une forme d'organisation sociale. En se basant sur une méthode phylogénétiquement comparative (c'est-à-dire un cadre bayésien) et en tenant compte de la variation intra-spécifique, nous montrons que l'organisation sociale ancestrale des mammifères n'était pas exclusivement solitaire mais variable; la vie en couple étant la principale organisation sociale ancestrale. Notre étude change notre compréhension de l'évolution sociale des mammifères et indique que la vie en couple a évolué très tôt, que la vie solitaire chez les mammifères actuels pourrait être une adaptation spéciale, et que le principal progrès dans l'évolution sociale des mammifères pourrait avoir été la tolérance entre mâles, permettant l'évolution de groupes multi-mâles.

IV.2 Abstract

It is generally believed that the ancestor of all mammals was solitary living. However, fossil evidence indicates a gregarious lifestyle in some early mammals and even in *Cynodonts*, ancestors of mammals. Here we created a database based only on primary peer-reviewed literature on the social organization of the 5740 extant mammalian species and found information for 806 species and 1622 populations. Of these, 412 species (51%) and 631 populations (39%) had a variable social organization with more than one form of social organization. Based on a phylogenetically comparative method (*i.e.* a Bayesian framework) and accounting for intra-specific variation, we show that the ancestral social organization of mammals was not exclusively solitary living, but variable, with pair-living being the main ancestral social organization. Our study changes our understanding of mammalian social evolution, and indicates that pair-living evolved early, that solitary living in extant mammals might be a special adaptation, and that the main advancement in mammalian social evolution might have been male-male tolerance, enabling the evolution of multi-male groups.

Keywords: Mammals, intra-specific variation, social organization, evolution

IV.3 Introduction

Mammalian species display a high diversity of social systems ranging from solitary living to large social groups and eusociality (Clutton-Brock 2021). Within mammalian species, the mating system is variable, with considerable inter-specific variation in extra-pair paternity (Cohas and Allainé 2009) and in the degree of multiple paternity within litters (Dobson et al. 2010). Social structure represented by social networks can vary widely, for example in primates (Sueur et al. 2011a). Most mammalian species show maternal care only but there are also species having biparental care or helpers at the nest (Skutch 1961; Cockburn 2006; Downing et al. 2021). This might be related to the social organization, for example whether mammals live solitarily, in pairs, or in groups. The social system of mammals varies in mating system, social structure, care system and social organization.

Kappeler (2019) suggested that animal social systems are composed of four inter-related components: the mating system, the social structure, the care system and the social organization. The mating system describes who mates with whom and the reproductive consequences. There are four major types of mating system, depending on the number of mating partners for males and females (Clutton-Brock 1989; Loue 2007): monogamy, polygyny, polyandry or polygynandry. The social structure describes the different interactions between individuals and the resulting relationships, for example in macaques (Thierry 2022), and is often described via social networks (Sueur et al. 2011b). The care system is about who cares for the dependent offspring (Kappeler 2019). Finally, the social organization describes the size, the sexual composition and the spatiotemporal cohesion of social units (Kappeler and van Schaik 2002). Three major categories of social organization occur: solitary living, pair-living, or group-living. These four components are inter-related, with for example the social organization (group composition) determining who can mate and interact with whom. Most information are available for the social organization that is relatively easier to measure in the field than the other components (Schradin et al. 2018).

Generally, the ancestral mammalian social organization is believed to be solitary living with pair and group-living deriving from it (Jarman 1974; Wemmer and Christen 1987; Lukas and Clutton-Brock 2013; Kappeler and Pozzi 2019). For example, Lukas and Clutton-Brock (2013) found in their comparative study that the ancestor of all mammals was solitary and suggest important social transitions from this primitive state. Using Bayesian phylogenetic comparative methods, Kappeler and Pozzi (2019) suggest for primates frequent transitions between solitary ancestors and pair-living which then evolved into group-living species. For primates again, Shultz et al. 2011 have shown that sociality progresses from solitary living first to large multi-male/multi-female groups, and then in some species to either pair-living or single-male harem systems. So far, in comparative studies on mammals there has been an agreement that solitary living was the ancestral state from which different forms of sociality evolved (Smith et al. 2017). Different ecological and life-history factors have been discussed to be associated to such social transitions.

Predation pressure and resource distribution (influencing competition) are known to be key factors exerting an evolutionary pressure on social organization (Crook and Gartlan 1966; van Schaik et al. 1989). In open habitats, species are more visible and thus vulnerable to predation (Crook and Gartlan 1966; Janson and Goldsmith 1995), which means that here individuals benefit more from living in groups (Markham and Gesquiere 2017). Seasonality in food availability influences breeding seasonality and might have a strong influence on sociality

(White 1998). Quantity and distribution of diet itself might influence sociality, with group-living being more likely if the food is plentiful and sharable (Jordan et al. 2022). In primatology, these ecological factors have been combined into so called socio-ecological models to predict whether these species live solitarily or in groups (Crook and Gartlan 1966; Emlen and Oring 1977; Terborgh and Janson 1986). The emerging socio-ecological models have been criticized for not taking phylogenetic relationships and life-history factors into account (Shultz et al. 2011).

Previous studies have shown that life history traits, such as body size or activity pattern can be related to sociality (Bekoff et al. 1981). In some taxa such as artiodactyla and primates, larger species are more likely to be group-living than smaller ones (Jarman 1974; Cheney et al. 1987), but in other taxa such as carnivores (with solitary large bears) this might not be the case. Sexual dimorphism is typically expected to be lowest in pair-living species and largest in group-living species, where several males experience contest competition for the access to females. In contrast, solitary species where males experiencing scramble competition might show a lower degree of sexual dimorphism, but in solitary carnivores such as mustelids, tigers, leopards and bears, males are considerably larger than females (Gittleman and Valkenburgh 1997). Solitary species are often assumed to be nocturnal, while diurnal species might be more likely to be group-living because they experience more predation (Wright 1998; Gursky 2000). Within the fast-slow continuum of life history strategies (Jeschke et al. 2008), short living species with large litters and only one breeding attempts are often assumed to be solitary living. On the contrary, long living species with small litters but multiple breeding attempts are assumed to be group-living (Lucas and Keller 2020). Previous studies succeeded in taking inter-specific variation in ecological and life-history factors into account but less so intra-specific variation.

Social organization itself varies not only between but also within species (Lott 1984). Intra-specific variation in social organization (IVSO) is common in several mammalian orders (Eulipotyphla: Valomy et al. 2015; strepsirrhines: Agnani et al. 2018; Artiodactyla: Miles et al. 2019; Macroscelidea: Olivier et al. 2022). Taking IVSO into account can change our understanding of social evolution. For example, previously it was believed that the ancestor of primates was solitary living but when accounting for IVSO, we found indication that it was rather pair-living (Olivier et al. 2023 (*in prep* Chapter 3)). Therefore, here we present the first study on the evolution of mammalian social organization that takes IVSO and all mammalian orders into account.

One additional difference between previous studies and our study is that we did not assume non-studied species to be solitary living nor did we use phylogenetic interference (assuming closely related species have the same social organization). For example, in one large comparative study on mammalian social systems, Lukas and Clutton-Brock (2013) assumed 397 out of 399 species of Eulipotyphla to be solitary living, when in fact only 16 had been studied, of which 9 were not exclusively solitary (Valomy et al. 2015). This example indicates the importance of data quality for comparative studies (Schradin 2017). So far, all comparative studies that were based on high quality data from primary literature and took IVSO into account failed to confirm solitary living to be the ancestral state in different mammalian orders (Dalerum 2007; Valomy et al. 2015; Miles et al. 2019; Olivier et al. 2022; *Chapter 2*).

In contrast to behavioral ecologists, palaeontologist do not consider the ancestor of all mammals to be solitary living. Therapsids belong to the stem mammals, *i.e.* the group from which modern mammals evolved. The therapsid *Lystrosaurus*, a dicynodont from the Perm-Triassic transition 255 million years ago, is believed to have formed large foraging herds

(Brusatte 2022). Dicynodonts were followed by cynodonts (living 260-230 million years ago), which gave rise to mammals (Box IV-1). There is good fossil evidence that some of these species were pair or group-living (Brink 1956; Groenewald et al. 2001; Jasinoski and Abdala 2017). Thus, 60 million year old fossils of the mammal *Pucadelphys andinus*, a stem-metatherian belonging to the Multituberculata (a side branch of the mammalian tree), indicate that this species was living in multi-male multi-female groups (Ladevèze et al. 2011). In sum, there is considerable evidence for the potential sociality of the ancestor of all mammals. Therefore, whether the ancestor was solitary living should not be assumed a priori but tested at posteriori.

The aim of this study was to determine the ancestral social organization of mammals. For this, we searched for each of the 5740 extent mammalian species whether the social organization had been studied in the field, recording all forms of social organization observed in each population. Using Bayesian statistical modelling taking IVSO into account on the population level, we evaluated the previous assumption that the ancestor of all mammals was solitary. Next, we tested whether ecological and life history factors were associated with specific forms of social organization. Specifically, we predicted diet to influence sociality with species feeding often on non-sharable food (insects, fish, and other animals) being more likely to be solitary living while species with clumped food (herbivores and frugivores) being more likely to be group-living. Species living in open habitats were predicted to be more likely to live in groups to reduce predation risk and species with small litter size were more likely to be group-living. As discussed, we predicted sexual dimorphism to be lowest in pair-living species and largest in group-living species. We also tested for possible effects of body mass, longevity and activity pattern on sociality and predicted small, nocturnal species to live solitarily while long-lived species could be more likely to live in groups. Finally, we tested for factors that could be related to the occurrence of IVSO. Specifically, we predicted that species having few options to reproduce might have developed evolved IVSO to be able to maximize their reproductive success under the current ecological conditions that might differ between generations. Therefore, short lived species might be more variable. Alternatively, individuals of long-lived species and species with more breeding attempts might experience more diverse environments during their lifetime making IVSO adaptive.

Box IV-1. Divergence in monotremes, marsupials and placentals

In contrast to what many believed, the ancestor of mammals (*i.e.* monotremes, marsupials and placentals) did not live 65 million years ago. Fossil discoveries in recent years have provided more information about the timeline.

The relationships between the three existing divisions of mammals (monotremes (prototheria), marsupials (metatheria) and placentals (eutheria)) have been and still are subject of much debate among taxonomists. Nevertheless, most morphological, genetic and molecular evidence favours a closer evolutionary relationship between marsupials and placental mammals than either has with the monotremes (van Rheede et al. 2006).

The divergence between the prototheria lineage and the theria (*i.e.* marsupial and placental) lineages occurred before the divergence between marsupial and placental mammals, which explains why monotremes retain some primitive traits thought to have been present in the synapsid ancestors of later mammals, such as egg laying. The time at which the monotreme lineage diverged from other mammalian lineages is uncertain. However, in a genetic study, estimates were about 220 million years ago (Madsen 2009). Through DNA analysis, the divergence between marsupials and placental mammals has been estimated at between 100 and 120 million years (Tyndale-Biscoe 2004).

Thus, in contrast to common believe, the ancestor of all mammals did not live 65 million years ago. Instead, the common ancestor of monotremes, marsupials and placentals lived approximately 250 million years ago.

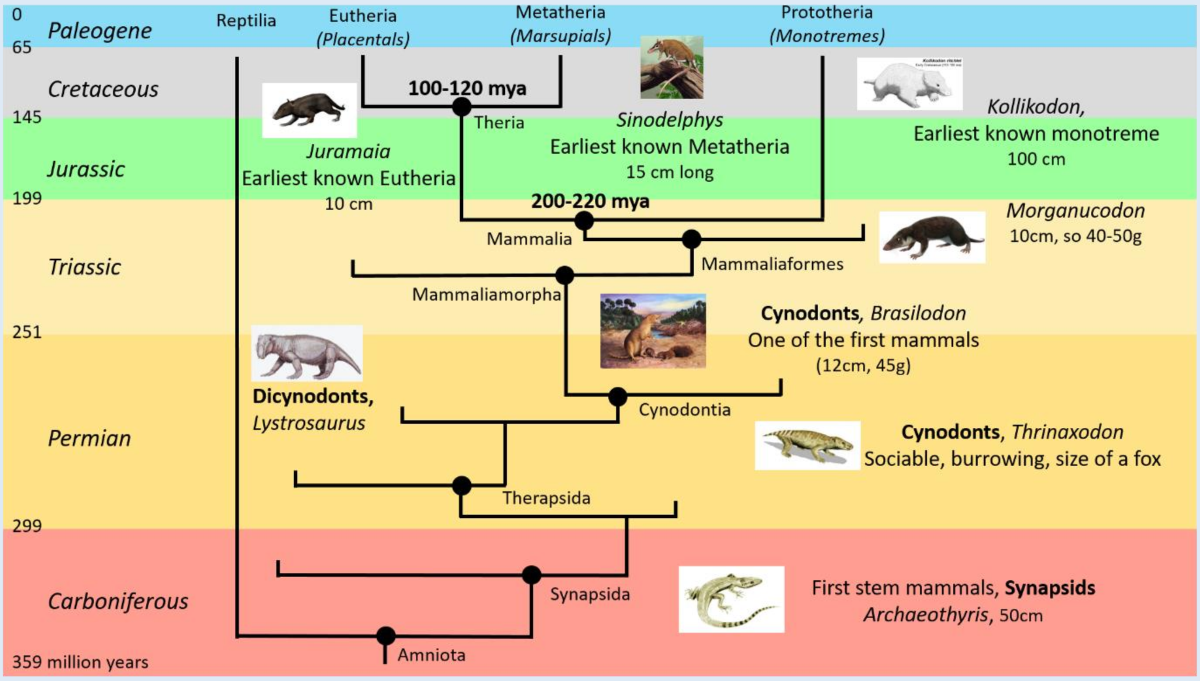


Figure Box IV-1: *Timeline and phylogenetic tree of the ancestor of all mammals and the latest fossils with some of their characteristics.*

IV.4 Materials and Methods

Data collection.— The 5740 species of mammals listed in the IUCN (International Union for Conservation of Nature) database (2019) were considered. We then conducted literature searches on field studies reporting the social organization for each of these mammalian species. The social organization of a species is described by the size, the sexual composition and the spatio-temporal cohesion of the group (Kappeler 2019). Here we strictly focused on the composition of groups, a central aspect of social organization. We defined social organization as solitary, pairs (MF), one male with multiple females (MFF), multiple males with one female (MMF), groups of multiple males and multiple females (MMFF), sex-specific groups, sex-specific solitary male and sex-specific solitary female (**Table IV-1**).

<u>Table IV-1:</u> The different forms of social organization recorded in our study and their definition. "Stable" refers to pairs or groups of the same individuals being repeatedly observed, also outside the context of mating.

Social organization	Definition
Solitary	Adult males and females forage independently and only meet for mating (do not stay together for periods longer than courtship and mating) and are otherwise alone. All identified dispersers were excluded. Cases where only one sex occurred alone were considered as potential dispersal or alternative reproductive tactics and were not accounted as a solitary social organization.
Pair-living (MF)	Repeated observations of one adult male and one adult female with or without dependent offspring. The home ranges of a pair overlap with each other to a great extent (>>80%) but not with others.
Groups of multiple males and one female and (MMF)	Observations of stable groups with multiple adult males and one adult female with or without dependent offspring.
Groups of one male and multiple females (MFF)	Observations of stable groups with one adult male and multiple adult females with or without dependent offspring.
Groups of multiple males and multiple females (MMFF)	Observations of stable groups with multiple adult males and multiple adult females with or without dependent offspring.
Sex-specific group	Both multiple adult male groups and multiple adult female groups occur in the population. Cases where only one sex formed-groups as an alternative reproductive tactic or non-reproductive tactic (bachelor groups) were not considered as a sex-specific social organization.
Sex-specific solitary male	Solitary adult males and groups of adult females occur in the population.
Sex-specific solitary female	Solitary adult females and groups of adult males occur in the population.

For each species, we searched the Latin name of the species and the term "social" (*e.g.* "*Lynx lynx* AND social"; "*Dugong dugon* AND social") in Web of Science (Thomson Reuters) and in Google Scholar between December 2019 and September 2022. If no study was found, only the Latin name was searched. For several species the Latin name changed over the years, in which case we repeated the search with the previous versions of their names. In Web of Science, search results were restricted to articles within the following three categories: “behavioral science”, “zoology” and “environmental science/ecology”. Only field studies from the primary literature were considered. Laboratory-based and captive studies were ignored, to ensure that the social organization observed by a given species also occurred in their natural habitat (*e.g.* many species can be kept in captivity in pairs, but this does not mean that pairs occur in nature). Studies in enclosures smaller than 1000 hectares, and studies that included manipulation of individuals (*e.g.* adding or removing individuals), groups or resources were discarded. Studies that did not report the sex or that could not determine if individuals were adults or subadults were not taken into account, following (Makuya et al. 2021). In the remaining articles, data for group composition were searched for in the methods, results, figures and tables section, avoiding any interpretations from the authors in the discussion. From each paper, we recorded the adult sex composition of all social units in a population using the definitions presented in Table IV-1. We reported how often each category of social units was observed *e.g.* how many solitary individuals, pairs or different groups were recorded.

We also considered data on home range sizes and overlap, for example from radio-tracking studies (see Table IV-1). However, overlap of home ranges alone does not indicate a group-living social organization. Many solitary species are non-territorial and show a lot of overlap between and within sexes. Only when individuals shared the sleeping sites or when the home ranges of several groups were clearly distinct from each other, were they considered to be pairs or groups.

We only recorded solitary living as a form of social organization when both sexes had been observed to be solitary, as single individuals of one sex may often represent dispersers. Whenever individuals were explicitly reported to be dispersers, they were not considered in the recording of social organization. Therefore, to record one social unit of solitary living, at least one solitary male and one solitary female were needed. For example, when 4 solitary males and 2 solitary females were reported, we recorded 2 solitary social units (the minimum between sexes). The same procedure was done with sex-specific groups, sex-specific solitary male and sex-specific solitary female. We only recorded sex-specific groups as a form of social organization when at least one group of males and one group of females had been observed. For example, when 10 groups of males and 4 groups of females were reported, we recorded 4 sex-specific groups social units. The same was done for sex-specific solitary male where the presence of at least one solitary male and a group of females was required to have a sex-specific solitary male social unit and for sex-specific solitary female (with at least one group of males and one solitary female was necessary). However, we did not record any sex-specific solitary female species and therefore excluded these social units from our analyses.

To be recorded to be pair- or group-living, individuals had to spend a longer period together than only for mating or due to foraging aggregation (for example solitary individuals attracted to the same clumped food search). Considering the huge variation in life history between mammalian species as well as duration of field studies (from weeks to decades), it was not possible to define a time period animals had to spent together to be recorded as pairs/groups that was suitable for all species and studies. Thus, whenever it was not clear from the presented data whether individuals observed together formed pairs/groups outside of the context of mating, these studies were not considered for the database (see also Makuya et al. 2022).

Data were collected at the population level by recording the total number of papers reporting a given social organization in a population. When the same observed individuals and their social units were included in more than one published paper, we considered only the most precise paper, *e.g.* papers where the precise number of social organizations and/or the sex of individuals was described, to prevent the same social unit from being counted several times. The total number of studies reporting social organization per population was then recorded in the database to control for any effects of research effort. For example, populations with multiple studies over decades might be more likely to show variation in social organization than populations with only one single study. Similarly, taxa exhibiting greater (or lesser) variation in social organization may be more or less likely to be investigated by researchers. Solitary species could be less studied because they are more difficult to observe. In addition, we recorded whether the study took place during the breeding season, during the non-breeding season, or throughout the year.

The database records for each population whether multi-level societies or fission-fusion societies occurred. A multilevel society is composed of nested social units with as core unit. Several MFF groups constitute a clan, and several clans form a band. Fission-fusion is a temporary subgrouping varying in size, composition and time association. When multilevel societies (Grueter et al. 2020) occurred within a population, indicating hierarchically structured social organization, we only recorded the composition of the core group defined in the study. In contrast, when fission-fusion societies occurred in the population, we recorded all forms of group composition observed, as this indicated that individuals of this population could exhibit multiple forms of social organization within their society over time. When sex was known, studies reporting groups of adult siblings or groups of a pair of breeding adults and their adult offspring were reported as multi males multi females groups as most studies did not represent genetic data on relatedness. For example, callitrichid primate multi males multi females groups were previously often believed to represent one breeding pair and adult offspring, but later genetic studies indicated this often to be incorrect, with more than one male and/or female breeding per group (Sussman and Garber 1987; Goldizen 1990).

Intrapopulation variation in social organization (IVSO).— IVSO was identified when different forms of social organization occurred within a population, indicating some degree of behavioral plasticity in this population´s social organization. However, the following cases were not regarded as IVSO: in cases of dispersing individuals (solitary individuals of one sex only) or in cases of alternative reproductive tactics (*e.g.* males following a group during the breeding season). Thus, when only one sex had two or more forms of social organization these were regarded as alternative reproductive or dispersal tactics.

Environmental disruption such as the death of a dominant breeder or predation of group-members can also change the social organization of a unit (Schradin 2013), but these changes do not reflect the evolved behavioral plasticity we want to explain. Thus, such environmental disruption events were not considered in our database but were recorded separately.

In contrast to previous studies that considered IVSO as a categorical variable (Dalerum 2007; Valomy et al. 2015; Jaeggi et al. 2020; Olivier et al. 2022) we treated it as a continuous variable. We calculated IVSO at the population level as the proportion of social units deviating from the most frequently observed social organization ('main social organization') within a population. Thus, we conceptualised and measured IVSO as a distinct trait capturing the overall degree of variation in social organization, which may co-evolve with the composition and frequency of specific social organizations within a population. For example, when in a population, 4 MFF and 6 MMFF social units were observed, we calculated the total number of social units (here 10) and assigned the degree of IVSO as follows:

$$1 - \frac{\text{Number of social units with the main social organization}}{\text{Total number of social units}} = 1 - \frac{6}{10} = 0.4$$

This avoided the use of arbitrary thresholds for categorizing the presence or absence of IVSO, retaining the continuous information provided by previous literature, and allowed us to consider how the evolution of specific forms of social organization and the overall degree of IVSO are related across species and populations.

Predictors of social organization.— We included the following predictors in our Bayesian model to account for potential social, ecological, life-history and methodological causes of variation in social organization: habitat type, body mass, diet, activity pattern, litter size, longevity, sexual dimorphism and number of studies per population (Table IV-2).

Table IV-2: *Predictors and from which database the information was used. The first database mentioned is where we used the most data from, the 2nd and 3rd database were used to add data for species not present in the first database.*

Predictors	Definition	Database
Habitat type	The type of habitat depending on whether it is open, closed, both, or water. Open: grassland, shrubland, rocky areas, savannah, desert. Closed: forest, wetland, cave, woodland. Both: artificial when a population lived in an open habitat (*e.g.* grassland) and in a closed habitat (*e.g.* forest). Water: sea, river, oceans, lake.	*Based on our own primary literature search.*
Body mass	Mean body mass (data of males and females combined); the standard deviation was used to	*Handbook Mammals of the World, Pantheria, AnAge.*

	account for measurement error.	
Diet	Percentage of the diet consisting of fruits and foliage throughout the entire year.	*Handbook Mammals of the World*
Activity Pattern	Diurnal, nocturnal or cathemeral.	*Handbook Mammals of the World, Pantheria, AnAge.*
Longevity	Mean longevity	*Pantheria, AnAge.*
Litter size	Mean litter size	*Handbook Mammals of the World, Pantheria, AnAge.*

Habitat type was recorded from the primary literature and categorized on IUCN classification. Given the large number of habitat categories that exist (15 habitats), we then classified them into open, closed, open and closed (both) or water. For the other predictors (body mass, diet, activity pattern, litter size, sexual dimorphism) we used three different databases to obtain the most accurate information for each species. Those three databases were the Handbooks Mammals of the World (Wilson, Mittermeier and Lacher 2013), the online database Pantheria and the online database AnAge. First, we compared the three databases to see if their information was similar (the correlations between the three databases were between 0.92 and 0.99). The most precise information (*e.g.* data for males, females, ranges and mean) was available in Handbook Mammals of the World. That is why we privileged the Handbook Mammals of the World books. If no information was found in the Handbook Mammals of the World, we then consulted the online database Pantheria and again if no information was found in the books or in Pantheria, we used AnAge. For longevity, no information was available in the Handbook Mammals of the World books, we used Pantheria and for species not present in Pantheria, AnAge.

The body mass was calculated by taking the mean body mass between males and females. The male body mass divided by the female body mass was used for sexual dimorphism.

The mean was taken for litter size when a range was provided in the literature. We classified activity pattern in three categories: nocturnal, diurnal and cathemeral.

Ancestral social organization.— To estimate the probability of each social organization and the degree of IVSO of the last common ancestor of all mammals we used predictors. Recent studies have revealed that the ancestor of all mammals was small (Cabreira et al. 2022 describing *Brasilodon* from 225 million years ago with a body mass of approximately 45g), nocturnal and insectivore (Meng et al. 2006; Cabreira et al. 2022). Body size, diet and activity pattern were therefore used to make more informed inferences about ancestral states whereas ancestral habitat types, litter size, sexual dimorphism or longevity were excluded from this model as there was no information available in the literature about a priori expectations on those variables for the ancestor.

Statistical analyses.— The same multilevel phylogenetic model was used as in chapter 2 (Methods section). To determine the ancestral social organization of all mammals, IVSO across mammals and the different ecological and life history factors associated, we developed multilevel phylogenetic models. All analyses were conducted within a flexible Bayesian framework to account for non-Gaussian outcome measures, measurement error in social and ecological data within taxa, as well as uncertainty in phylogenetic relationships across taxa (Hadfield and Nakagawa 2010; McElreath 2020). Our analyses relied on one of the most recent and up-to-date mammalian phylogenies from the VertLife project, ensuring that evolutionary relationships were accurately represented between all species in our dataset. Main social organization was modelled as a multinomial response variable (Koster and McElreath 2017), while IVSO was treated as a binomial response, representing the number of social units deviating from the main social organization out of the total number of social units observed.

Multi-response models were estimated to assess phylogenetic and ecological effects and to conduct robust ancestral state reconstruction of the main social organization and the degree of IVSO expected in an ancestral mammalian populations. We used, weakly regularizing priors to have more realistic assumptions about the estimators and to reduce the risks of inferential bias caused by multiple testing and measurement and sampling error (Lemoine 2019).

The original database can be found at: *https://github.com/CharlotteAnaisOLIVIER/Social_OrganizationIVSO_Mammals.*

For all analyses, as in chapter2, two generalized multilevel phylogenetic models, one for describing the probability of each social organization with a multinomial distribution and the other for describing overall IVSO with a binomial distribution were estimated. For population *p* for species *s*, the multinomial model predicted the number of units observed in category *i* as a function of the total number of units observed n_{ps} and a vector of parameters θ_{ps} for the relative probabilities of each category compared to the base category, which in this case is MMF social organization (a category unlikely to be the ancestral state).

$$\text{Social organization}_{ps} \sim \text{Multinomial}_{\text{K}}\left(n_{\text{ps}}, \boldsymbol{\theta_{ps}}\right)$$

$$\text{logit}\left(\theta_{ps}^{(i)}\right) = \mu_0^{(i)} + \boldsymbol{x}'_{ps}\boldsymbol{\beta}^{(\boldsymbol{i})} + \alpha_{\text{phylo(s)}} + \alpha_{\text{species(s)}} + \alpha_{\text{order(s)}} + \alpha_{\text{population(p)}}$$

$$\text{for } i, \dots, K-1$$

The parameters $\theta_{ps}^{(i)}$ for each category *i* (Solitary, MF, MFF, MMFF, sex-specific group and sex-specific solitary male) as compared to K (MFF) were predicted on the transformed logit scale by a category-specific intercept $\mu_0^{(i)}$, fixed effects $\boldsymbol{\beta}^{(\boldsymbol{i})}$ (research effort and ecological predictors), where $\boldsymbol{x}'_{ps}$ is the transposed vector of population- and/or species-specific predictors, and by the random effects α, which capture Brownian Motion phylogenetic effects

$\alpha_{\text{phylo(s)}}$ as well as any deviations from these phylogenetic predictions at the order, species, and population level. $\alpha_{\text{population(p)}}$ is as an observation-level random effect capturing overdispersion from the expected variance.

By adjusting for any species-level effects, the K-1 intercepts $\boldsymbol{\theta_{ps}}$ provide appropriate relative probabilities of non-MMF compared to MMF social organization for an average ancestral population. These values can be transformed to the absolute scale using the logistic function, which facilitates calculating the probability of social units in an average ancestral population showing each of the K social organizations. In particular, for MFF and any other social organization i

$$\Pr(\text{MMF}) = \frac{1}{1 + \sum_{i}^{K-1} \exp\left(\text{logit}\left(\theta_0^{(i)}\right)\right)} \qquad \Pr(i) = \frac{\exp\left(\text{logit}\left(\theta_0^{(i)}\right)\right)}{1 + \sum_{i}^{K-1} \exp\left(\text{logit}\left(\theta_0^{(i)}\right)\right)}$$

Note that this standard parameterization of the multinomial model can be equivalently specified with K intercepts, where $\theta_0^{Solitary} = -\sum_{i \neq Solitary}^{K-1} \theta_0^{(i)}$. This approach allows for modelling predictors directly on the probability of each category.

The variance explained in social organization by each set of effects can be calculated on the transformed scale using model predictions for the fitted data. Specifically, the total latent variance for social organization i is given by

$$V_{T^{(i)}} = V_{\boldsymbol{\beta}^{(i)}} + V_{\alpha_{\text{phylo}}^{(i)}} + V_{\alpha_{\text{species}}^{(i)}} + V_{\alpha_{\text{order}}^{(i)}} + V_{\alpha_{\text{population}}^{(i)}} + \left(\frac{\pi}{\sqrt{3}}\right)^2$$

where $\left(\frac{\pi}{\sqrt{3}}\right)^2$ is the theoretical variance of the logit scale. The latent variance explained (R^2), also known as the repeatability or phylogenetic signal (λ) can then be estimated by

$$R^2_{\boldsymbol{\beta}^{(i)}} = V_{\boldsymbol{\beta}^{(i)}} \,/\, V_{T^{(i)}}$$

$$R^2_{\boldsymbol{\alpha}^{(i)}} = V_{\boldsymbol{\alpha}^{(i)}} \,/\, V_{T^{(i)}}$$

$$\boldsymbol{\lambda}_{(i)} = V_{\alpha_{phylo}{}^{(i)}} \,/\, V_{T^{(i)}}$$

The same approach is taken for predicting the total probability τ_{ps} of IVSO given the number of social units n_{ps} for population p of species s using a Binomial distribution

$$\text{Overall IVSO}_{ps} \sim \text{Binomial}\left(n_{ps}, \tau_{ps}\right)$$

$$\text{logit}\left(\tau_{ps}\right) = \mu_0 + \boldsymbol{x}'_{ps}\boldsymbol{\beta} + \alpha_{\text{phylo(s)}} + \alpha_{\text{species(s)}} + \alpha_{\text{order(s)}} + \alpha_{\text{population(p)}}$$

The proportion of social units expected to deviate from the main social organization observed in the population or, equivalently, the probability of deviating for a randomly selected social unit is predicted by the probability τ_{ps}.

Ancestral state reconstructions are commonly carried out with intercept-only random effects models, in which the global model intercept is interpreted as the expected ancestral state after marginalizing over any species-level phylogenetic or stochastic effects; multiple regression models are then used separately to identify relevant selection pressures across the sample. However, as the size and depth of the sampled phylogenetic tree grows, so too does the potential bias introduced into a reconstruction by unmeasured temporal trends and processes of non-random convergent evolution. These concerns are particularly acute for our dataset, which contains unbalanced samples across all major clades within the mammalian order and covers a span of approximately 225 million years. Therefore, we conducted our reconstruction of mammalian social organization in the context of a broader multiple regression model accounting for the effects of key social and ecological factors thought to be relevant to understanding the adaptive niche of ancestral mammals, and which may also be associated with directional change in social organization and IVSO across extant mammals. We assumed that ancestral mammals were like *Brasilodon*, 225 million years ago : with a small body size (~45 g or -1.9 SD z-score log mean body size), insectivore, and nocturnal (**Figure Box IV-1**).

Our reconstruction was adjusted for any biased sampling caused by differential research effort within mammalian orders. Thanks to Bayesian framework, we avoided the limitations of null-hypothesis testing, and relied on multiple sources of information provided by posterior distributions of model parameters and predictions. Median posterior estimates and median absolute deviations (MADs) were used to characterize the central tendency and relative dispersion of estimated effects, while 90% Bayesian credible intervals (CIs) and posterior probabilities of positive or negative effects (*i.e*. p+ or p−) were used to assess the uncertainty in the magnitude and direction of these effects. 90% Bayesian CI excluding zero indicates greater than 0.95 posterior probability in support of a directional effect. Values closer to 1 indicate greater support for the directional effect (+,-) and values closer to 0 indicate greater support for the opposite directional effect (-,+). All models were estimated in R (R Core Team 2020) and the brms package.

IV.5 Results

Data description.— Around 15 000 articles were analysed for information on social organization and a total of 2170 articles contained useable data. In proportion to the number of extant species, we found that primates were the mammalian order with the most field studies in the primary literature (886 studies) followed by carnivores (282 studies), cetartiodactyls (242 studies), rodents (257 studies) and chiropters (177 studies; **Figure IV-1A**).

Despite the very large number of studies carried out in primates (886), we only found information about social organization for 50% of the primate species (**Figure IV-1B**). While for some orders with only one or two species, all species of the order have been studied (for example elephants, order Proboscidea), for most orders much less than 50% of the species have been studied regarding their social organization (**Figure IV-1B**).

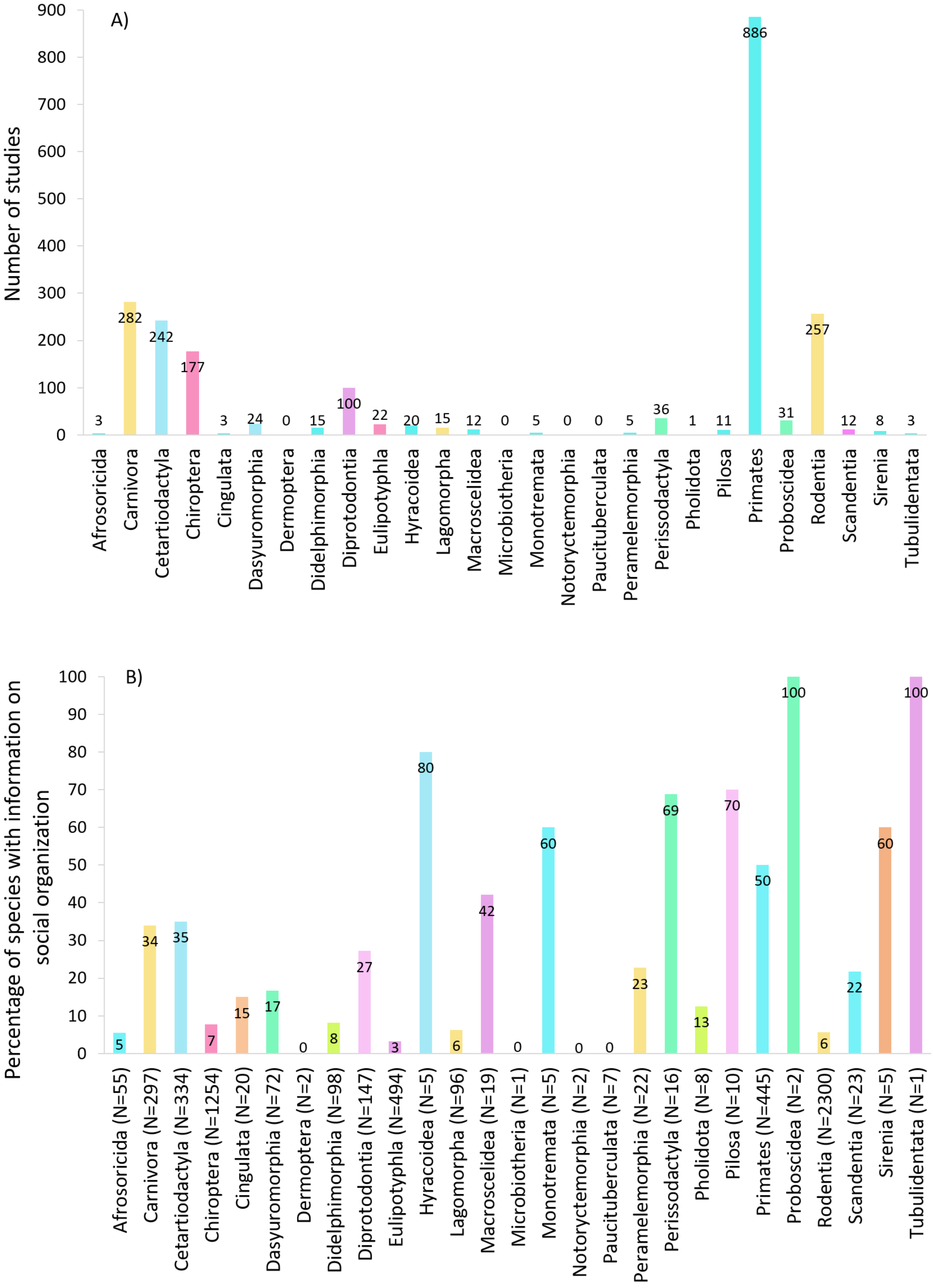


Figure IV-1*: A)** *Percentage of field studies (total N= 2170) on social organization for each order.* ***B) *Percentage of species with information on social organization for each order (percentages are indicated on each bar of the histogram). Orders are classified in alphabetical order with next to each order the number of extant species.*

Out of the 5740 mammalian species, we found information in the primary literature for 806 species and 1622 populations. Of these, 412 species (51.12%) and 631 populations (38.90%) had a variable social organization with more than one form of social organization (Table IV-3).

__Table IV-3:__. The total number of species for each mammalian order is indicated as well as the number of species and populations with information on their social organization. The number of species and populations with more than one form of social organization is also provided.

Subclass	Clade	Superorder	Order	Nbr species	Species with SO data	Pops with SO data	Nbr species with IVSO	Nbr Pops with IVSO
Theria	Metatheria	Ameridelphia	**Didelphimorphia**	98	8	14	3	2
			Paucituberculata	7	0	0	0	0
		Australidelphia	**Peramelemorphia**	22	5	5	1	1
			Microbiotheria	1	0	0	0	0
			Dasyuromorphia	72	12	21	7	10
			Notoryctemorphia	2	0	0	0	0
			Diprotodontia	147	40	100	16	36
	Eutheria	Afrotheria	**Afrosoricida**	55	3	3	0	0
			Macroscelidea	19	8	12	7	8
			Tubulidentata	1	1	3	0	0
			Hyracoidea	5	4	12	2	2
			Proboscidea	2	2	21	2	8
			Sirenia	5	3	8	1	2
		Boreoeutheria	**Lagomorpha**	96	6	14	4	5
			Rodentia	2300	131	211	54	63
			Scandentia	23	5	11	4	4
			Dermoptera	2	0	0	0	0
			Primates	445	223	498	140	216
			Eulipotyphla	494	16	20	9	12
			Chiroptera	1254	96	160	45	67
			Cetartiodactyla	334	117	214	70	111
			Perissodactyla	16	11	31	9	20
			Pholidota	8	1	1	0	0
			Carnivora	297	101	246	34	60
		Xenarthra	**Cingulata**	20	3	3	0	0
			Pilosa	10	7	10	2	2
Prototheria			**Monotremata**	5	3	4	2	2
TOTAL				**5740**	**806**	**1622**	**412**	**631**

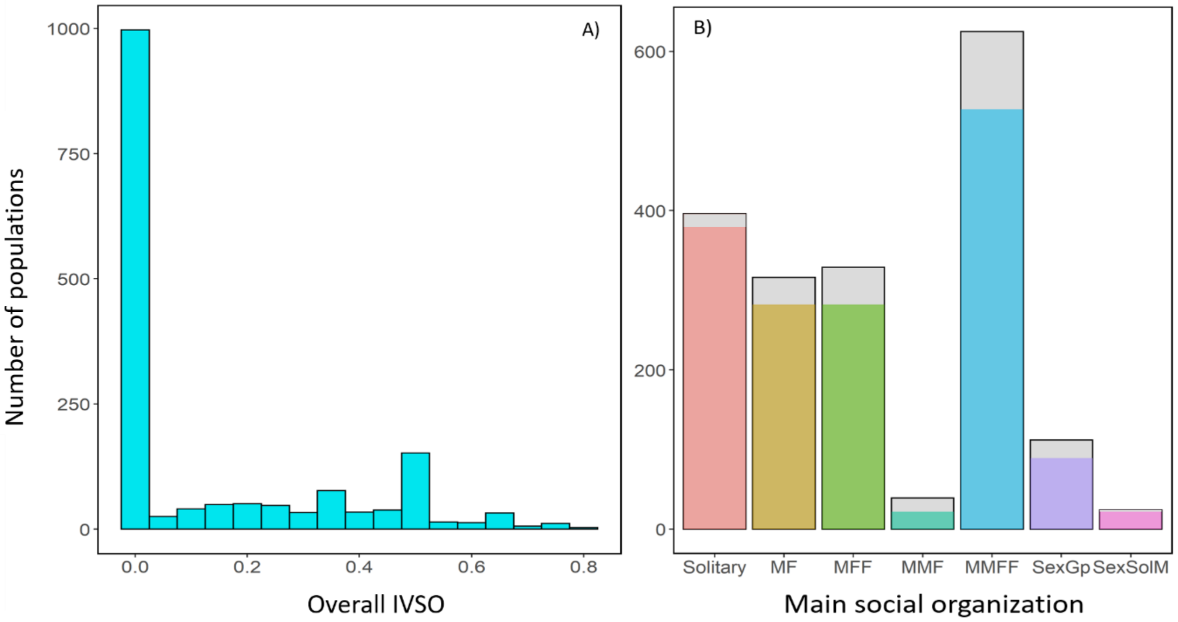


__Figure IV-2:__ ***A)*** *Total number of populations in our dataset exhibiting intra-specific variation in social organization (IVSO).* ***B)*** *Total number of populations in our dataset exhibiting each form of social organization as the main (most common form). Gray bars represent uncertainty in the main social organization for populations exhibiting two or more forms of social organization with equally high frequency (for example 50% of social units are solitay, 50% are pair-living). MF : pair-living; MFF : one male multiple females group; MMF : multiple males one female group; MMFF : multi males multi females groups; SexSpGp : Sex-specific group; SexSpSolM : Sex-specific solitary males.*

While most populations did not show IVSO (61.32%), there was substantial variation between populations in the level of variation in social organization (**Figure IV-2A**). In our database, the most common main social organization was living in multi-male multi-female groups (MMFF; 576±49 populations = 33.46%) followed by solitary living (388±8 populations = 22.55%). We observed relatively high rates of groups of one male multiple females (main social organization MFF; 306±24 populations = 17.78%) and moderate rates of pair-living (MF; 299±17 populations = 17.38%). Sex-specific groups (100±11 populations = 5.8%), one female multiple males groups (MMF; 30±8 populations = 1.75%) and sex-specific solitary male (22±2 populations = 1.28%) were observed at low rates (**Figure IV- 2B**).

Effects of ecological and life history predictors on social organization.— Overall, we did not find effects of any of the predictors on the overall proportion of IVSO across populations.

Pair-living was more common in species with high sexual dimorphism with larger females than males (-1.5 SD; median Δ probability = 0.52, 90% CI [0.13, 0.80]) compared to species with high sexual dimorphism but with males larger than females (+1.5 SD; **Figure IV-3**). In contrast, sex-specific solitary male social organization was more likely in species with high sexual dimorphism with males being heavier than females (+1.5; median Δ probability = 0.21, 90% CI [0.30, 0.70]). For longevity, short lived species were more likely to be solitary living (median Δ probability = 0.47, 90% CI [0.1, 0.75]) compared to long lived species who tended to be sex-specific solitary male (median Δ probability = 0.22, 90% CI [0.01, 0.76]; **Figure IV-3**). Solitary and pair-living were in turn more likely among smaller-bodied species (-1.5 SD) compared to large species (+1.5 SD; median Δ probability of solitary = 0.26, 90% CI [0.01, 0.73]; median Δ probability of pair-living = 0.31, 90% CI [0.04, 0.68]). Conversely, larger species were more likely to have a sex-specific solitary male social organization than smaller ones (median Δ probability = 0.18, 90% CI [0.00, 0.72]). Solitary was more common with nocturnal than diurnal activity (median Δ probability = 0.16, 90% CI [0.01, 0.48]). Multi-male multi-female groups were more likely associated with a water type habitat (median Δ probability = 0.22, 90% CI [0.13, 0.71]; **Figure IV-4)**. No clear effects were observed for differences in litter size and diet on the probability of social organization (**Table IV-4**).

Table IV-4 : Table summarising significant links between specific forms of social organization and the included predictors.

Social organization	Sexual dimorphism	Longevity	Body size	Litter size	Activity pattern	Diet	Habitat
Solitary	-	Short lifespan	Small bodied	-	Nocturnal	-	-
Pair	Larger females than males	-	Small bodied	-	-	-	-
Single male multiple females	-	-	-	-	-	-	-
Multiple males single female	-	-	-	-	-	-	-
Multi-male multi-female	-	-	-	-	-	-	Water
Sex-specific group	-	-	-	-	-	-	-
Sex-specific solitary male	Larger males than females	Long lifespan	Large bodied	-	-	-	-
IVSO	-	-	-	-	-	-	-

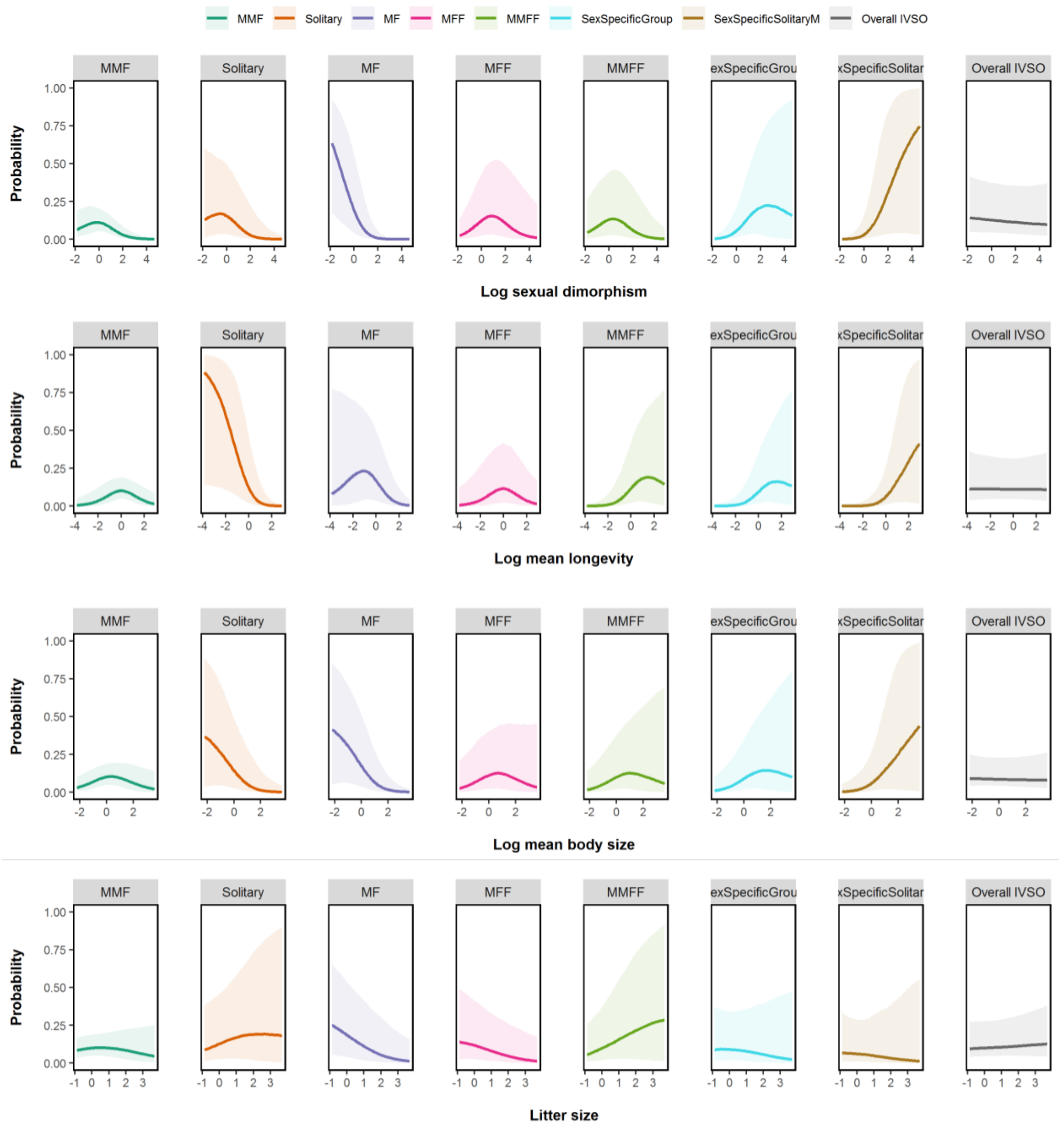


Figure IV-3: *Total effects of the ecological and life history factors (sexual dimorphism, longevity, body mass and litter size) on social organization and overall IVSO (exSpecificGrou : sex-specific groups; SpecificSolitar : sex-specific solitary male). Thick lines indicate posterior medians and ribbons indicate 90% Bayesian CIs.*

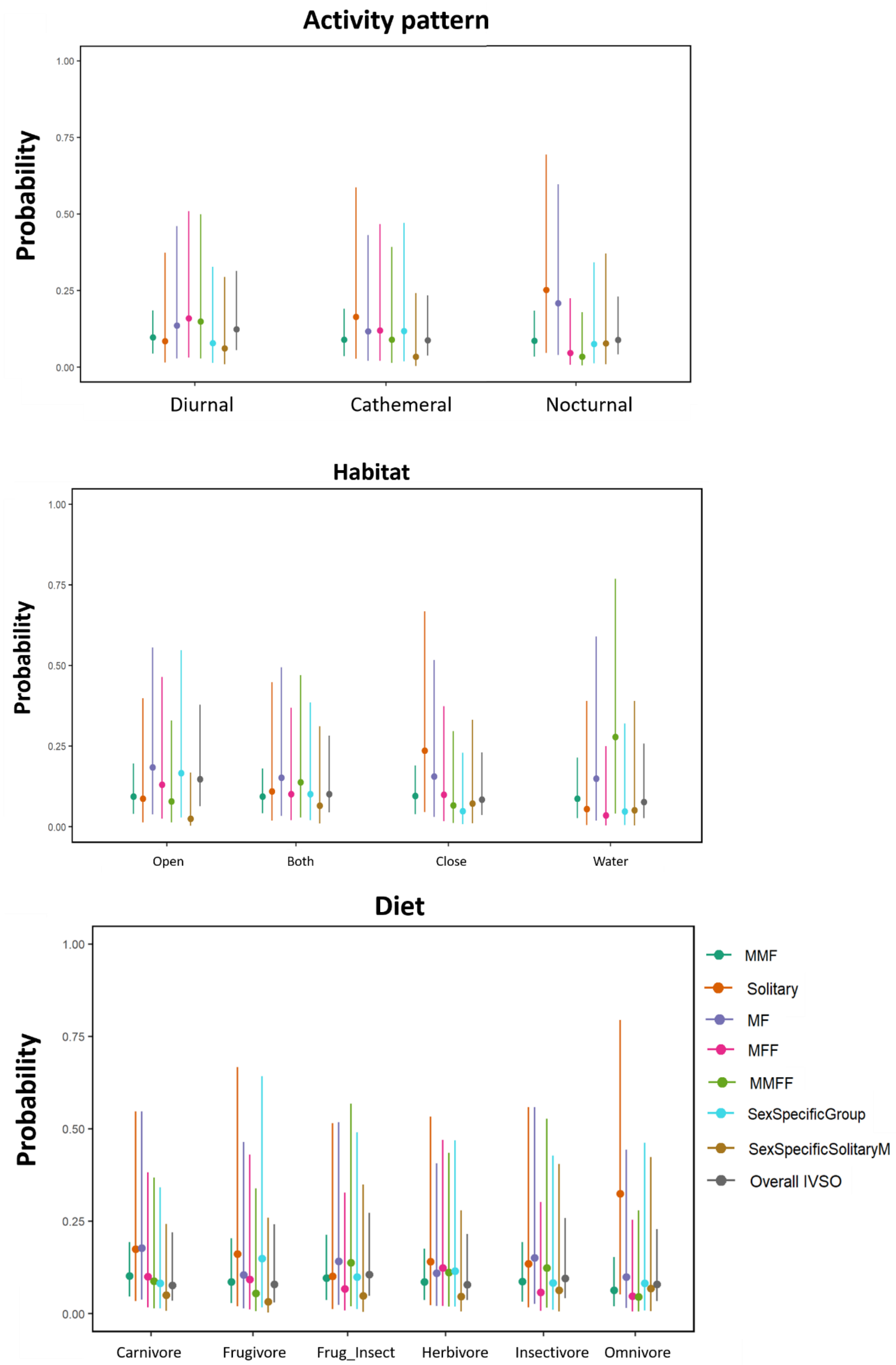
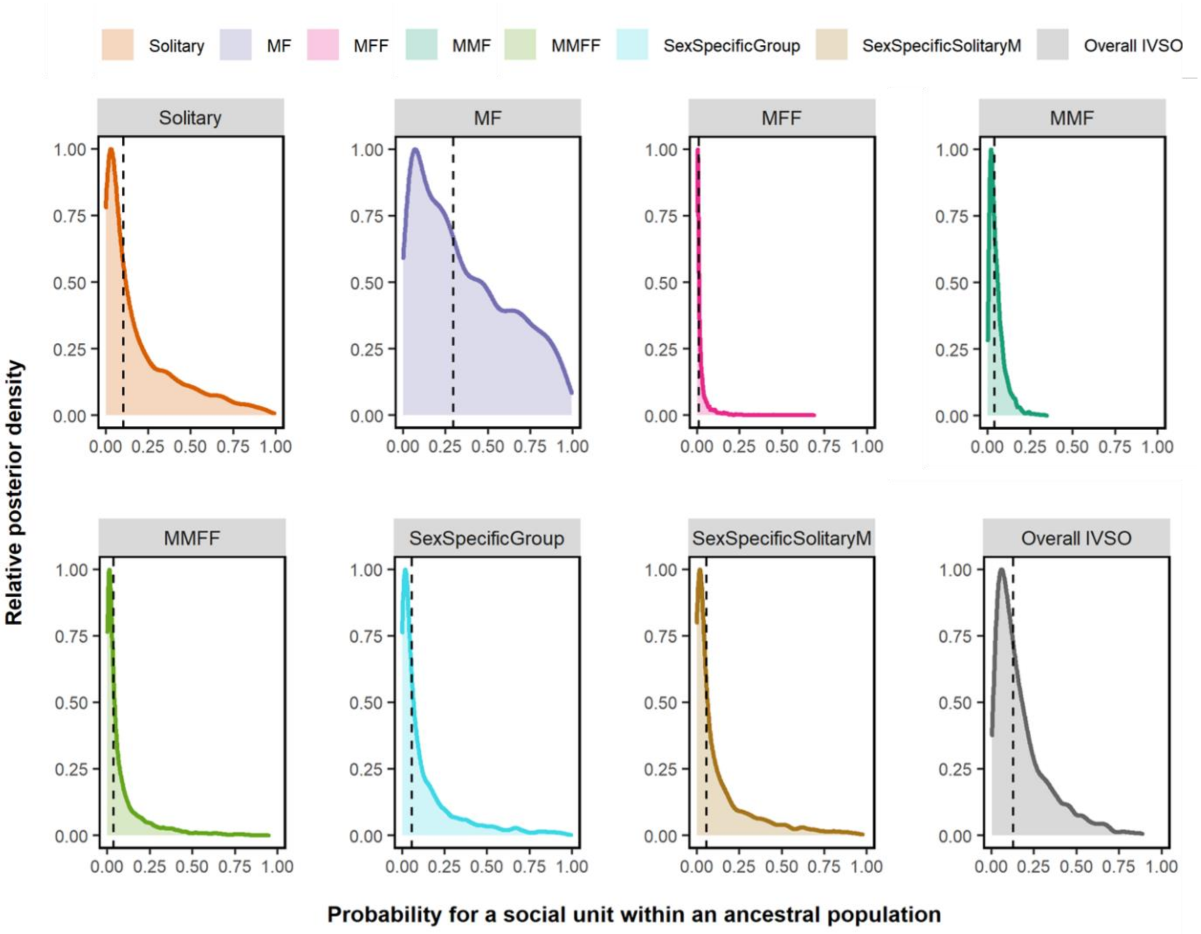


Figure IV- 4: *Total effects of* ***A)*** *activity pattern,* ***B)*** *habitat and* ***C)*** *diet (Frug_Insect : frugivore and insectivore) to predict ancestral social organization and IVSO. Thick lines indicate posterior medians and ribbons indicate 90% Bayesian CIs.*

Ancestral social organization.— Under the assumption that the ancestor of all mammals was nocturnal, insectivore and with a small body size, pair-living units are the most likely ancestral social organization (median probability = 0.30, 90% CI [0.03, 0.80]), compared to solitary (median Δ probability = 0.10, 90% CI = 0, 0.69), MFF groups (median Δ probability = 0.01, 90% CI = 0.01, 0.12), MMF groups (median Δ probability = 0.04, 90% CI = 0.01, 0.15) and MMFF groups (median Δ probability = 0.03, 90%% CI = 0.01, 0.38; **Figure IV-5**). Despite the large uncertainty, we found a posterior probability between pair-living and solitary of 0.68, meaning that there is 68% probability that the ancestral social organization is rather pair than solitary-living. Comparing pair-living to the other forms of social organization it is always much more likely to be the ancestral social organization (95% more likely compared to MFF, 89% compared to MMF, 83% compared to MMFF, 76% compared to sex-specific group and 75% compared to sex-specific solitary male).



*<u>Figure IV-5:</u> **Ecologically informed predictions of social organization in an ancestral mammal population.*** *Predicted probabilities of a social unit exhibiting each social organization and some form of IVSO within ancestral populations, assuming the ecological conditions (nocturnal, insectivore and small), as well as average within-order sampling effort. Scaled posterior densities are shown, with posterior medians indicated by the dotted line.*

The probability for overall IVSO was 0.13 (90% CI [0.02, 0.53]). Thus, approximately 13% of social units in an ancestral population deviated from the main social organization, which was pair-living. Thus, in an ancestral population containing 10 social units, we expect ~87% of those units to be pair-living, but also ~13% to deviate from pair-living.

IV.6 Discussion

The aim of this study was to determine the social organization of the common ancestor of mammals. To this end, we have developed an innovative approach that contrasts with previous studies in several aspects. We have built a database based exclusively on field studies reported with data in primary literature without making any assumptions on the social organization of species. We also used a strict classification of social organization, as well as innovative statistical models that account for variation in social organization in a continuous way.

In contrast to previous studies that found solitary to be the ancestral social organization for all mammals (Lukas and Clutton-Brock 2013), our results suggest that, under the assumption of a small, nocturnal and insectivore ancestor, pair-living was the most likely ancestral state for all mammals, an ancestor that lived approximately 225 million years ago. Our results are consistent with other studies showing that pair-living may be the ancestral social organization of several mammal groups when variation was taken into account (Artiodactyla ; Jaeggi et al. 2020; Macroscelidea ; Olivier et al. 2022, Primates ; Olivier et al. (in prep)). Finally, we showed that the ancestral social organization of mammals was variable, with approximately 13% of the individuals in the population deviating from pair-living. Thus, by considering variation in the social organization of populations, focusing only on primary literature and field studies, we found that the ancestral state was variable with pair-living as the main social organization.

There is considerable uncertainty for our finding that the ancestor of mammals was pair-living, which had a probability of only 30%. However, when comparing pair-living social organization with the other social organizations, we find that the probability of pair-living being ancestral is 68% to 95% more likely than the alternative form of social organization. However, our results might come from finding very few solitary species. It is possible that solitary species are understudied, biasing our results. The results of this study should therefore be taken with caution.

Our analysis is based on traits of the 225 million years old fossil *Brasilodon* that has been described as a most early mammal (Cabreira et al. 2022). Our result could change according to the fossil trait chosen. However, all potential ancestors for mammals (*e.g. Brasilodon*, *Morganucodon*) were small, nocturnal and insectivore. Hence, for mammals, whichever we choose, results will remain unchanged. Our uncertainty comes from the fact that there is not much information on life history factors for early mammals. Indeed, the more precision and predictors we have, the more precise the estimation of the ancestral social organization would be. Furthermore, the broad ecological niches occupied by the different extant orders implicate that the factors leading to a specific form or social organization (such as solitary, MF or MFF) might differ between orders. Because of that great variability within all mammalian orders, it would have been interesting for each order to centre the different predictors, thus reducing the uncertainty.

The evolution of organisms is often assumed to tend towards more complex life forms and pair-living is considered to be a more complex social organization than solitary living (Lukas and Clutton-Brock 2013). Thus, finding pair-living to be ancestral might come as a surprise to many. Further, solitary living might be more complex than generally believed and pair-living might be less complex, representing a simple tactic to increase reproductive success.

Solitary living might induce specific problems that do not occur when living in pairs or groups. Indeed, unlike group-living, a solitary individual will in all cases disperse to find a new territory. It will also have to know its territorial neighbours and in the breeding season, depending on the density of the population, it may take time to find a suitable mate. Furthermore, by living alone, an individual will miss out on all the benefits of group-living: predation avoidance and finding food more easily.

Pair-living has often been regarded as an intermediate social organization between solitary and group-living (Lukas and Clutton-Brock 2013; Shultz et al. 2011). This social organization has many advantages allowing males and females to increase their reproductive success. Males can ascertain a high degree of paternity, while females benefit from reduced male harassment, and the risk of infanticide is reduced in pair-living species compared to solitary ones (Lukas and Huchard 2014). In addition, pairs can defend a territory more effectively than if they were solitary and therefore have access to more resources (Tecot et al. 2016). Our work is a further step in understanding the evolution of mammalian behavior and more specifically of social organization. We therefore recommend that we now study the different transitions that can exist between social organizations.

However, other hypotheses suggest that complexification is not the rule and that "simpler" traits may be selected if they are more beneficial in a given environment (Spencer 1895; Wheeler 1928). This phenomenon of regression in the complexity of social organization has for example been observed among the orangutans who transitioned back to solitary from a social ancestor (Kappeler 1999).

Until now, many studies have focused on the transition from solitary to pair-living (Shultz et al. 2011; Lukas and Clutton-Brock 2013; Kappeler and Pozzi 2019). However, our study shows that pair-living is ancestral. The most common main social organization in extant mammals is multi-male multi-female groups followed by solitary living and one male multiple females groups, while pair-living is one of the least common forms of social organization.

The study of transitions from pair to group-living (the more recent social organization) would provide interesting information allowing us to understand the benefits that led males to tolerate each other within a group (social structure). Even if pair-living is the social organization of the common ancestor of mammals, it may have evolved from another social organization in the past. Like behavior, social organization is a very flexible trait from an evolutionary point of view (little phylogenetic influence). Solitary living could be the ancestral state of reptiles, located more at the root of the phylogenetic tree. It would then be interesting to include reptiles and birds as well in the future.

To understand how social organization has evolved, we wanted to know how much variation in mammal social organization and IVSO is explained by phylogeny, life history traits and environmental factors. Body size, sexual dimorphism, longevity and activity patterns were related to certain social organization but did not well explain the proportion of variation in social organization and IVSO. This leaves a sizable portion of unexplained variation among species. Thus, other predictors should be considered. Two main evolutionary pressures explain the evolution of social organization: resource defence and predation risk (Crook and Gartlan 1966; van Schaik and van Noordwijk 1989). While some food sources like fruits are more easily defended than others like insects, our study did not contain a good proxy (diet) for resource defence on the species level. As predation pressure is of major importance, it should be considered in future models. However, measuring predation pressure in field studies is extremely difficult and the few existing data are often not comparable between studies. It has been shown that a harsh environment (low rainfall and high temperature) favoured sociality in marsupials while climatic conditions of tropical rainforests were associated with solitary social organization (Qiu et al. 2022). Climatic data such as temperature or precipitation rate are excellent environmental factors that should be studied.

To understand the incredible diversity of social systems in mammals, we created a database of all species studied in the field. Despite the fact that since the 1950s an increasing number of studies on the behavior of mammals have been conducted, we found information for only 806 out of the 5,740 mammal species that inhabit our planet. Many more field studies have been conducted but did not properly report data for the social organization of the studied species, for example by not specifying the sexual composition of groups (Makuya et al. 2021). Unfortunately, these studies could not be considered for our database. Our study reveals a considerable lack in the study of mammalian behavior and the importance of field studies for reporting accurate data concerning the social organization of species or populations.

Comparative phylogenetic studies allow reconstructions of the social organization of the common ancestor of mammals based on the social organization of modern mammals. Palaeontology, another field of science, could verify these estimates by studying the fossils of the ancestors of mammals. Until the end of the last millennia, it was believed that the early mammals living in the Jurassic and Cretaceous with the dinosaurs were solitary, nocturnal, dull unspecialised generalists looking like shrews or mice (Brusatte et al. 2012). However, a wealth of newly discovered fossils from China revealed that they were in fact ecologically highly diverse, including tree-climbers, diggers, semi-aquatic species, and even gliders (reviewed in (Brusatte et al. 2012). Recent discoveries concerning fossils of early mammals and their ancestors have shown that the ancestor of mammals might have been more social than previously thought (Groenewald et al. 2001; Ladevèze et al. 2011; Jasinoski and Abdala 2017). Here we show that their social organization might also have been diverse, as already the ancestor was socially variable and not exclusively solitary, but mainly pair-living, further revolutionising our view of mammalian evolution.

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Chapter 4

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V. Chapter 4: Global Change and Conservation of Solitary Mammals

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V.1 Résumé

Nous soutenons ici que la compréhension du système social des espèces peut nous aider à les conserver. De nombreux mammifères en voie de disparition vivent solitairement. Nous montrons ici que la compréhension des contraintes et de la valeur adaptative de la vie solitaire est importante pour appréhender la manière dont les mammifères solitaires seront affectés et pourront répondre aux différents aspects du changement global. Les espèces solitaires pourraient, par exemple, être plus vulnérables au changement global que les espèces sociables car elles ne bénéficient pas des avantages de la vie en groupe qui pourraient atténuer le changement.

V.2 Abstract

Here we argue that understanding the social system of species can help us to conserve them. Many endangered mammals are solitary living (Clutton-Brock, 2021). We show how understanding the constraints and the adaptive value of solitary living is important to understand how solitary mammals will be affected and can respond to the different aspects of global change. For example, solitary species might be more vulnerable to global change than sociable species as they miss benefits of living in groups that could mitigate change.

V.3 Global change Impacts biodiversity

Global change is a major threat to biodiversity (Harley, 2011; Pimm, 2009; Thornton et al., 2014). Anthropogenic-induced global change includes habitat loss (Galbraith et al., 2002), fragmentation (Fahrig, 2003), and climate change (Chapin III et al., 2000), all of which are accelerating at a rate unprecedented in earth's history (Etterson and Shaw, 2001). While the factors causing global change are known, the speed and strength at which it occurs is still unsure and we do not know the way in which species will be able to cope and adapt to these changes. Global change occurs at an unprecedent rate and is expected to have severe impacts on ecosystems (Friedlingstein, 2008), decreasing biodiversity (Vitousek et al. 1997; Sih et al. 2011).

V.4 Understanding the social system of species, including solitary ones, can help us to conserve them

In order to overcome and slow biodiversity loss, we need studies informing conservation programs, including those on mammals. There are many ways to prevent the decline of mammal species. One of them is through understanding and analyzing behavior, because changes in behavior can allow for resistance towards change, and constraints on behavioral flexibility restrict resilience (Rymer et al., 2016). Animal social systems have always been a key subject in behavioral ecology as it gives us information about the mating system, the care system, the social organization and the social structure of species (Kappeler, 2019). These four components of social systems are interrelated and influence each other. This has revealed stunning interspecific diversity in the size, composition, and cohesion of social units, as well as in the patterning of reproductive skew, cooperation, and competition among their members (for mammals see (Clutton-Brock, 2021)). Within mammals, species display a wide variety of social systems ranging from solitary living in many carnivores, to pair-living in some primates, to groups in some species, such as elephants (Loxodonta africana) and marmosets (Callithrix jacchus). By understanding the social system of a species we are able to predict how a species will respond to global change, and how its responses will be constrained, important information to decide on the best conservation efforts for each species.

V.5 Solitary species miss the benefits from group-living and might be more vulnerable to global change than sociable species

Conservation efforts for solitary species might differ from those of group-living species. The social system of a species induces costs and benefits that are reliant on the environment, especially with regards to competition for resources (mates, food shelter), and how the social system impacts on predation risk (Kappeler et al., 2013). The net outcome of these costs and benefits will change when the environment changes. Species that live in groups might be buffered from these changes due to the benefits of group-living, especially improved foraging and predator avoidance (Krause and Ruxton, 2002). The extent that solitary species show behavioral flexibility to cope with changes in resource availability and predation pressure is unknown, *i.e.* the extent that individuals can alter their behavior reversibly in response to changing environmental conditions (Gordon, 1991). This is why we need to study the behavioral flexibility of solitary species under varying environmental conditions to assess their vulnerability to global change (Huey et al., 2012). As solitary species miss the benefits from group-living they might be more vulnerable than sociable species.

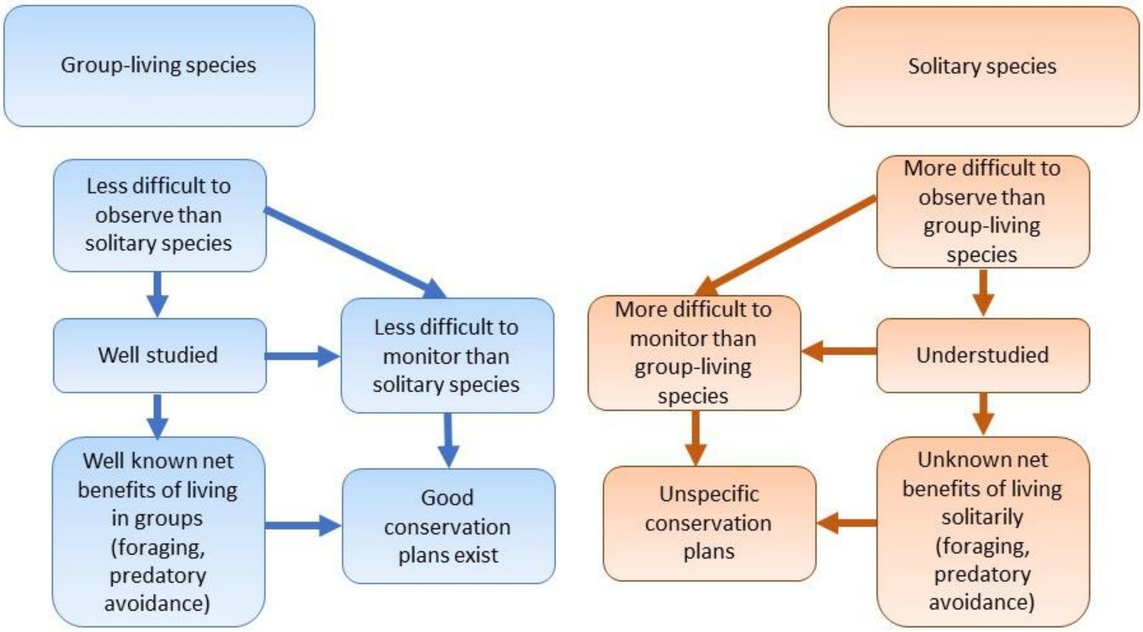
V.6 Allee effect and solitary species

The Allee effect describes a positive correlation between individual fitness and population density, with individuals benefitting from the presence of conspecifics (Allee WC, 1927). When living in groups, individuals can benefit from the Allee effect, by reducing predation pressure and gaining easier access to mating partners (Stephens and Sutherland

1999). The Allee effect can thus be seen as a driving force behind animal spatial structure and sociality (Stephens and Sutherland 2000). Due to climate change, (obligate) sociable species might suffer from fitness costs induced by reduced group sizes. However, even solitary species might benefit from higher population density making it easier to find mating partners or reducing predation pressure (because predators have more prey to choose from), unless – as in sociable species – high population density increases intra-specific competition. Thus, so far it is unknown in how far the correlation between fitness and population density differs between sociable and solitary species, nor do we know at which population density positive Allee effects are overrun by negative effects of intra-specific competition. Therefore, in both sociable and solitary species the Allee effect should be taken into account when predicting how changes in population density induced by climate change affect extinction risk.

V.7 Solitary species might be understudied when compared to sociable species

Solitary species might be understudied when compared to sociable species, especially with regards to their social behavior (**Figure V-1**). First, for decades researchers rather studied sociable than solitary species as the focus of behavioral ecology was on the benefits of group-living and aspects like alloparental care (Clutton-Brock, 2021). Second, species that live solitarily are often more difficult to observe as they are nocturnal and shy, live in dense habitat (many small mammals), or have huge home ranges (solitary carnivores). In addition, the fact that they live alone makes them more difficult to monitor (**Figure V-1**). The combination of a research focus on sociable species and the discrete nature of solitary species explains why they are understudied with regards to behavior, their trade-offs (energy, resources, time), and how these trade-offs might change and affect their resilience under conditions of global change.



<u>Figure V-1</u>: *While social species (left) are well studied and understood with regards to their social biology, solitary species (right) are understudied. This is likely to affect the quality of species specific conservation plans (middle).*

V.8 To conserve mammalian biodiversity, we need to understand why solitary living is an adaptive trait

679 of the 5500 mammalian species are endangered (IUCN redlist) and many of them are solitary living. The first mammal that became extinct as a direct cause of climate warming was the solitary Bramble Cay mosaic-tailed rat (Melomys rubicola; Fulton, 2017; Waller et al., 2017). It became extinct because of an ocean inundation, *i.e.* high water levels and storm surges caused by an increased frequency of extreme weather events, which were caused by anthropogenic climate change (Waller et al., 2017). Other well-known examples of endangered solitary mammals that are threatened by climate change include polar bears (Ursus maritimus),

snow leopards (Panthera uncia), tigers (Panthera tigris), and panda bears (Ailuropoda melanoleuca). It can be expected that many less well monitored solitary small mammal species are threatened by climate change.

Many endangered species are solitary and thus understanding constraints and the adaptive value of solitary living is important to conserve them. The persistence of mammals being solitary living after 170 million years of mammalian evolution (Rowe, 1988) indicates that it is an adaptive social system for many environments. To conserve mammalian biodiversity, we need to understand why solitary living is adaptive for many species. However, while for decades the costs and benefits of group-living have been studied, it is not known what makes solitary living adaptive. Without knowing the costs and benefits of solitary living we will not know how the trade-offs that solitary species face will change with global change. At the moment, we do not even know which are their most restricting trade-offs, whether it is with regards to food, shelter, predation, or maybe finding mating partners.

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VI. General discussion

In my thesis, I showed that intra-specific variation in social organization is common in mammals, occurring in 51 % of studied species. Taking this variation into account changes our understanding of mammalian social systems and social evolution: 1. Macroscelidae (elephant-shrews) cannot be considered to be an order consisting only of pair-living species, 2. the ancestor of primates living approximately 69 million years ago was rather pair- than solitary living, which is important to consider if we want to understand why some extant primate species are pair-living and 3. the ancestor of all mammals living approximately 225 million years ago was already socially variable with more social units consisting of pairs than of solitary living individuals. Ecological and life history factors had surprisingly little effect on what social organization extant macroscelidae, primates and mammals are having. Thus, my results have significant implication for our understanding of social evolution and mammalian conservation.

VI.1 How much variation in social organization exists in mammals at the species and population level?

VI.1.1 More variation than initially expected

Previously, it was believed that each species had a specific social organization and studies focused on inter-specific variation in social organization. While intra-specific variation in social organization was soon discovered and reviewed by Lott in 1984, it only became later a major research topic, for example by the long term studies on African striped (Schradin et al. 2012, 2018). Consequently, IVSO has been studied comparatively in several mammalian taxa including Eulipothyphla (Valomy et al. 2015), even-toed ungulates (Artiodactyla; Miles et al. 2019), strepsirrhines (Agnani et al. 2018), and New World monkeys (Platyrrhines; Agnani 2016), suggesting that variable social organization in mammals may be more common than previously thought.

To see how frequently IVSO has been found in mammals I reviewed what we know about the social organization of Macroscelidea, Primates and all mammals at the population and species level. I started my thesis by studying the order of Macroscelidea (**Chapter 1**) which is the only mammalian order where all species are considered to live exclusively in pairs. In this chapter, I found that there was variation in social organization not only between but also within species. Of the 19 species of Macroscelidea, information was available for only eight species and 12 populations. Seven of the eight species of elephant shrews and 10 of the studied 12 populations showed pair-living. However, seven species and nine populations exhibited intra-specific variation in social organization: two species and four populations were also solitary living and two other species (and 2 populations) also lived in groups of one male with multiple females. The last three species and three populations were solitary, pair- and group-living. Finally, one species and four populations were exclusively solitary. Therefore, variation was present in most species and populations and pair-living was not the exclusive form of social organization.

Following this, I have been interested in recording the social organization of all primates (**Chapter 2**), the most studied mammalian order. Of the 445 primate species, information on their social organization was available for 223 species and 498 populations (Agnani 2016; Pilisi

2019). Out of 223 species, more than half (140) showed variation in their social organization. The average degree of IVSO in primate species was 0.2 meaning that out of 10 social units, 2 did deviate from the main social organization. With this, primate species show considerable levels of variation in social organization.

In my third chapter, all mammalian species that have been studied in the field were included in the analysis (**Chapter 3**). Among the 5740 extant mammal species, I found information about their social organization (published in primary literature) for 806 species (14% of all species) and 1622 populations. 412 species (51.12%) and 631 populations (38.90%) had a variable social organization with more than one form of social organization. The mean IVSO in all populations was about 14%. These results demonstrated that within mammals, species show a considerable amount of variation in their social organization.

VI.1.2 Limitations and perspectives

My doctoral research used mammals as the main model of study, developing for the first time a database on social organizations in all mammalian species at the species and population level and taking into account the variations that have been reported. This database started in 2015 (~10% of species : Valomy et al. 2015; Agnani 2016; Pilisi 2019) and was then completed during my 3 years of PhD. For this, I read more than 15 000 articles and about 2 170 articles have been used to complete the database. I have shown how common IVSO is in mammals. However, accurate information for most species is still lacking. In order to succeed in these ambitious comparative studies, a very rigorous methodology had been necessary to have the most accurate database possible.

The aim was to collect information on what was already known from published data rather than from opinions, as often expressed even for species not studied in the field (only in captivity) or even species never studied at all (Schradin 2017). Hence, review articles were excluded from my study to avoid relying on assumptions rather than data. Furthermore, when the sex or age of individuals was unknown, these studies were not considered, as the adult sex composition is crucial to define social organization (Makuya et al. 2021). This was the case for many species of artiodactyls and cetaceans. The sexual composition is difficult to determine in species that form large herds (Moehlman 1998; Rudman 1998), when individuals are not captured to be sexed and individually marked, when there is no sexual dimorphism, or when observing individuals in certain habitats is complicated (*e.g.* aerial whale watching of *Eubalaena australis;* Groch et al. 2005)). The decision to use only field data was also reducing the number of useable studies for my analyses (as many species have been studied only in captivity). Still, this was important to ensure that the social organization observed for a given species also occurred in their natural habitat (*e.g*. many species can be kept in captivity in pairs, but this does not mean that pairs occur in nature). Similarly, one of the challenges of my bibliographical research was the observation bias of certain social organizations. For example, in some cetacean species (*Monodon monoceros;* Marcoux et al. 2009), many solitary female social units were observed because it was easier to categorise a female with her young than a group of whales whose sexual composition was not known. The contrary might also be relevant as solitary species are often assumed to be more difficult to observe and might then be less studied (*e.g.* carnivores; Olivier et al. 2022). Therefore, in each of the Bayesian phylogenetic mixed effect models using this database, research effort was considered to reduce bias towards more studied or easily studied species.

One method to obtain a larger amount of data would have been to contact an expert for each mammalian species or taxa, but this would have taken much longer. In future, more insights from scientists working on individuals in the wild and therefore having access to information on the respective social organization will be needed. Proper data reporting is essential when working on comparative studies, especially on social evolution (Schradin 2017). This is what we suggested in an article in 2021 entitled "*Field studies need to report essential information on social organization – independent of the study focus*" (Makuya, Olivier and Schradin 2021). Indeed, although social organization is measured in many field studies, these data are often not correctly reported. During the process of building the mammalian social organization database, several field studies indicated that they had collected data on social organization but this information was not presented in a way that we could reliably determine the composition of social units. Considering how costly and time-consuming it is to conduct field studies, it seems aberrant not to report such valuable information. It is therefore highly recommended to always provide the following information regarding social organization: the proportion of population studied, the frequency of trapping/observation events, occupancy of sleeping sites, the sex of individuals studied, the home range overlap and the composition of social units. These recommendations are also important for databases in other taxa, such as fish (Tanaka et al. 2018) and birds (Griesser and Suzuki 2016).

Our study provides the first-step towards considering variation in social organization. However, we acknowledge that there are limitations in our study, including not considering group size or the number of breeding individuals in a group. Given our already very rigorous methodology, we decided not to take group size into consideration due to the limited data available on the subject. For example, only few studies reported group size; instead, it was simply reported that a group of multiple males and females had been observed. However, the number of social units and the sexual composition of the group were considered. Nevertheless, group size could be considered for future studies. Indeed, if within a population a pair and a group of 80 individuals are observed, the consequences in terms of genetics and evolution will be different than if within a population there is one pair and a group of three individuals. This could therefore limit the study of the genetic and evolutionary aspects of social organization and its variation. If social organization is explained from a genetic point of view (Kappeler 2019) then our categorisation does not take into account the proportions of alleles that are responsible for a certain social organization within a population. However, the proportion of alleles is decisive for understanding the evolution of a trait (in this case social organization) over time. Thus, the consideration of variation in group size may be a determining factor in the evolution of social organization as it can affect group cohesion, sexual composition, association patterns, and reproductive skew (Markham and Gesquiere 2017; Kappeler 2019). In the future, carrying out the same study but on a smaller scale (considering the limited data) to account for group size would allow us to better understand the evolution of social organization.

Like group size, the number of breeders (mating system) could be a step forward in our study as it would allow us to understand the genetic and evolutionary aspects of IVSO. For the same mechanisms as mentioned above, the genetic mixing within a population will not be the same according to the number of breeders within a population, which should also influence the evolution of the trait (in this case social organization) over time. For example, there will be different evolutionary consequences if a population consists of a pair of reproductive individuals and a group of 8 reproductive individuals than if it consists of a pair and a group of 2 breeders with 6 non-breeders. As population dynamics allows a better understanding of the evolution of organisms, considering the number of breeders in future studies would be an important improvement.

Intraspecific variation in social organization has been observed in all classes of vertebrates (Lott 1984) and even in insects (Müller et al. 2007). For example, pied kingfishers (*Ceryle rudis*), depending on the nesting and breeding sites, can live in pairs, in family groups with philopatric adult offspring or even in one male multiple females groups (Reyer 1980, 1984). Similar to that, burying beetles (*Nicrophorus vespilloides*) depending on the size of the carrion for which they compete (Müller et al. 2007) can be solitary, in pairs, or form communal groups with two or more breeding females (Eggert 1992). Therefore, to better determine how and why IVSO has evolved within populations and species, other clades such as insects, birds or even reptiles could be considered.

VI.2 Does our understanding of the ancestral social organization change when we take variation into account?

In this thesis, I investigated whether taking IVSO into account changes our estimation of ancestral social organization. Previous studies determining ancestral states considered only one form of social organization per species. Yet, I have shown that many species exhibit variation in their social organization. For this purpose, a rigorous methodology was established consisting of 1. Only taking data from primary peer-reviewed literature 2. Considering only field studies 3. Considering the variation in our analysis and 4. Developing innovative statistical tools that can take variability into account. In this thesis, I have shown that my methodology led to different results than what was found in previous studies.

In chapter 1, I focused only on Macroscelideas to begin my investigations. For this order, I considered IVSO as a category (yes/no) with statistical methods involving phylogenetic Bayesian mixed-effect models. That is, when within a species or population several social organizations were observed, we characterised the general social organization of the species or population as 'Variable'. This categorisation did not allow us to distinguish a population with solitary and pair-living individuals from a population with pair and group-living individuals. Such models had already been used to study the ancestral state of artiodactyls (Jaeggi et al. 2020) and later of marsupials (Qiu et al. 2022). In chapter 1, we tested how considering IVSO could change our understanding of the ancestral state of Macroscelidea. When only the main social organization was considered and as such IVSO ignored, the ancestral state was pair-living. In contrast, when IVSO was accounted for, we found that the ancestor of Macroscelidea was probably variable in its organization, with pair-living being one possible form in the ancestral population. Throughout this study, I was able to show that in an order with few species, the consideration of IVSO can considerably change our view of the ancestral social organization.

In chapters 2 and 3 of my thesis, we wanted to improve our models and find a way to treat IVSO statistically more accurately. The problem was that with 8 forms of social organizations (solitary, MF, MFF, MMF, MMFF, Sex-specific group, Sex-specific solitary M and sex specific solitary F), the number of possible IVSO combinations was extremely high: 8^8 *i.e.* 16 777 216 possibilities. For this reason, we have developed a Bayesian mixed-effects statistical tool that takes variation into account in a continuous manner to improve our statistical modelling and ensure that it is as close as possible from reality. Compared to previous studies that found the ancestor of primates and mammals to be solitary (Shultz et al. 2011; Lukas and Clutton-Brock 2013), I showed that the ancestor of primates and mammals was variable with pair-living as the main social organization. By 1. considering IVSO, 2. primary literature from field studies, 3. a very strict classification of social organization and 4. a new statistical approach, I found results that differed considerably from previous studies that used simplified databases and statistics. In how far each of these four improvements lead to my novel results cannot clearly be said. For example, it may not be only considering variation that changes our perception of the ancestor compared to previous studies but also our statistical methodology associated with our rigorous database. However, not considering IVSO would of course mean that we could never find IVSO to be an important aspect of ancestral social organization. Thus, my thesis may represent the most reliable analyses of ancestral social organization in mammals to date.

VI.3 Which ecological and life history factors are associated to the different forms of social organization (including variation)?

VI.3.1 Summary of results

The incorporation of ecological and life history trait factors into our studies had two purposes. The first one was to determine which factors were related to social organization and IVSO in mammals. The second, was to determine the characteristics of these factors (those influencing social organization and IVSO) in the common ancestor in order to predict its social organization. These factors, also called predictors, were therefore used to answer one of our main questions: what was the ancestral social organization?

Ideally, predation risk and resource distribution are the mains factors related to social organization and should be the best predictor of social organization (Crook and Gartlan 1966; van Schaik et al. 1989). However, predation risk and resource availability to which the mammalian ancestor was exposed is unknown and there are also very few information for all actuals mammal species. Therefore, we used proxies for these two factors *i.e.* predictors highly correlated to predation risk and resource distribution (see Table VI-1).

In chapter 1, we examined the influence of body mass, habitat diversity and population density on the social organization and IVSO of Macroscelidea (Table VI-1). Surprisingly, we did not find any correlation between social organization and those factors although other studies have found such relationships (*e.g.* correlation between population density and social organization, see Schradin in 2020). This might be related to our small sample size of only 9 species and 12 populations. Thus, even though we found important variation in social organization within and between populations, we could not explain this variation by the ecological and life history factors included in our analysis.

In chapter 2, we tested again different associations between social organization and IVSO with ecology and life history traits previously outlined in chapter 1 (without population density because of the limited data). In addition to body mass and habitat type, we tested new factors such as locomotion, activity pattern, diet and foraging style. Predictions and results are summarized in Table VI-1. We did not find any effects for differences in locomotion, habitat type and diet on the probability of social organization, and none of these ecological predictors consistently explained variation in the overall proportion of IVSO across populations. In contrast to Macroscelidea (Chapter 1), we found a relation between body mass and social organization. This might be explained by an increase in sample size in primates or by evolutionary constraints specific to this phylogenetic group. Indeed, primates and Macroscelidea may not be subject to the same evolutionary pressures on social organization. Hence, a factor (such as body mass) could be highly related to social organization in primates and have a less important effect in Macroscelidea. Alternatively, there may be an evolutionary pressure which has a greater impact on social organization, thus masking the effect of body mass on Macroscelidea's social organization.

__Table VI-1__: Table summarizing which predictors were used in each chapter to determine the associations with social organization as well as the predictions for each chapter and the associated results. -: No significant effect of the predictor was found-

Chapters	Predictors tested	Predictions	Results
1. Macroscelidea	Body mass	Solitary species are smaller.	-
	Habitat diversity	IVSO increases with variability in habitats.	-
	Population density	Pair-living is associated with low population density.	-
2. Primates	Body mass	Solitary species are smaller.	Pair-living species were smaller. Species with multi-male, multi-female groups were larger.
	Habitat type	Group-living species live in open habitats.	-
	Locomotion	Solitary species are more often arboreal.	-
	Activity pattern	Solitary species are more often nocturnal.	Pair-living were more often nocturnal.
	Diet	Clumped food (leaves and fruit) is associated with group-living	-
	Foraging style	Group foragers will be group-living.	-
3. Mammals	Body mass	Group-living are larger and solitary species are smaller.	Larger species were more likely to be sex-specific solitary male than smaller ones. Solitary and pair-living species were smaller-.
	Habitat type	Group-living species live in open habitats.	Multi-male multi-female groups are more likely

			associated with water habitat type.
	Activity Pattern	Solitary species are nocturnal.	Solitary species were more often nocturnal than diurnal.
	Diet	Carnivore species (feeding on non-sharable food) are more likely to be solitary living than frugivore species (feeding on clumped food).	-
	Sexual dimorphism	Sexual dimorphism is lowest in pair-living species and largest in group-living species.	Pair-living was more likely in species with high sexual dimorphism (females larger than males). Sex-specific solitary male social organization was more likely in species with high sexual dimorphism (males larger than females).
	Longevity	Long living species is associated to group-living.	Short lived species were more likely to be solitary living than long lived species who tended to live in sex-specific solitary male groups.
	Litter size	Group-living species are more likely to have small litter size.	-

In chapter 3, some factors studied in chapter 2 (body mass, activity pattern, diet and habitat type) were analysed again with a much larger sample size including all mammals to test for a correlation with social organization and IVSO. In addition, other life history traits such as, sexual dimorphism, longevity and litter size were investigated. Predictions and results are summarized in **Table VI-1**. Specifically, we predicted IVSO to increase with diversity in habitats (Schradin et al. 2018). IVSO might have evolved in species having few options to reproduce to maximize their reproductive success (at the expense of survival) and in species living in ecological conditions that might differ between generations.

However, in a highly variable environment, the selection pressures on the social organization could change rapidly from one year to the next favouring different social organization over time (called fluctuating selection). This type of selection should be most visible in species with a short life cycle (low longevity and low reproduction). Thus, short lived species and species with fewer breeding attempts might be more variable. Alternatively, long-lived species and species with more breeding attempts might experience more diverse environments during their lifetime making IVSO adaptive. This is true if IVSO is explained by phenotypic plasticity. It is adaptive for an individual that will encounter variable living conditions to be able to modify its social organization over time (phenotypic plasticity). However, we did not find any effect of any of the factors on the overall proportion of IVSO across populations.

As in Chapter 2, body mass and activity pattern were related to social organization: solitary species were more likely to be nocturnal and small while larger ones were more likely to live in groups. Overall, we found considerable correlations between our proxies of predation risk and resource distribution. Nevertheless, it is important to not confuse correlation with causality. Indeed, we do not know in which direction evolution occurred. For example, environmental factors (resource distribution and predation risk) may induce selection pressures, which will also act on other biological traits than social organization, thus some phenotypic traits (such as body mass or activity pattern) may have co-evolve with social organization. This is what has been found in primates, which demonstrates a co-evolution between shifts from solitary forager to multi-male/multi-female aggregations with the switch from a nocturnal to a diurnal lifestyle (Shultz et al. 2011).

VI.3.2 Limitations and perspectives

Our method allowed us to estimate the ancestral social organization of mammals as accurately as possible. Nevertheless, I recognize that some points could be improved. In particular, in chapters 2 and 3, social organization and IVSO were at the population level while predictors were at the species level. A study with population-level predictors would give more precise results (as variation for example of body mass or diet also occurs within populations), but in the current state of the literature, this study would be limited for the majority of the populations. Moreover, I propose to expand the third chapter of my thesis by considering other predictors. Resource defence and predation risk (Crook and Gartlan 1966; van Schaik and van Noordwijk 1989) could be studied through population density as it was done by Schradin in 2020. When population density is high, striped mice tend to live in groups, whereas a solitary life is privileged when density is low. As predation risk is of major importance, conducting the same study with predation pressure factors would be of interest to determine what sort of correlation exists. For example, testing the effect of predation pressure (on artiodactyls for example) on social organization would be one option. In high predation sites, individual vigilance rate was significantly greater than in low predation site (Skinner and Hunter 1998) and species living in groups benefit from the vigilance of others as well as the reduction of predation risk. Thus, we would expect that predation pressures favour group-living. Sadly, data on predation rate are very rare.

Climatic factors could also be linked to social organization. Indeed, environmental uncertainty resulting from climatic variation is likely to be an important driver of temporal variation in selection pressure and therefore is expected to impact the evolution of social behavior (Jetz and Rubenstein 2011). Harsh environments (low rainfall and high temperature) are associated to sociality in marsupials while stable climatic conditions of tropical rainforests are associated with solitary social organization (Qiu et al. 2022). Climatic data such as temperature or precipitation rate as well as their variation are excellent environmental factors that should be studied. Due to time constraints, I was not able to study the links between IVSO, social organization and climate. However, for each of my populations where I collected information, I integrated the population's GPS localisation into my database. Thus, as Qiu did in 2022 for marsupials, climatic data can be added to the populations in my database.

A sizable portion of IVSO remained unexplained by proxies of resource distribution and predation risk. Therefore, it is possible that the proxies we have used are not appropriate ones for IVSO or that the variation in social organization is not correlated with resource distribution and predation risk. As with social organization, climatic factors could be related to IVSO's evolution. I expect populations living in highly variable climates, *i.e.* with large temperature variations or large rainfall variability (rainy and dry seasons), to have a more variable social organization to adapt to their environment. For example, studies have shown that the social phenotype is influenced by local environmental conditions, which could induce plasticity in sociality in crows and bees (Baglione et al. 2002; Field et al. 2010, 2012).

Another goal of future studies might be performing experiments in the laboratory to determine whether variation in social organization is due to social flexibility or local adaptation through genetic differentiation such as "animal model analyses" or "common-garden studies" (see review by Stirling et al. 2002; Schradin 2013; Merilä and Hendry 2014). Although it is not logistically feasible to carry out experiments on social mammals due to their large time scales, a more simplified system, such as that of insects (Fisher 2023) , might provide the adequate conditions to physically manipulate the environment and ultimately understand which factors induces a variation in social organization.

VI.3.3 From social organization to conservation

In times of global change, understanding how individuals react to environmental change can help us to design better conservation plans. With climate change the distribution of resources is expected to change drastically. The social organization of a species is presumed to be a key factor in maximising fitness in relation to the distribution of resources. Therefore, populations having a social organization that will not be able to maximise their fitness under the new resource distribution should be affected by global changes. Thus, we may assume that, species that can adapt by changing their social organization (*e.g.* by becoming more solitary if resources become increasingly scarce) can probably cope better with change than species with a fixed social organization. Thus, the degree of IVSO of a species may help identify which species are most vulnerable to environmental change, such that a species with a low degree would be less vulnerable.

Global change may impact species differently depending on their social organization. For example, because of the small patches of habitat induced by fragmentation (caused by human activity), species living in groups might decrease in their group size. As a consequence there may be a reduction in genetic mixing increasing risk of extinction. For example, in red squirrels, greater isolation and lower immigration of individuals has led to lower population densities, increasing their probability of extinction (Verboom and Apeldoorn 1990; Verbeylen et al. 1997). On the other hand, due to fragmentation, solitary species that live in different patches may not be able to find each other to reproduce, leading to a decrease in population density (*e.g.* lynx). As the threats are not the same according to the type of social organization, management measures might be different for solitary than for group-living species (*e.g.* creation of ecological corridors for solitary species (Blazquez-Cabrera et al. 2019); protection of big patches of habitat for group-living species (Tulloch et al. 2016)).

In general, regardless of the threats, the measures of population reinforcement or reintroduction also differ according to the social organization of the species. It seems essential to know the social organization of a species to release the good number of individuals at the same time. For example, releasing two individuals of a solitary species at the same time and place could lead to avoidable territory competition and compromise their settlement. On the other hand, social species could be released at the same time and place, thus facilitating group formation.

Höglund in 1996, argued that the social system of any given species may limit its distribution and affect its local extinction risk. More research in this area is obviously needed. However, because variation occurs in several taxa, the social system, *i.e.* the behavioral ecology, of any given species needs to be considered not only when conservationists are facing practical problems (re-introductions) but also when modelling demographic stochasticity.

In my last chapter (chapter 4), I argued that because many endangered mammals are solitary living (Clutton-Brock 2021), it is of major importance to understand the constraints and the adaptive value of solitary living. This will enable us to identify how solitary mammals will be affected and can respond to the different aspects of global change. Solitary species might be more vulnerable to global change than sociable species as they miss benefits of living in groups that could mitigate change. Moreover, if a sudden and quick global change occurs, impacting the benefits of a certain social organization, species with social flexibility might be less threatened. Our studies could therefore have impact on the conservation of mammalian species.

VI.4 What was the ancestral social organization of all mammals?

VI.4.1 The ancestor was variable

Macroscelidea was the only mammalian order where all species were considered to be pair-living (Ribble and Perrin 2005; Rathbun and Rathbun 2006; Lukas and Clutton-Brock 2013). In Chapter 1, my results suggest that the ancestor of Macroscelidea was in fact variable with pair-living as one of the main social organizations. I then focused on Primates, the most studied order among mammals. Unlike Shultz in 2011, who suggested that the primate ancestor was solitary, I showed that the primate ancestor was variable with pair-living as the main social organization by taking into consideration variation in social organization and under the assumption of a small, nocturnal and arboreal ancestor. Finally, when I studied all extant mammals, the most likely ancestral social organization was also variable with pair-living as the main social organization. These results differ from Lukas and Clutton-Brock (2013) whose methodology presents several limitations: 1. They assigned a single social organization per species, without considering the variation that exists within and between populations 2. They used field data as well as captive data and, for some species, assumptions and information not based on the primary literature 3. They categorised many species as 'socially monogamous', a mix between social organization and mating system.

This major discovery of my thesis therefore changes our understanding of the evolution of mammalian social organization and should be of interest not only to specialists, but also to museums for example.

VI.4.2 What about the fossil evidence?

Our results are consistent with various fossils found by palaeontologists. Indeed, fossils of cynodonts (mammaliaforms living between 260 and 230 million years ago) from the Triassic period have been found in groups of juveniles and adults (Jasinoski and Abdala 2017). Furthermore, the absence of sexual dimorphism associated with the small number of adults found together indicates that this species might have been pair-living, which would further corroborate our results. Similarily bones of about 20 individuals Trirachodon from the lower Triassic (250 million years ago) were found together indicating a group-living social organization for this cynodont (Groenewald et al. 2001). Hence, the paleontological evidence supports my results suggesting that the ancestor of mammals was sociable and lived in pairs. Our priors are based on an ancestor belonging to Brasilodon that was to our knowledge small, insectivore and nocturnal (Cabreira et al. 2022). Brasilodon is assumed to be one of the first mammals. We could also have based our studies on other common ancestors such as Morganucodon, but this would not have changed our results as they had the same characteristics as Brasilodon (small, nocturnal and insectivore). It is important to continue to collaborate with palaeontologists to get as much information as possible about the life history traits and lifestyle of early mammals and their ancestors (mammaliformes). This would allow us to use new additional predictors and increase the accuracy of our results of the ancestral state. For example, longevity, a variable for which we have found a correlation with social organization could be considered.

A new step in understanding the evolution of social organization would be to determine the ancestral state of clades within mammals. Indeed, monotremes and theria mammals (placentals and marsupials) separated 220 million years ago (Madsen 2009). Therefore, new analyses based on the same methodology and database could be conducted to predict the ancestral social organization of theria (placentals and marsupials), only metatheria (marsupials), only eutherian (placentals) or only prototheria (monotremes; **Figure VI-1**). This would allow to confront the different hypotheses concerning transitions of social organization over time (e.g. complexification of the organization).

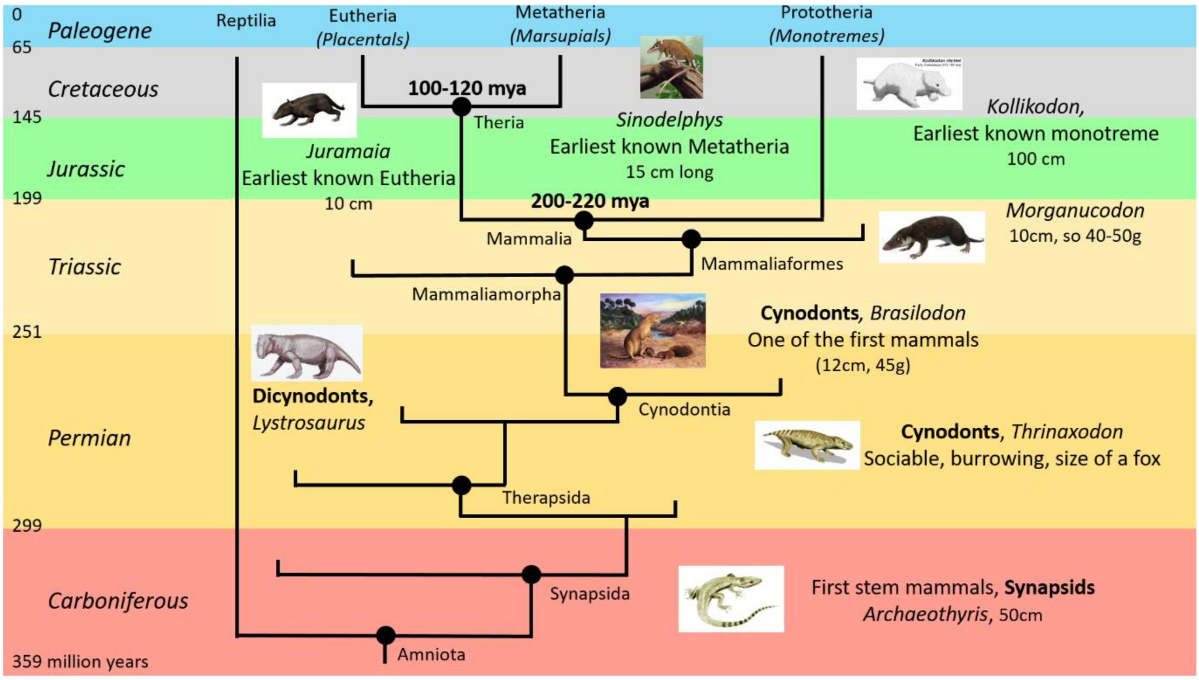

__Figure VI-1:__ Timeline of the evolution of mammals over the last 359 million years and the fossils discovered.

VI.4.3 Evolutionary transitions

Through comparative phylogeny approaches, it is possible to study how social organization evolved over time. According to Kappeler (2019) one of the main questions in these approaches is the degree to which a social trait is correlated with phylogeny. In Chapter 2 and 3, we found that variation in social organization was moderately explained by phylogeny. Consequently, traits related to social organization can vary in response to ecological and social factors. Our results are consistent with previous studies showing that compared to morphological and physiological traits, behavioral and social traits tend to exhibit relatively weak phylogenetic signal (Blomberg et al. 2003; Kamilar and Cooper 2013; Strier et al. 2014).

The discovery of an ancestral pair-living social organization could change the perception of the different transitions in social organization. Indeed, Lukas and Clutton-Brock in 2013 proposed that pair-living was derived from solitary living while Shultz (2011), proposed that pair-living was rather a derived state from group-living. However, a more recent study in primates showed that transitions between solitary and pair-living were frequent, later giving rise to group-living social organization (Kappeler and Pozzi 2019). Thus, in addition to the transition between clades, the transition in social organization among species should be considered using our database through Bayesian phylogenetic comparative methods, or by developing new statistical tools as we have done which would also consider the degree of variation of each population.

VI.4.4 Variation in social system and co-evolution

Finally, our study focused only on variation in one component of the social system: social organization. However, variation in care system, social structure (Sterck et al. 1997; Clutton-Brock and Janson 2012; Kappeler et al. 2013; Koenig et al. 2013) and mating system has also been extensively studied (Emlen and Oring 1977; Greenwood 1980; Thornhill and

Alcock 1983; Clutton-Brock 1989; Shuker and Simmons 2014). For example, mating system in fallow deer (*Dama dama*) varies according to ecological factors such as buck density, doe density, habitat structure and tree cover (Langbein and Thirgood 1989).

The relationships between components of social system, suggest that they have evolved together (Rubenstein 2012). For example, a certain social organization can give us clues to potential mating systems: a solitary species is unlikely to have a monogamous type of mating system. Similarly, species that live in pairs are more likely to have biparental care compared to solitary species (Kokko and Jennions 2008). However, there is no normal pattern, as in pair-living species paternal care can be absent and present in some group-living species (Tecot et al. 2016). The fact that the components of the system do not vary arbitrarily, shows us the presence of a mutual contingency (Kappeler 2019; **Figure VI-2**). Thus, if co-evolution between the different components of the social system occurs, then the mating system, the care system or the social structure could be used to predict the evolution of the social organization.

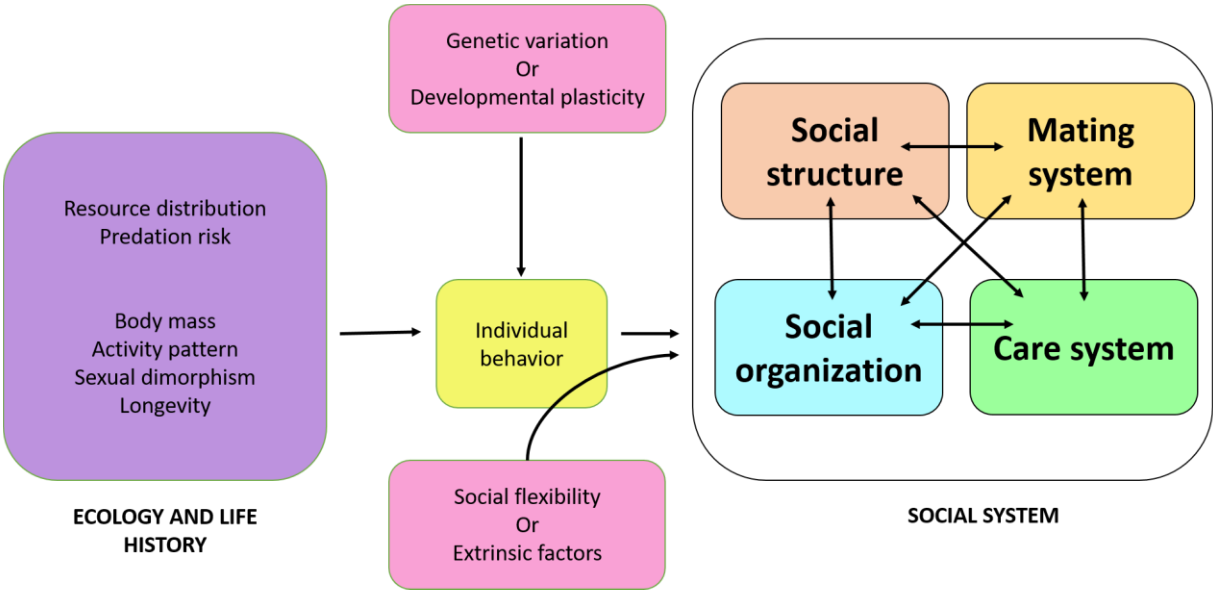

__Figure VI-2:__ Schematic representation of the mechanisms influencing individual behavior and their influence on social system (social organization, mating system, care system and social structure).

VI.5 Concluding remarks

In this thesis, I wanted to understand mammalian social evolution by considering IVSO. One particularity of my thesis is the application of a unique methodological combination: peer-reviewed field data, consistent classification of social organization, consideration of variation in social organization, and use of innovative statistics. Under the assumption that the ancestor was small, nocturnal and insectivore, we found for the first time that the ancestor social organization was more likely to be variable with pair-living as the main social organization. Our results differed from what has been previously found when IVSO was not considered, changing our understanding of mammalian social evolution. Especially important, is the statistical method of using IVSO as a continuous variable, which could and should also be applied to any other variable traits. Overall, my thesis reveals the importance of inter-disciplinarity science that is useful to support any scientific statements. In this case, palaeontology is used for direct prediction on the ancestral social organization of mammals based on fossil evidence. In addition, understanding the evolution of social organization and IVSO in times of global change may allow to identify the most vulnerable species and ensure appropriate management according to their social organization. Finally, my thesis, besides contributing further to our understanding of mammalian social evolution, represents one further step on the comprehension of our own social ancestry, and our current life: Being variable is common, being solitary might not be primitive but adaptive.

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Appendices

Appendix A :

Olivier, C. A., Schradin, C., & Makuya, L. (2022). Global Change and Conservation of Solitary Mammals. *Frontiers in Ecology and Evolution*, *10*, 906446. https://doi.org/10.3389/fevo.2022.906446

Appendix B :

Olivier, C. A., Jaeggi, A. V., Hayes, L. D., & Schradin, C. (2022). Revisiting the components of Macroscelidea social systems: Evidence for variable social organization, including pair-living, but not for a monogamous mating system. *Ethology*, *128*(5), 383–394. https://doi.org/10.1111/eth.13271

Appendix C :

Qiu, J., **Olivier, C. A.**, Jaeggi, A. V., & Schradin, C. (2022). The evolution of marsupial social organization. *Proceedings of the Royal Society B: Biological Sciences*, *289*(1985), 20221589. https://doi.org/10.1098/rspb.2022.1589

Appendix D :

Makuya, L., **Olivier, C. A.**, & Schradin, C. (2021). Field studies need to report essential information on social organisation–independent of the study focus. *Ethology*, *128*(3), 268–274. https://doi.org/10.1111/eth.13249

Appendix E :

Schradin, C., Drouard, F., Lemonnier, G., Askew, R., **Olivier, C. A.**, & Pillay, N. (2020). Geographic intra-specific variation in social organization is driven by population density. *Behavioral Ecology and Sociobiology*, *74*(9), 113. https://doi.org/10.1007/s00265-020-02896-z

Appendix A

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OPINION
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Global Change and Conservation of Solitary Mammals

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INTRODUCTION

Here we argue that understanding the social system of species can help us to conserve them. Many endangered mammals are solitary living (Clutton-Brock, 2021). Here we show how understanding the constraints and the adaptive value of solitary living is important to understand how solitary mammals will be affected and can respond to the different aspects of global change. For example, solitary species might be more vulnerable to global change than sociable species as they miss benefits of living in groups that could mitigate change.

GLOBAL CHANGE IMPACTS BIODIVERSITY

Global change is a major threat to biodiversity (Pimm, 2009; Harley, 2011; Thornton et al., 2014). Anthropogenic-induced global change includes habitat loss (Galbraith et al., 2002), fragmentation (Fahrig, 2003), and climate change (Chapin et al., 2000), all of which are accelerating at a rate unprecedented in earth's history (Etterson and Shaw, 2001). While the factors causing global change are known, the speed and strength at which it occurs is still unsure and we do not know the way in which species will be able to cope and adapt to these changes. Global change occurs at an unprecedent rate and is expected to have severe impacts on ecosystems (Friedlingstein, 2008), decreasing biodiversity (Vitousek et al., 1997; Sih et al., 2011).

UNDERSTANDING THE SOCIAL SYSTEM OF SPECIES, INCLUDING SOLITARY ONES, CAN HELP US TO CONSERVE THEM

In order to overcome and slow biodiversity loss, we need studies informing conservation programs, including those on mammals. There are many ways to prevent the decline of mammal species. One of them is through understanding and analyzing behavior, because changes in behavior can allow for resistance toward change, and constraints on behavioral flexibility restrict resilience (Rymer et al., 2016). Animal social systems have always been a key subject in behavioral ecology as it gives us information about the mating system, the care system, the social organization and the social structure of species (Kappeler, 2019). These four components of social systems are interrelated and influence each other. This has revealed stunning interspecific diversity in the size, composition, and cohesion of social units, as well as in the patterning of reproductive skew, cooperation, and competition among their members (for mammals see Clutton-Brock, 2021). Within mammals, species display a wide variety of social systems ranging from solitary living in many carnivores, to pair-living in some primates, to groups in some species, such as elephants (*Loxodonta africana*) and marmosets (*Callithrix jacchus).* By understanding the social system of a species we are able to predict how a species will respond to global change, and how its responses will be constrained, important information to decide on the best conservation efforts for each species.

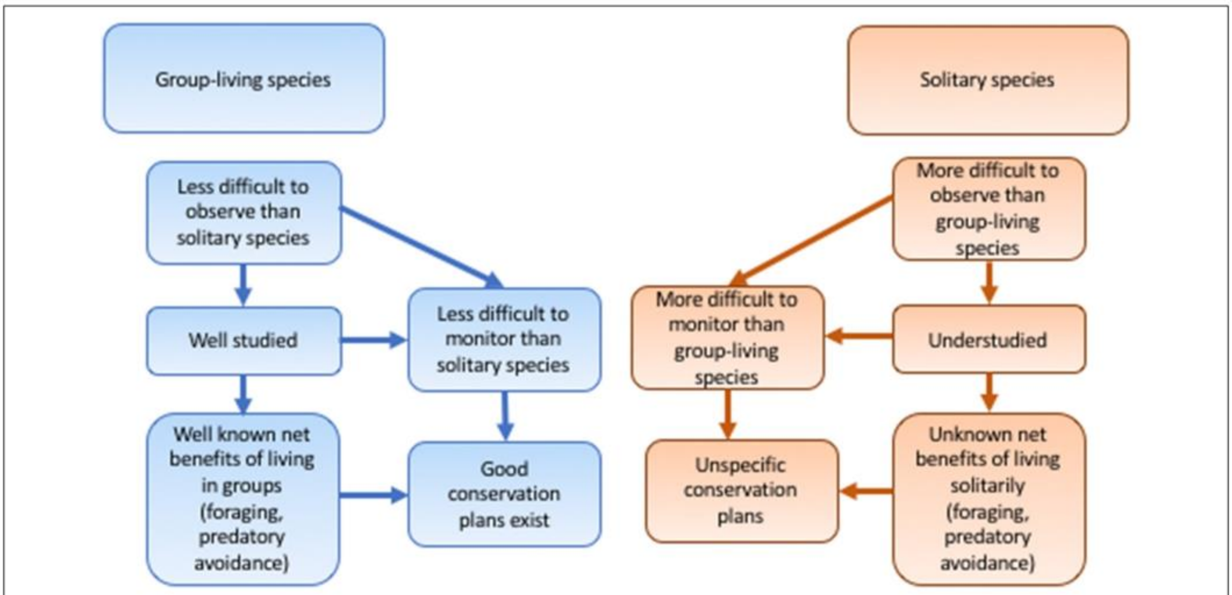

FIGURE 1 | While social species **(left)** are well-studied and understood with regards to their social biology, solitary species **(right)** are understudied. This is likely to affect the quality of species specific conservation plans **(middle)**.

SOLITARY SPECIES MISS THE BENEFITS FROM GROUP-LIVING AND MIGHT BE MORE VULNERABLE TO GLOBAL CHANGE THAN SOCIABLE SPECIES

Conservation efforts for solitary species might differ from those of group-living species. The social system of a species induces costs and benefits that are reliant on the environment, especially with regards to competition for resources (mates, food shelter), and how the social system impacts on predation risk (Kappeler et al., 2013). The net outcome of these costs and benefits will change when the environment changes. Species that live in groups might be buffered from these changes due to the benefits of group living, especially improved foraging and predator avoidance (Krause and Ruxton, 2002). The extent that solitary species show behavioral flexibility to cope with changes in resource availability and predation pressure is unknown, i.e., the extent that individuals can alter their behavior reversibly in response to changing environmental conditions (Gordon, 1991). This is why we need to study the behavioral flexibility of solitary species under varying environmental conditions to assess their vulnerability to global change (Huey et al., 2012). As solitary species miss the benefits from group-living they might be more vulnerable than sociable species.

ALLEE EFFECT AND SOLITARY SPECIES

The Allee effect describes a positive correlation between individual fitness and population density, with individuals benefitting from the presence of conspecifics (Allee, 1927). When living in groups, individuals can benefit from the Allee effect, by reducing predation pressure and gaining easier access to mating partners (Stephens and Sutherland, 2000). The Allee effect can thus be seen as a driving force behind animal spatial structure and sociality (Stephens and Sutherland, 2000). Due to climate change (obligate) sociable species might suffer from fitness costs induced by reduced group sizes. However, even solitary species might benefit from higher population density making it easier to find mating partners or reducing predation pressure (because predators have more prey to choose from), unless—as in sociable species—high population density increases intra-specific competition. Thus, so far it is unknown in how far the correlation between fitness and population density differs between sociable and solitary species, nor do we know at which population density positive Allee effects are overrun by negative effects of intra-specific competition. Therefore, in both sociable and solitary species the Allee effect should be taken into account when predicting how changes in population density induced by climate change affect extinction risk.

SOLITARY SPECIES MIGHT BE UNDERSTUDIED WHEN COMPARED TO SOCIABLE SPECIES

Solitary species might be understudied when compared to sociable species, especially with regards to their social behavior (**Figure 1**). First, for decades researchers rather studied sociable than solitary species as the focus of behavioral ecology was on the benefits of group-living and aspects like alloparental care (Clutton-Brock, 2021). Second, species that live solitarily are often more difficult to observe as they are nocturnal and shy, live in dense habitat (many small mammals), or have huge home ranges (solitary carnivores). In addition, the fact that they live alone makes them more difficult to monitor (**Figure 1**). The combination of a research focus on sociable species and the discrete nature of solitary species explains why they are understudied with regards to behavior, their trade-offs (energy, resources, time), and how these trade-offs might change and affect their resilience under conditions of global change.

TO CONSERVE MAMMALIAN BIODIVERSITY, WE NEED TO UNDERSTAND WHY SOLITARY LIVING IS AN ADAPTIVE TRAIT

Six hundred and seventy nine of the 5,500 mammalian species are endangered (IUCN redlist) and many of them are solitary living. The first mammal that became extinct as a direct cause of climate warming was the solitary Bramble Cay mosaic-tailed rat (*Melomys rubicola*; Fulton, 2017; Waller et al., 2017). It became extinct because of an ocean inundation, i.e., high water levels and storm surges caused by an increased frequency of extreme weather events, which were caused by anthropogenic climate change (Waller et al., 2017). Other well-known examples of endangered solitary mammals that are threatened by climate change include polar bears (*Ursus maritimus*), snow leopards (*Panthera uncia*), tigers (*Panthera tigris*), and panda bears (*Ailuropoda melanoleuca*). It can be expected that many less well-monitored solitary small mammal species are threatened by climate change.

Many endangered species are solitary and thus understanding constraints and the adaptive value of solitary living is important to conserve them. The persistence of mammals being solitary living after *170* my of mammalian evolution (Rowe, 1988) indicates that it is an adaptive social system for many environments. To conserve mammalian biodiversity, we need to understand why solitary living is adaptive for many species. However, while for decades the costs and benefits of group living have been studied, it is not known what makes solitary living adaptive. Without knowing the costs and benefits of solitary living we will not know how the trade-offs that solitary species face will change with global change. At the moment, we do not even know which are their most restricting trade-offs, whether it is with regards to food, shelter, predation, or maybe finding mating partners.

AUTHOR CONTRIBUTIONS

C-AO, CS, and LM conceived of and wrote the manuscript. All authors approved the final manuscript.

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Appendix B

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RESEARCH ARTICLE

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Revisiting the components of Macroscelidea social systems: Evidence for variable social organization, including pair-living, but not for a monogamous mating system

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Abstract

Elephant-shrews (Macroscelidea) have long been considered the only mammalian order to be completely monogamous, based on observations of their pair-living social organization. We reviewed primary studies on the four components of social systems (social organization, mating system, social structure, and care system) in elephant-shrews to evaluate whether they truly are monogamous. To identify gaps in our knowledge of their social system, we reviewed evidence for a pair-living social organization, mate fidelity (mating system), pair bonds (social structure), and biparental care (care system). Field data were available for eight species and seven were often pair-living. However, these seven species exhibited intra-specific variation in social organization; two of these species were also solitary living, two species were also group-living, and the remaining three species were both solitary and group-living. The eighth species was exclusively solitary. We reconstructed the ancestral social organization of Macroscelidea using Bayesian phylogenetic mixed-effects models and found that variable social organization, rather than exclusive pair-living, was the most likely ancestral state, though there was high uncertainty. No socio-ecological factors (body size, population density, and habitat) predicted a specific social organization. Observations of mating have been rare, such that no firm statements can be made. However, one unpublished study indicated high levels of extra-pair paternity. Regarding social structure, there was no evidence of pair-bonding, but there was evidence of mate guarding. Only maternal care has been observed, with females having very short nursing bouts. Evidence suggests that despite having often a pair-living form of social organization, Macroscelidea should not be described as a monogamous order, as little or no evidence supports that designation, nor are they exclusively pair-living (social organization) and we urge further field studies on Macroscelidea social systems.

KEYWORDS

Elephantulus, intra-specific variation, *Macroscelides*, *Petrodromus*, *Rhynchocyon*, sengi, social flexibility

1 | INTRODUCTION

Kappeler (2019) suggested that animal social systems are composed of four inter-related components: social organization, social structure, mating system, and care system. The social organization describes the size, sexual composition, and spatiotemporal cohesion of a group (Kappeler & van Schaik, 2002). Three major categories of social organization occur: solitary living, pair-living, or group living. The social structure describes the different interactions between members of the same group and the resulting relationships. The mating system describes who mates with whom and the reproductive consequences (e.g., paternity). There are four types of mating system, depending on the number of mating partners for males and females (Clutton-Brock, 1989; Loue, 2007): monogamy, polygyny, polyandry, or polygynandry. Finally, the care system is about who cares for the dependent offspring (Kappeler, 2019).

Over the last decades, the study of animal social systems has undergone significant progress due to long-term studies and advances in technology (e.g., genotyping; Clutton-Brock, 2021). Often the focus has been on specific social systems such as monogamy (Kleiman, 1977; Lukas & Clutton-Brock, 2013; Mock & Fujioka, 1990). Initially, pair-living (a form of social organization) was often regarded to be indicative of a monogamous social system in mammals (Kleiman, 1977, 1981). However, genetic fingerprinting revealed that extra-pair paternity is common in many pair-living species (Cohas & Allainé, 2009), leading to the realization that seemingly monogamous relationships do not necessary predict genetic outcomes (i.e., genetic monogamy). As a result, some researchers introduced the term "social monogamy" (Dobson et al., 2010; Gowaty & Buschhaust, 1998) to distinguish social behavior within pairs from genetic monogamy. Recent reviews from multiple research groups advocate abandoning the term "social monogamy" and using the term "monogamy" only in the context of mating systems (Fernandez-Duque et al., 2020; Garber et al., 2016; Huck et al., 2020; Kappeler & Pozzi, 2019; Kvarnemo, 2018; Tecot et al., 2016). Arguments against the use of the term "social monogamy" are centered on the importance of distinguishing between the different components of social systems for understanding their evolution. For example, if one wants to understand why animals live in pairs, it is not necessary to assume that they mate monogamously, only, that pair-living adds to a higher fitness than alternative forms of social organization. It is therefore necessary when describing the social system of a species, that social organization, mating system, social structure, and care system are considered (Kappeler, 2019).

Describing all four components of a social systems is a challenge, for a number of reasons. For example, it was previously assumed that "socially monogamous" species are pair-living (social organization), have pair bonds (social structure), and engage in biparental care (Kleiman, 1977; Mock & Fujioka, 1990). However, it is well known that several pair-living taxa do not fit this syndrome (Kleiman, 1977), such as dwarf antelopes (Bovidae) that do not exhibit biparental care (Komers, 1996), elephant-shrews (Macroscelididae) that do not have pair bonds (i.e., individuals showing a preference for a specific opposite sex-individual, which can be tested experimentally: Carter et al., 1995a, 1995b; Garnier & Schradin, 2019) or exhibit biparental care (Rathbun & Rathbun, 2006). Most confusion, however, arises from the inconsistent use of the term "monogamy" (see above and Kappeler, 2019; Solomon & Ophir, 2020), which should be restricted to describe the mating system where reproduction occurs mainly within pairs (Kappeler, 2019; Kappeler & van Schaik, 2002; Mock & Fujioka, 1990). For understanding the evolution of pair living, the different components of social systems should be studied separately from each other (Fernandez-Duque et al., 2020; Huck et al., 2020; Kappeler, 2019).

A species' social organization is typically characterized by the most frequent form, an approach that ignores intra-specific variation (Schradin et al., 2018). For example, the greater white-toothed shrew (*Crocidura russula*) has a variable social organization including solitary, pair, and group-living (Cantoni & Vogel, 1989; Ricci & Vogel, 1984). Intra-specific variation in social organization (IVSO) has now been reported in many mammalian taxa, including Artiodactyla (Jaeggi et al., 2020), Carnivora (Dalerum, 2007), Eulipotyphla (Valomy et al., 2015), and Strepsirrhini (Agnani et al., 2018). IVSO may be more common in other mammalian taxa as well, where variation has been possibly ignored to emphasize the most frequent or the most interesting form of social organization (Schradin et al., 2018). A consideration of IVSO and variation within the three other components of social systems can transform our understanding of social evolution (Jaeggi et al., 2020; Schradin et al., 2018).

The mammalian order Macroscelidea (elephant-shrews or sengis) includes 19 extant species in four genera, all occurring in Africa, ranging in body mass from 27 to 700 g (Rathbun & Dumbacher, 2015; Rovero et al., 2008) and occupying a diversity of habitats including deserts, semi-deserts, savannahs, rocky mountains, lowland forests, and tropical rain forests (Kingdon et al., 2013; Rathbun, 1979). Macroscelidea is the only mammalian order for which all extant species are believed to be monogamous (Lukas & Clutton-Brock, 2013; Rathbun & Rathbun, 2006; Ribble & Perrin, 2005), though this typically refers to a pair-living social organization (Schubert et al., 2009). Theory predicts that the ability of males to monopolize access to females, which depends on ecological factors and population density, will greatly influence mating systems (Emlen & Oring, 1977). The main hypothesis for monogamy in Macroscelidea is that low population density, possibly due to their insectivorous diet, makes it unfeasible for males to defend more than one female (Ribble & Perrin, 2005; Schubert et al., 2009). Males generally mate-guard a single female, leading to pair-living and potentially monogamous mating (Fitzgibbon, 1997; Ribble & Perrin, 2005; Schubert et al., 2009). Thus, their small body size combined with low population density is believed to have favored the evolution of monogamy.

The long-held assumption that all elephant-shrews are monogamous might have led to an underappreciation of variation in their social systems. The last detailed review on monogamy in elephant-shrews was published more than 40 years ago (Rathbun, 1979), and was updated within the discussion of a more recent case study (Rathbun & Rathbun, 2006). Therein, the importance of considering

TABLE 1 Types of social organization reported in field studies on elephant-shrews

Social organization	Definition
Solitary living	Both resident adult solitary males and solitary females occur in the population (excluding dispersing individuals)
Pair	One adult female and one adult male share a home range, with or without dependant offspring
One male multi female groups	Multiple breeding females and one breeding male share a home range

intra-specific variation for understanding the social systems of elephant-shrews, which were still considered to be all monogamous, was emphasized (Rathbun & Rathbun, 2006). To date, no review has differentiated between the four different components of social systems in elephant-shrews or summarized the observed intra-specific variation.

The overall aim was to describe all four components of the social system of elephant-shrews, taking intra-specific variation into account. First, we conducted a systematic review of the primary literature on elephant-shrew social organization, mating systems, social structure, and parental care. This approach allowed us to evaluate the empirical evidence suggesting that elephant-shrews are pair-living and monogamous. Second, we compared our dataset on elephant-shrew social organization—the component of the social system with the most data—with other available datasets that also used secondary sources to summarize their social systems (Heritage, 2018; Lukas & Clutton-Brock, 2013; Nowak & Wilson, 1999). Third, we report the results of phylogenetic comparative analyses to estimate the ancestral state of all elephant-shrews. Social organization was the only component for which sufficient data were available to conduct such an analysis. Based on previous reports, we expected the ancestral social organization to be pair-living. Body mass and habitat diversity differ widely between species and could influence their social organization. For example, living in variable habitats can affect density or grouping pattern of a population, through food availability or predation pressure (Geist, 1974). We therefore expected that variability in social organization will increase with variability in habitats (Schradin et al., 2018). Population density is the factor most emphasized to have influenced the evolution of pair-living in elephant-shrews (Rathbun & Rathbun, 2006) and mammals more broadly (Lukas & Clutton-Brock, 2013 but see Dobson et al., 2010), such that we predicted pair-living to be associated with low population density, making it difficult for a male to associate with more than one female.

2 | MATERIALS AND METHODS

2.1 | Literature searches

The 19 species of elephant-shrews were identified using the IUCN (International Union for Conservation of Nature) database (2019). Literature searches on the four social system components were conducted in Web of Science (Thomson Reuters) and in Google Scholar between November 2019 and March 2020 using specific key words (see the different sections below). This search yielded 166 articles that were scanned for information on social systems. Additional papers cited in those 166 articles were also studied. Data were recorded at the population-level.

2.2 | Social organization

For each species, the current and previously used Latin name of the species and the term "social" was searched. If no literature on social organization was found, the search was repeated in Web of Science and Google Scholar, only with the Latin name (for 10 species). To obtain information on social organization, only peer-reviewed literature from studies conducted in the field about elephant-shrews were taken into account, and reviews and studies in captivity were ignored. For each study, the following keywords were searched throughout the PDFs: "social," "solitary," "group," and "pair". All figures and tables were examined. Data on social organization were found in 11 papers on eight species.

Seven categories of social organization including solitary living, pair-living, and different forms of group-living (one male with multiple females, multiple males with multiple females, one female with multiple males, and multiple females and multiple males) were defined, of which only three were reported in the elephant-shrew studies (Table 1). For our study, we only considered adult and mature individuals. For each paper, we recorded the number of social units reported as solitary, pair-living, or group-living. Individuals of a species were considered as solitary only if both sexes have been observed to be solitary, as single individuals of one sex could represent dispersers. Identified dispersers were always ignored. For solitary living, we used the smaller number of the two sexes to have a number comparable to pairs (e.g., when four solitary males and three solitary females were observed, we recorded "3" solitary social units). Individuals of a species were considered as being pair-living when a male and a female have a significant overlap of their home ranges with each other but not with other individuals. Populations in which two or more forms of social organization were recorded were categorized as variable resulting in four possible social organizations within populations: solitary, pair-living, group-living, and "variable" (solitary/pair; pair/group; solitary/pair/group). In addition, we recorded whether the study took place during the breeding season, during the non-breeding season, or throughout the year.

2.3 | Mating system

For the mating system, peer-reviewed literature from studies conducted in the field and in captivity were taken into account. Searches included the following key words: "monogamy," "polygamy," "polyandry," "polygyandry," and "promiscuity." In addition, we report data presented on a poster available on researchgate (Peffley et al., 2009).

2.4 | Social structure

For the social structure, peer-reviewed literature from studies conducted in the field and in captivity were taken into account. Searches were made using the following key words: "solitary foragers," "pair bond," "aggression," and "mate guarding." This resulted in five suitable studies on social structure. Information on pair-bonds, aggression toward offspring, foraging, time spent between individuals, chasing, mate guarding, and aggression between females or between males was recorded as present or absent.

2.5 | Care system

For the care system, peer-reviewed literature from studies conducted in the field and in captivity were used. Searches were made using the following key words: "maternal care," "paternal care," "offspring," "direct paternal care," "indirect paternal care," and "absentee strategy" which are common terms for Macroscelidea (Rathbun, 1979). Indirect paternal care represents behaviors shown by the fathers independent of the presence of offspring which are beneficial for the offspring (while direct paternal care is a direct response to the presence of offspring) (Kleiman, 1977). This resulted in six suitable studies of care systems. We reported whether maternal and paternal care was observed.

2.6 | Dataset comparison

We compared our data with the database from Lukas and Clutton-Brock (Lukas & Clutton-Brock, 2013). Additionally, we compared our database with information in secondary literature, specifically in Walker's Mammals of the World Volume II (Nowak & Wilson, 1999) and the Handbook Mammals of the World (Heritage, 2018), compiled by taxon-specific experts. This comparison was only made for social organization, the only category for which sufficient data from peer-reviewed literature were available.

2.7 | Predictors for social organization

We included the following predictors in our Bayesian model described below: body mass, population density, number of studies per population, and habitat heterogeneity (see Tables S1–S3). Habitat heterogeneity represents the maximum number of habitats per population. Habitat type was reported from the primary literature and categorized on IUCN classification as shrubland, rocky areas, bushlands, desert, or forest. Habitat heterogeneity and whenever possible, body mass and population density, were extracted from the same study in which data on social organization had been reported. If no information was available in that same study, we searched for other studies of the same population (two species). Finally, if no information was available, we searched the primary literature for data on the same species in other populations (one species).

2.8 | Phylogenetic comparative analysis

All statistical analyses were conducted in R v.3.6.1 (The R foundation for statistical computing). To analyze social organization, Bayesian phylogenetic mixed-effects models were used in order to account for the multilevel structure of the dataset (populations nested within species) and the phylogenetic relationships among species (de Villemereuil, 2014). To represent the phylogenetic relationships and their uncertainty a sample of 100 phylogenetic trees was downloaded from the online database VertLife (http://vertlife.org/data/). The parameter used to create the tree was "Mammals birth death node dated completed tree." We used the R package *brms* (Bürkner) to fit multinomial models to the response variable social organization, wherein each population could occupy one of several mutually exclusive states. We created three models. In model 1, the social organization (solitary, pair-living, group-living, and variable) was the response variable. In model 2, the response variable was separated into all possible combinations (solitary + pair-living, pair + group-living, and solitary + pair-living + group-living) to estimate the most likely ancestral social organization. In model 3, we used the main (i.e., the modal or most common) form of social organization, defined as the social organization for which the most social units were observed (solitary, pair-living, and group-living) as the response variable. In this model, variability was not included except for one species, *Macroscelides flavicaudatus*, where an equal number of social units were solitary and pair-living.

For each model, we also calculated the percentage of the difference between the probability of two different social organization using the posterior samples (e.g., all samples for the probability of variable social organization minus all samples for the probability of pair-living) and whether the probability of that difference was greater than zero (i.e., the proportion of the resulting samples >0); the ability to compute such contrasts between model parameters is a notable strength of Bayesian inference (McElreath, 2019), whereas frequentist models are limited to comparing estimated parameters to 0. Hence we can directly express the model's greater confidence that a given social organization had a higher probability than others, which cannot be learned by merely comparing each social organization's mean probability and confident intervals. Thus, even if the exact probability of each social organization is estimated with high uncertainty (large 95% CIs), we can have more confidence in the probability of differences between the probabilities of two social organizations.

We included the following predictors in our models: body mass, population density, number of studies per population, and habitat heterogeneity (number of habitat per population) (see Tables S1–S3). The number of studies per population (one or two) was added to control for research effort. The number of studies per population and habitat heterogeneity were centered on one. Body mass and population density were centered on their mean.

Our model converged well with Rhat values (potential scale reduction factor) ≤1.01. The likelihood of each social organization being the ancestral state was inferred from the intercepts of the model, that is, the probability of each social organization when predictors were at their means. Pair-living was the reference category in our two models.

The phylogenetic signal (λ) was calculated as the proportion of variance captured by the phylogenetic random effects (Nakagawa & Schielzeth, 2013):

$$\lambda = \frac{\sigma_p^2}{\sigma_p^2 + \sigma_r^2 + \sigma_d^2}$$

σ_p^2 represents the variance of the phylogeny random effect, σ_r^2 is the variance of the species-level random effect, and σ_d^2 is the distribution-specific variance equal to $\pi^2/3$ (Nakagawa & Schielzeth, 2013).

3 | RESULTS

3.1 | Social organization

Data on social organization were reported for 12 populations of eight species (Table 2). One species (*Macroscelides micus*) was only reported to be solitary living whereas the other seven species had variable social organizations. Two species were solitary and pair-living, three species were solitary, pair- and group-living, and two species pair- and group-living (Table 2). Of the 12 studied populations, one population was solitary (*Macroscelides micus*) and two populations of *Petrodromus tetradactylus* were pair-living. The other 10 populations (75%) had a variable social organization (Table 2).

3.2 | Mating system

Our search generated only one paper that reported observations of mating in the field (Rathbun, 1979). A male *Rhynchocyon chrysopygus* chased the female and then copulated with her during 2 s with five rapid copulations. Schubert et al. (2012) found in captive experiments that female *Macroscelides proboscideus* showed as many sexual interactions with a neighboring male as with her pair partner, and that males actively aimed to mate with non-pair neighboring females. In an unpublished poster on a study using micro-satellites to determine paternity in *Macroscelides proboscideus*, Peffley et al. (2009) found for the population studied by Schubert et al. (2009) that only two out of six mother-offspring families resulted from serially monogamous mating. From a sample of 19 offspring, the male of the pair was the sire of only seven. At least six offspring were sired by another male than the female's social mating partner.

3.3 | Social structure

Our search generated six studies reporting information about social interactions (Table 3). Individuals living together had little social interaction, there were no pair-bonds, and they were solitary foragers (Rathbun, 1979). Mate guarding was said to occur in five species (Table 3). In *Elephantulus myurus* (Ribble & Perrin, 2005) and in *Rhynchocyon chrysopygus* (Fitzgibbon, 1997), males defended territories containing females, and these territories were quickly taken over by other males after the pair male disappeared (resulting in a change of the adult sex ratio). This was regarded as evidence of male mate guarding. The same association pattern has been interpreted as mate guarding in several other species, where males followed their females when in estrus, though mate guarding was not measured directly (Rathbun, 1979). The only study that directly measured mate guarding was in *Macroscelides probiscideus*, where males reduced the distance to their female in the periods they were receptive (Schubert et al., 2009). Similarly, in the solitary species *Macroscelides flavicaudatus*, males associated with females when these were receptive, but then male left, searching for other females (Sauer, 1973). Moreover, both sexes defend a territory and are very aggressive towards conspecifics of the same sex (FitzGibbon, 1997; Rathbun, 1979). Schubert et al. (2012) found in captive experiments no evidence for pair-bonding, but individuals of both sexes readily interacted with opposite sex conspecifics with which they were not paired.

In several species, aggression towards young was observed around weaning. Some species tolerated their weaned offspring for periods ranging from 21 to 40 days old (Rathbun, 1979; Schubert et al., 2012) while in *Elephantulus rufescens*, parents tolerated one of their young for the entire period of 193 days. In *Elephantulus rufescens*, some offspring can remain in their parents' territory long after reaching adulthood (Rathbun, 1979).

3.4 | Care system

We found information on the care system for six of the 19 species (Table 4). The precocial young were visited and nursed by the mother for very short periods of 10–60 s, which has been called an absentee strategy (Rathbun, 1979). During this period, the female was not engaged in other care activities, such as cleaning or huddling the offspring. Maintenance of pathways by males to allow offspring to move quickly and escape from a predator was reported for five species (Table 4) and interpreted as indirect paternal care while no direct paternal care was observed.

TABLE 2 The different forms of social organization reported in the primary literature. Numbers refer to the numbers of social units observed

Species	Population	Solitary	Pair-living	One male several females	References
Elephantulus intufi	Erongo Wilderness Lodge Okapekaha Farm, Namibia	—	6 (BOTH)	1[a] (BOTH)	Rathbun and Rathbun (2006)
Elephantulus myurus		5 (BOTH)	18 (BOTH)	—	—
	Weenen Nature Reserve, South Africa	1 (BS)	12 (BS)	—	Ribble and Perrin (2005)
	Goro Game Reserve, South Africa	2 (BS) 2 (NBS)	4 (BS) 2 (NBS)	—	Hoffmann et al. (2019)
Elephantulus rufescens	Bushwacker, Kenya	2 (ALL)	7 (ALL)	1[a] (ALL)	Rathbun (1979)
Macroscelides flavicaudatus	Namib Desert, Namibia	2 (BS)	2 (BS)	—	Sauer (1973)
Macroscelides micus	Eastern Goboboseb Mountains, Namibia	2 (BS)	—	—	Rathbun and Dumbacher (2015)
Macroscelides proboscideus	Goegap Nature Reserve, South Africa	1 (BOTH)	32 (BOTH)	1[a] (BOTH)	Schubert et al. (2009)
Petrodromus tetradactylus		—	5 (BOTH)	1 (BS)	—
	Tembe Elephant Park, South Africa	—	4 (NBS)	—	Oxenham and Perrin (2009)
	Arabuko Sokoke Forest, Kenya	—	1 (BOTH)	—	Fitzgibbon (1995)
	Sodwana Bay National Park, South Africa	—	—	1 (BS)	Linn et al. (2007)
Rhynchocyon chrysopygus		1 (ALL)	12 (ALL)	3 (ALL)	—
	Arabuko Sokoke Forest, Kenya	—	5 (ALL)	2[a] (ALL)	Fitzgibbon (1997)
	Gedi Forest	1 (ALL)	7 (ALL)	1[a] (ALL)	Rathbun (1979)

Note: No data could be found on social organization of the remaining species (*Elephantulus brachyrhynchus, Elephantulus edwardii, Elephantulus fuscipes, Elephantulus fuscus, Elephantulus pilicaudus, Elephantulus rozeti, Elephantulus rupestris, Rhynchocyon cirnei, Rhynchocyon petersi and Rhynchocyon udzungwensis*).

Abbreviations: ALL, non-seasonal breeding throughout the year; BOTH, breeding and non-breeding season; BS, breeding season; NBS, non-breeding season.

[a] One male and several female association (group-living) lasted 2 weeks for Elephantulus intufi, 42 days for Elephantulus rufescens, 5–6 weeks for *Macroscelides proboscideus*, 6 weeks, 2 and 3 months for Rhynchocyon chrysopygus.

3.5 | Dataset comparison

In our database, the most frequent form of social organization observed of six of the eight species of Macroscelidea was pair-living (Table 5), while one species had a solitary main social organization (*M. micus*) and another had an equal number of solitary and pair-living social units, hence a variable main social organization (*M. flavicaudatus*). Thus, our results of main social organization were similar to what was reported by Lukas and Clutton-Brock (2013). Seven (87.5%) of the species with information available showed IVSO and the only species (12.5%) with a single form of social organization was solitary. This high prevalence of IVSO was not represented in the database of Lukas and Clutton-Brock (2013), in which 15 (93.3%) of the elephant-shrew species were reported to be pair-living and one (6.7%) to be solitary (Table 5 and Tables S4). They reported *Petrodromus tetradactylus* to be solitary, which we found to be variable with pair and group-living, while the species we reported to be solitary, *Macroscelides micus*, was studied after the paper from Lukas and Clutton-Brock (2013) by Rathbun and Dumbacher (2015) (see Tables S4).

The Handbook Mammals of the World (Heritage, 2018) reported all elephant-shrew species to be pair-living. Walker's Mammals of the World (Nowak & Wilson, 1999) reports data on eight species, with five (62.5%) of them showing IVSO, two (25%) being pair-living, and one (12.5%) being solitary living (Table 5).

3.6 | Phylogenetic comparative analysis

The phylogenetic mixed effects models showed no significant effects of habitat heterogeneity, population density, body mass, and number of studies on social organization (see Tables S5–S7). The phylogenetic signal for model 1 was moderate (mean = 0.35, 95% CI = 0.008–0.75). Variable social organization had the highest probability as ancestral state (mean probability = 0.67, 95% CI =0–1) compared to solitary living (mean = 0.15, 95% CI = 0–1.0), group-living (mean = 0.09, 95% CI =0–0.85), and pair-living (mean = 0.08, 95% CI = 0–0.69). Despite the large confident intervals surrounding the exact probability of each social organization, we can express greater confidence about the differences between these probabilities; namely, we are 82% confident

TABLE 3 The different components of social structure identified in our primary literature research

Species	PB	ATO	SF	Time MF	Chase	MG	Ag FF	Ag MM	References
Elephantulus myurus	—	—	—	—	—	Yes	—	—	Ribble and Perrin (2005)
Elephantulus rufescens	No	Yes (40 days old)	Yes	—	—	Yes	Yes	Yes	Rathbun (1979)
Macroscelides flavicaudatus	No	—	Yes	No	—	Yes	—	—	Sauer (1973)
Macroscelides proboscideus	No	Yes (21 days old)	—	—	Yes	Yes	—	Yes	Schubert et al. (2012) and Schubert et al. (2009)
Petrodromus tetradactylus	No	—	yes	—	—	—	Yes	Yes	Rathbun (1979)
Rhynchocyon chrysopygus	—	no (193 days old)	Yes	No	Yes	Yes	Yes	Yes	Rathbun (1979); FitzGibbon (1997)

Abbreviations: Ag FF, aggression between neighboring females; Ag MM, aggression between neighboring males; ATO, aggression toward their offspring; Chase, chase conspecific that entered their territory; MG, mate guarding; PB, Pair-bond; SF, solitary foragers; Time MF, Male and female spend considerable time together.

TABLE 4 Care system identified in literature for Macroscelidea

Species	Direct maternal care	Direct paternal care	Indirect paternal care	References
Elephantulus intufi	Yes	No	Yes	Rathbun and Rathbun (2006)
Elephantulus myurus	—	No	Yes	Ribble and Perrin (2005)
Elephantulus rufescens	Yes	No	Yes	Rathbun (1979)
Macroscelides flavicaudatus	Yes	—	—	Sauer (1973)
Rhynchocyon chrysopygus	Yes	No	Yes	Rathbun (1979) FitzGibbon (1997)
Rhynchocyon petersi	—	No	Yes	Baker et al. (2005)

TABLE 5 Social organization of Macroscelidea reported in primary literature and compared to three published databases (Lukas & Clutton-Brock, 2013, the book Mammals of the World by Nowak & Wilson, 1999, and the Handbook Mammals of the World by Heritage, 2018)

	Our study	Our study (main social organization)	Lukas and Clutton-Brock (2013)	WMW 1999	HMW 2018
Number of species with information on social organization	8	8	15	8	10
Number of species showing IVSO	7 (87.5%)	1 (12.5%)	0	5 (62.5%)	0
Number of exclusively solitary species	1 (12.5%)	1 (12.5%)	1 (6.66%)	1 (12.5%)	0
Number of exclusively pair-living species	0	6 (75%)	14 (93.33%)	2 (25%)	10 (100%)
Number of exclusively group-living species	0	0	0	0	0

Note: Note that Lukas and Clutton-Brock as well as Handbook Mammals of the World only report the most frequently observed form of social organization and did not consider IVSO.

Abbreviations: HMW, Handbook of the Mammals of the World; WMW=Walker's Mammals of the World.

that variable was more likely than pair-living, 32% confident that group-living was more likely than pair-living, and 38% confident that solitary was more likely than pair-living (Figure 1; Tables S8).

In order to understand which kind of variable social organization was the most likely ancestral state, a second analysis was conducted using all different categories of variable social organization (model 2; Figure 2; Tables S9). The phylogenetic signal of this analysis was moderate (mean = 0.32, 95% CI = 0.0027–0.74). Solitary + pair-living + group-living was the most likely ancestral state (mean = 0.29, 95% CI = 0–1), followed by pair + group-living ((mean = 0.28, 95% CI = 0–1) and solitary + pair-living (mean = 0.19, 95% CI = 0–1). Those three social organizations were part of the category "variable" in our first analysis (Figure 1) and were respectively 60%, 67%, and 45% more likely than pair-living (Figure 2; Tables S9). The probability that the ancestral social organization was solitary was relatively low (mean = 0.12, 95% CI = 0–0.99). Group-living (mean = 0.06, 95% CI = 0–0.52) and pair-living (mean = 0.05, 95% CI = 0–0.32) were the least likely ancestral social organization.

In model 3, we calculated what the ancestral state would be if we only took the main social organization into account, neglecting variability (Figure 3). The phylogenetic signal was again moderate (mean = 0.36, 95% CI = 0.00008–0.8). Pair-living was the most likely ancestral state (mean probability = 0.58, 95% CI = 0–1), but again with large uncertainty. Group-living (mean = 0.08, 95%

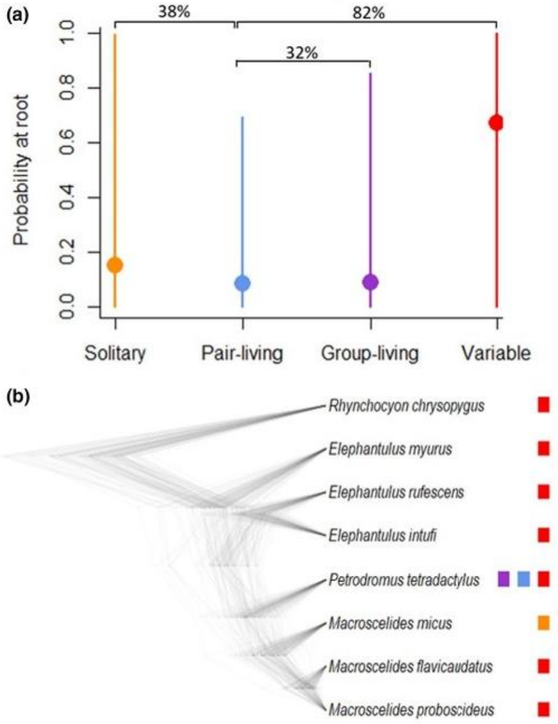

FIGURE 1 (a) The likelihood of each social organization (solitary, pair-living, group-living, and variable) being the ancestral state ("probability at root"). Percentages represent the probability that the difference between the estimated probabilities of different social organizations compared to pair-living was greater than 0 (e.g., variable is 82% more likely than pair-living). (b) Phylogeny of the eight Macroscelidea species with data on social organization from 12 populations. Colored boxes at the tip of phylogenetic tree correspond to social organization(s) observed within species (orange = solitary; blue = pair-living; violet = group-living; and red = variable), and if two populations of the same species had different social organization, then two boxes are shown

CI = 0–0.74), solitary (mean = 0.20, 95% CI = 0–1), and solitary/pair-living (mean = 0.14, 95% CI = 0–1) had lower mean probabilities and similar uncertainties (Figure 3; Tables S10).

4 | DISCUSSION

Our comprehensive review of the literature on Macroscelidea indicated that their best studied social system component is social organization. The most frequent form of social organization was pair-living, though all pair-living species exhibited a variable social organization, including either solitary and/or group-living. Our approached revealed that (1) elephant-shrew social organization is best characterized as variable, (2) the ancestral form of social organization could not be reliably determined, but pair-living had the lowest probabilities when IVSO was taken into account, and (3) there is no empirical evidence that any of the species typically exhibit a monogamous mating system.

4.1 | Social system

Consistent with a previous report (Rathbun & Rathbun, 2006), our literature review indicates that Macroscelidea have a variable form of social organization, with pair-living occurring in 87.5% of the species, solitary living occurring in 75% of the species, and group-living occurring in 62.5% of the species. While pair-living is common in many species of Macroscelidea, it is neither the only form of social organization nor the main form of social organization in all species. Solitary living occurred in most species and was as common as pair-living in one species and the only form of social organization for another species. Importantly, pair-living was mainly derived from the extensive home range overlap of one male and one female with each other but not with other individuals. Thus, even though spatial organization indicated pair-living, individuals spent most of their time alone, and other researchers might categorize these individuals as solitary rather than pair-living. In some cases, the home ranges of two females and one male overlapped heavily such that the social units were categorized as single male/multi-female groups. These associations lasted for a few weeks up to several months (Fitzgibbon, 1997; Rathbun, 1979; Schubert et al., 2009), which is long for species that lives between 2 and 4 years (Rathbun, 1979). Typically, such groups occurred because of the death/disappearance of the male of a neighboring pair (Rathbun, 1979; Schubert et al., 2009). However, pairs were more stable than groups in *Elephantulus rufescens* (pairs = 1 year, groups=2 months; Rathbun, 1979), *Rhynchocyon chrysopygus* (pairs = up to 16 months, groups = up to 3 months; Fitzgibbon, 1997), and *Macroscelides proboscideus* (pair = 2 years, groups = 5–6 weeks; Schubert et al., 2009).

Our study suggests that the long-held assertion that Macroscelidea is the only monogamous mammalian order (Lukas & Clutton-Brock, 2013; Rathbun, 1979; Rathbun & Rathbun, 2006; Ribble & Perrin, 2005; Handbook Mammals of the World 2018) is an over-simplification of elephant-shrew mating systems. The only available information regarding the mating system is from an unpublished study that was presented as a poster, representing data from the study population of Schubert et al., 2009 (samples had been collected by Schradin & Schubert). These non-peer-reviewed data indicate that *M. proboscideus* are not genetically monogamous and that females tend to reproduce with more than one male (Peffley et al., 2009). Many pair-living mammal species do not have a monogamous mating system but show extra-pair paternity, varying between 0 and 92% (Cohas & Allainé, 2009). Future studies will have to investigate how common extra-pair paternity is in the different Macroscelidea species.

4.2 | Dataset comparison

We found that 75% of the species had pair-living as their most frequent form of social organization. In comparison, the Handbook Mammals of the World (Heritage, 2018) considers all species of

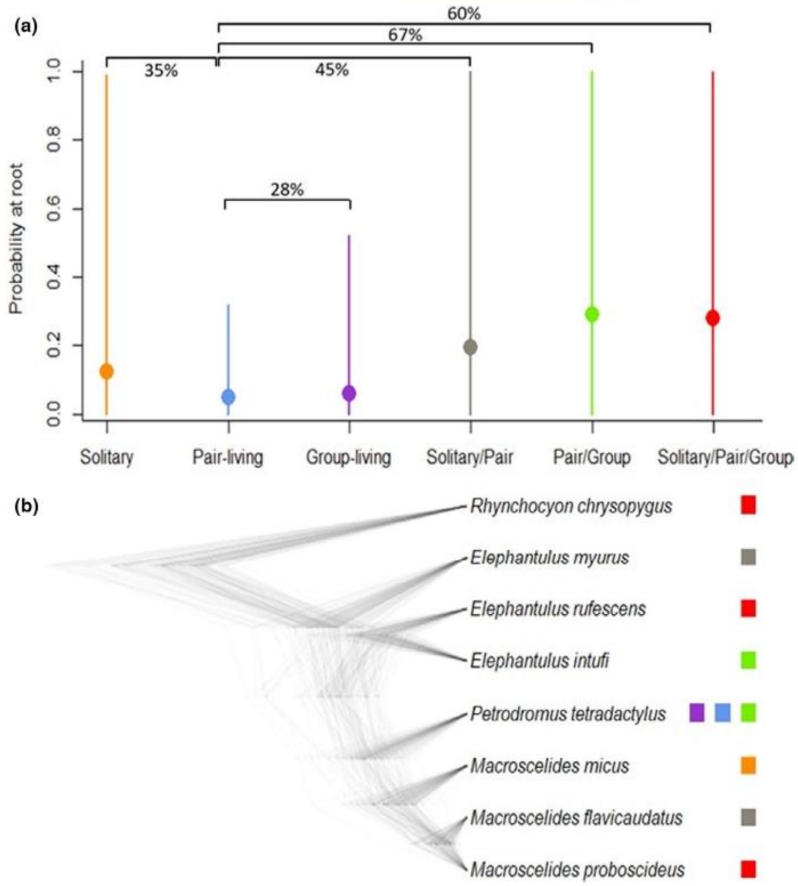

FIGURE 2 (a) The likelihood of each social organization (solitary, pair-living, group-living, solitary + pair-living, pair + group-living, and solitary + pair-living + group-living) being the ancestral state ("probability at root"). Percentages represent the probability that the difference between the estimated probabilities of different social organizations compared to pair-living was greater than 0. (b) Phylogeny of the eight Macroscelidea species with data on social organization from 12 populations. Colored boxes at the tip of phylogenetic tree correspond to social organization(s) observed within species (orange = solitary; blue = pair-living; violet = group-living; gray = solitary + pair-living; green = pair + group-living; and red = solitary + pair-living + group-living), and if two populations of the same species had different social organization, then two boxes are shown

elephant-shrews to be pair-living and Lukas and Clutton-Brock (2013) reported 93% of species as pair-living. There are several explanations for these differences. We relied only on information from field studies, whereas Lukas and Clutton-Brock (2013) also included data from captivity and assumed that species without data have the same form of social organization as closely related species. Thus, their database comprised of 15 species while we only found field data for eight species. The references in their database include one paper making the general statement that Macroscelidea are monogamous (Rathbun & Rathbun, 2006), one paper reporting data from captivity (Lawes & Perrin, 1995), one paper that cannot resolve the social organization of the studied species (*Petrodromus tetradactylus*; Jennings & Rathbun, 2001), as well as one paper that does not provide data on social organization (Koontz & Roeper, 1983). Interestingly, the only species which they do not regard to be monogamous but solitary, *Petrodromus tetradactylus*, was reported by us to be group or pair-living. Our results compare well with the expert opinions published in the book Walker's Mammals of the World (Nowak & Wilson, 1999). Like us, they report data for only eight species, 12.5% of which were believed to be solitary, 25% to be pair-living, and 62.5% to be variable. Based on these differences, we argue that our database based on primary field studies is the most robust of these datasets.

4.3 | Phylogenetic comparative analysis

We could not reliably identify the ancestral form of social organization, but found in all analyses a moderate phylogenetic signal indicating that social organization is influenced by phylogenetic history. Considering a posteriori the small sample size and the high variation between species and populations, this is not surprising. Nevertheless, the phylogenetic analyses revealed that variable social organization was 82% more likely to be the ancestral state than pair-living.

Most Macroscelidea had a variable type of social organization which was also the most likely ancestral form of social organization. More precisely, it was solitary + pair-living + group-living followed by pair + group-living that were the most likely ancestral forms of social organization. The uncertainty surrounding these inferences was large. Of note is that the previous assumption, of a pair-living ancestral social organization was the least supported. Importantly, when considering the variation reported from the field, pair-living always received very little support as the ancestral form. In contrast, when we considered only the main social organization (and ignored variation), pair-living became the most likely ancestral form of social organization, but with a lower mean probability than the variable ancestral state in the first analysis. What we can hypothesize is that the ancestor of all Macroscelidea was able to be pair-living, but with

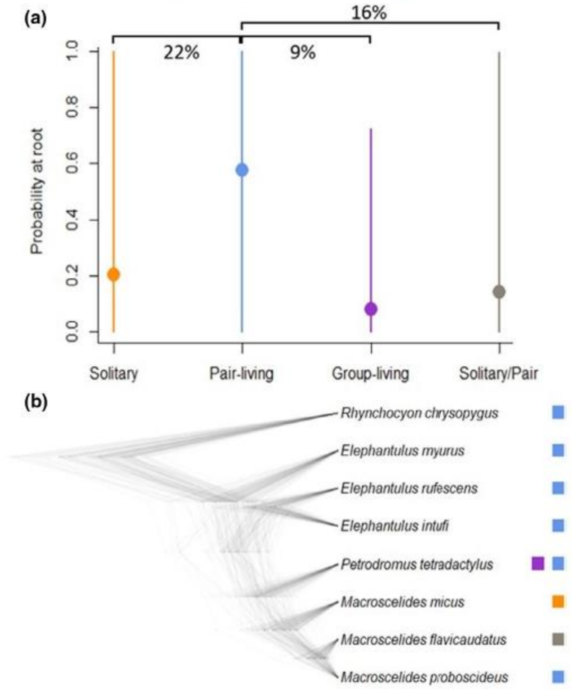

FIGURE 3 (a) The likelihood of each main form of social organization (solitary, pair-living, group-living, and solitary with pair-living) being the ancestral state ("probability at root"), ignoring the observed variation. Percentages represent the probability that the difference between the estimated probabilities of different social organizations compared to pair-living was greater than 0. (b) Phylogeny of the eight Macroscelidea species with data on social organization for 12 populations. Colored boxes at the tip of phylogenetic tree correspond to social organization(s) observed within species (orange = solitary; blue = pair-living; violet = group-living; and gray = solitary and pair-living), and if two populations of the same species had different social organization, then two boxes are shown

significant variation in its social organization that also allowed for solitary and group-living.

Low population density has been considered as the main factor leading to pair-living in animals (Emlen & Oring, 1977) and specifically in Macroscelidea, since it makes it difficult for males to defend more than one female (Rathbun & Dumbacher, 2015; Rathbun & Rathbun, 2006). However, we found no indication that social organization was related to population density. This might be because the lowest population densities (reported for two species of the genus *Macroscelides*) were associated with solitary living, which is in contrast to Rathbun and Rathbun's (2006) prediction of an increased incidence of pair-living with decreasing population density. Body mass and habitat type, two factors varying widely between populations and species, also had no influence on social organizations. Thus, even though we found important variation in social organization within and between populations, we could not explain this variation by the ecological and life history factors included in our analysis. To gain a better understanding of the evolution and diversity of Macroscelidea social organization, more field studies would be needed, especially on the 11 species for which we could not find any data.

4.4 | Social monogamy versus sengi syndrome

Aspects of the care system and of the social structure have been discussed in the literature to be associated with monogamy. Social monogamy has been characterized by pair-living, monogamous mating, biparental care, pair bonding, and mate guarding (Lukas & Clutton-Brock, 2013; Mock & Fujioka, 1990). Direct paternal care is absent in Macroscelidea, though indirect paternal care, that is, behaviors of the male which benefit the offspring but which are shown to be independent to the presence of offspring, has been reported for several species (Rathbun, 1979). However, indirect paternal care did not evolve because of its benefits for the offspring, but because it has direct survival benefits for the males, such as improved ability to escape predators (Rathbun, 1979; Ribble & Perrin, 2005). Macroscelidea is the only taxon where indirect paternal care has been discussed in detail, possibly to fit the proposed social monogamy. There is also general consensus that pair-bonding (i.e., individuals showing an attachment to a specific opposite-sex individual, Carter et al., 1995a, 1995b) does not exist in Macroscelidea (Rathbun & Rathbun, 2006).

In Macroscelidea, individuals of a pair spend little time together (Fitzgibbon, 1997; Koontz & Roeper, 1983; Rathbun, 1979) apart from the period when the female is receptive (Fitzgibbon, 1997; Schubert et al., 2012). This represents the behavioral pattern of many solitary living species (Schülke & Kappeler, 2003). Females defend territories against other females and males against other males (Rathbun, 1979). Mate guarding has been observed in several elephant-shrew species (FitzGibbon, 1997; Rathbun, 1979; Sauer, 1973; Schubert et al., 2012). This tactic consists of a male keeping within a short distance to a female as long as she is receptive, possibly to prevent male competitors to have access to that female (Huck et al., 2004). For example, in *M. probscideus*, a male and female sharing a home range were much closer to each other in the period during which the female was sexually receptive than when she was not (Schubert et al., 2009). Our evaluation of the four components of social systems independently in Macroscelidea shows that this taxon is in general neither pair-living nor monogamous, and thus not "socially monogamous."

It was recognized early on that Macroscelidea did not fit the typical description of social monogamy (Kleiman, 1977; Rathbun & Rathbun, 2006). Instead, Rathbun & Rathbun, 2006 discussed a "sengi syndrome" for small mammals with the sengi typic morphology: compact body, large head and long and narrow snout. Species falling under this syndrome have a relatively long life expectancy, produce few precocial young and have an insectivorous diet, which can explain a conserved social organization of pair-living even though the different species inhabit diverse habitats. The sengi syndrome has been discussed in relation to their phylogenetic ancestry (Rathbun & Rathbun, 2006). We found that phylogeny has a moderate effect on social organization, suggesting that social organization is somewhat constrained by phylogenetic history, but can also adapt to local ecology. Indeed, the phylogenetic signal in all of our three models had a much higher mean probability compared to other studies (e.g., 0.05 in Jaeggi et al., 2020 on Artiodactyla social organization). Thus, our study is not in contrast to the suggested sengi syndrome but indicates that instead of fixed pair-living, a flexible social organization including solitary and pair-living is likely part of this syndrome.

5 | CONCLUSIONS

The Macroscelidea (elephant-shrews or sengis) have been regarded for decades as the only mammalian order in which all extant species are monogamous. Reviewing field studies of the last five decades we found that the social organization of elephant-shrews is much more flexible than previously recognized and not all species are pair-living. More species must be studied in the field to reliably infer the ancestral form of social organization and the ecological and life history factors related to Macroscelidea social evolution. Our analysis predicts a socially variable ancestor that had pair-living as one of several possible forms of social organization. Paternity studies are needed to determine the genetic mating system, but the flexible social organization predict that extra-pair paternity is common and that Macroscelidea are not a monogamous order. In sum, elephant-shrews are not exclusively pair-living, do not fit the definition of socially monogamous (Kleiman, 1977; Rathbun & Rathbun, 2006), and there is no evidence for a genetically monogamous mating system.

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CONFLICT OF INTEREST

The authors and co-authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Additional supporting information may be found in the online version of the article at the publisher's website in our Supplementary Material.

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SUPPORTING INFORMATION

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Appendix C

PROCEEDINGS B

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Research

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THE ROYAL SOCIETY
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The evolution of marsupial social organization

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It is generally believed that marsupials are more primitive than placentals mammals and mainly solitary living, representing the ancestral form of social organization of all mammals. However, field studies have observed pair and group-living in marsupial species, but no comparative study about their social evolution was ever done. Here, we describe the results of primary literature research on marsupial social organization which indicates that most species can live in pairs or groups and many show intra-specific variation in social organization. Using Bayesian phylogenetic mixed-effects models with a weak phylogenetic signal of 0.18, we found that solitary living was the most likely ancestral form (35% posterior probability), but had high uncertainty, and the combined probability of a partly sociable marsupial ancestor (65%) should not be overlooked. For Australian marsupials, group-living species were less likely to be found in tropical rainforest, and species with a variable social organization were associated with low and unpredictable precipitation representing deserts. Our results suggest that modern marsupials are more sociable than previously believed and that there is no strong support that their ancestral state was strictly solitary living, such that the assumption of a solitary ancestral state of all mammals may also need reconsideration.

1. Introduction

Social systems are believed to evolve from a simple state of solitary living to more complex forms, including pairs, and groups, some of which show communal or even cooperative breeding [1,2]. The environment is seen as a major driver of social evolution [3]. In birds [4], mammals [5] and humans [6], cooperative breeding occurs more often in harsh environments with low rainfall and variable climate. However, so far no comparative study tested whether the association between environmental harshness and sociality is also found in taxa which do not contain cooperative breeders.

Animals' social systems are composed of four parts [7]: social organization (group size and composition), social structure (the interaction between individuals), mating system (who mates with whom) and the care system (who takes care of the offspring). These components are connected in complex ways [7]. Most information is available for social organization [8], which can influence social structure, mating and care system, and therefore the entire social system [7]. Social organization differs not only between species, but also within species. Intra-specific variation in social organization (IVSO) occurs when the composition of social units of a species varies, for example between solitary, pairs and / or different forms of group-living [8]. Several mammalian taxa have a more variable social organization than we used to believe [9–11]. Consideration of IVSO is important when studying social evolution because it more accurately describes the social organization than a simple categorization [8].

Social organization is the product of individual social tactics that evolved to maximize inclusive fitness in natural habitats [12]. The habitat type may have an effect on individual social tactics, affecting the social organization of the population. For example, arid environments may favour sociality by limiting dispersal opportunities [4,13–15], while moist and temperate habitats are often the home of solitary species [15]. Thus, the social organization might be habitat specific, and species occupying multiple habitats may show IVSO as a response to different types of habitats.

Habitats vary depending on the local climatic conditions. From tropical rainforests to arid deserts, climate plays an important role in controlling the environment and drives species evolution [16]. Seasonal changes in local climate might cause periodic changes in habitat quality, which may lead to seasonal variation in social organization. Many studies found a link between climate-related environmental harshness and sociality [5,15,17]. Arid environments with low and unpredictable rainfall are positively correlated with the care system, i.e. the occurrence of non-breeding helpers in birds [17] and mammals [5], but we know little about how environmental variations influences variation in social organization.

As a diverse clade of animals, mammals show high variability in social organization, possibly depending on habitat and climate, as studied in some placental taxa [15,18]. Marsupials are the only extant members of Metatheria, which is one of the three extant clades of mammals, together with monotremes and eutherians (= placental mammals). Fossil records suggested the divergence between the ancestors of placentals and marsupials happened around 160 Ma [19]. The care system of marsupials is normally exclusive maternal care with paternal care being very rare, and there are no reports of cooperative breeding [20]. This makes marsupials a good system to study the relationship between climate, environmental harshness and social organization independent from variation in the care system. Most marsupial species are believed to be solitary living, but other forms of social organization have also been observed [21]. For example, some kangaroo species like *Macropus parryi* and *Macropus giganteus* can form fission–fusion societies or permanent social groups of up to 50 individuals [22]. While many field studies on marsupials have been published in the last decades, no recent review about their social organization exists. Recently, using modern statistical approaches, marsupials were used as a model to study brain size [23] and life-history evolution [24] in mammals with a supposedly relatively simple social system. However, their social evolution is poorly understood, though there is indication that in large generalist grass feeders like kangaroos (macropods) occupying open habitats are more social than cryptic, nocturnal, selectively browsing fruit and fungus feeders [25]. However, to our knowledge no phylogenetically comparative study about the evolution of marsupial social organization was ever done.

We established a marsupial social organization database based on primary literature reporting field data, taking the occurrence of IVSO into account for the first time. Our first objective was to infer the ancestral form of marsupial social organization and whether species living in multiple habitats are likely to show a high degree of IVSO. Our second objective was to test the prediction that sociality is favoured in harsh environments, predicting more social species living in environments with high ambient temperature and low rainfall (arid and semi-arid environments) and high variation in both. For Australian rodents, it was previously found that sociality evolved in response to harsh environment of low rainfall and high-temperature variability [15]. Our study represents an independent test of this hypotheses, by focussing on other mammalian taxa living in the same environment, using the same climate data source. Therefore, while objective 1 considered all marsupials, for objective 2 we focused on Australian marsupials only.

2. Material and methods

(a) Ancestral state of social organization of all marsupials

Our aim was to create a database based exclusively on published primary data, without the consideration of interpretations or generalizations of the authors, and in doing so contribute to improving the quality of future comparative studies. We only considered primary literature that reported actual field data on social organization in their methods or results section. This was important for the main aim of our study which is to consider IVSO and not only the most common form of social organization believed to occur in one species. Reviews making generalizations were not considered.

We searched for publications about social organization of marsupials on Web of Science and Google Scholar from June 2020 until April 2021. Our search included all 345 marsupial species categorized by the IUCN (International Union for Conservation of Nature) database in 2021 (https://www.iucnredlist.org/). Each species was searched by its scientific name (genus and species) and the keyword 'social' (e.g. *Acrobates pygmaeus* AND social). If no results were found, a second search was conducted using only the scientific name (genus and species). For each study, title and abstract were read to determine whether the study was based on a wild population and if it might contain data about social organization. By reading the article titles from the search results we marked 697 articles and downloaded 456 of them after reading the abstract. For 105 articles (mainly old articles from local journals), we were not able to obtain a PDF or copy; thus, we could not check them for suitability nor add them to our database [26].

To address our main interest of identifying primary data on IVSO (deviation from the main form of social organization), methods, results, figures and tables of all 456 articles were checked. Further, the full text was searched for the following keywords: 'social', 'solitary', 'pair' and 'group'. Two hundred fifty-three articles did not contain useable data on social organization. Based on our criteria, 83 articles could not be included in the analyses [26], as the authors only stated the main form of social organization, but did not present the data on the composition of social units, the sex of individuals, occupancy of sleeping sites, home range overlap or the proportion of the individuals marked and studied in the study area [27]. In other words, these studies were excluded because either IVSO was ignored as a possibility, or if the existence of IVSO was reported, it was impossible to determine the degree of it. Electronic supplementary material section S8 presents an alternative analysis focussing only on the main form of social organization ignoring IVSO, including these studies excluded from our main analysis. As would be predicted, this model overemphasizes the probability of solitary living being ancestral.

We found data on social organization that matched our inclusion criteria in 120 of all articles. The data in these articles were recorded at the population level ($n = 149$ populations) and covered 65 species [26]. The phylogenetic distribution of those species [26] shows that while there is very limited knowledge for the Ameridelphia, the available data for the Australidelphia are relatively evenly distributed among families. We also compared our database with two previously published databases (electronic supplementary material, section S4).

We were able to classify the social organization of each social unit reported in the 120 articles as one of six possible forms: (i) solitary; (ii) pair-living; and four forms of group-living, namely (iii) single male multiple female group, (iv) single female multiple male group, (v) sex-specific group (group of only males or only females) and (vi) multi-male multi-female group. For analyses, we used the category 'stable group' if all social units showed the same category of group-living, while if more than one category occurred, this was categorized as IVSO (see details below). Social organization was only based on the number of adults present and we did not consider pups and juveniles (Joeys). Solitary individuals were recorded separately by sex; a social unit was recorded as solitary only when both sexes were solitary. Many species show sex-specific dispersal. Thus, when solitary living was only reported for individuals of one sex, this was not considered as evidence for a solitary social organization, since the data might represent dispersing individuals. As most species have dispersing individuals that are solitary for a short time, including this transitional phase as a separate social organization would basically mean that all species show IVSO, in which case it would not make sense to study why and when it occurs. Instead, apart from studies on IVSO, separate studies on the proximate causes and ultimate function of dispersal are needed. To facilitate comparison to pairs (one male and one female), the number of solitary social units was determined by the sex with the smaller number of solitary individuals (e.g. when 10 solitary males and 5 solitary females were observed, we recorded five solitary social units). The same method was applied for sex-specific groups.

IVSO was recorded when more than one form of social organization was observed in the same population. Populations where 2 or more forms of group-living but no other forms of social organization occurred were categorized as 'variable group'. Otherwise, to reduce the numbers of IVSO categories for the statistical analysis, we combined the four forms of group-living as 'group' when the population had both group-living and non-group-living social units. Therefore, IVSO consisted of five categories: (i) solitary + pair (SP), (ii) solitary + group (SG), (iii) pair + group (PG), (iv) solitary + pair + group (SPG) and (v) variable group (VG). Together with the three non-IVSO categories: solitary (S), pair (P) and stable group (G, only one forms of group-living reported), we have eight combinations of social organization, but as SG did not occur in any population, this was effectively reduced to seven. If males and females live separately in two different forms of social organization (for example, group-living females and solitary males), this population was classified as having a sex-specific social organization and not IVSO, since there was no variation within either sex. Fission–fusion groups characterized by temporal variation in group size and composition [28] are common in some kangaroo species [29]. All observed variation in social organization in a fission–fusion population was recorded. Environmental disruption events, such as the accidental death of a group member, represent external incidents that can change the social organization of the social unit. Three cases of social organization change due to environmental disruptor were not considered for further analysis because they do not represent a change in social organization in response to ancestrally relevant conditions [26].

To better estimate the ancestral state and the possible ecological factors that may have an influence on the evolution of social organization, we obtained body mass from the *Handbook of the Mammals of the World* [30] and centred it to the body mass of Australia's oldest known marsupial fossil [31]. By comparing the M2 mesiodistal length, we estimated the body mass of the 30 Myr old ancestral species *Djarthia murgonensis* would be similar to *Antechinus stuartii* as 37.75 g, which is smaller than most of the modern species in our database and much smaller than the mean (4871 g). The number of studies per population was recorded to control for research effort. We determined the habitat type(s) in which the study took place, categorized and recorded based on IUCN classification (www.iucn.org) as desert, forest, rocky areas, savannah, grassland, shrubland, wetlands or artificial. Habitat heterogeneity was then determined as the maximum number of habitats occupied per population.

(b) Ancestral state of social organization and climate in Australian marsupials

To test how climate would affect social organization, we focused on Australian marsupial species to control for other environmental variable that differ between Australia and South America, such as competition with placentals that mainly occurs in South America but not Australia (apart from small rodents and bats). We obtained long-term climate data from the online dataset of Australian Bureau of Meteorology (http://www.bom.gov.au/climate). For each studied population, we obtained local climate data at the GPS coordinates reported in the articles. Climate data were obtained for 51 Australian marsupial species.

High-resolution (0.05 × 0.05 degree) grids downloaded from climate dataset were converted to raster grids in QGIS 3.10. Based on the monthly precipitation and monthly mean maximum temperature data from 1910 to 2019, we calculated six variables to represent climate conditions: annual mean precipitation (mm), annual mean maximum temperature (°C) and coefficient of variation to represent within-year variation (seasonality) and between-year variation (predictability) for both precipitation and temperature (for details see electronic supplementary material, section S1). Six maps were generated in QGIS, one for each climate variable. For populations with precise GPS locations, data were directly obtained from the climate maps. When the location was not specified in the paper (one population of *Distoechurus pennatus* in the state of Victoria), we ran 'zonal statistics' analysis to obtain mean value of the area.

(c) Statistical analysis

Phylogenetic comparative analyses were conducted by R v.3.6.1, using the R packages brms [32,33], RStan [34] and Rethinking [35]. All R codes and data are available at our online dataset [26].

Climate data are often correlated with each other. Thus, we first performed a principal component analysis to reduce the six climate variables (see above) to a smaller number of components. The first two principal components (PC1 and PC2) explained 82% of the variation (electronic supplementary material, table S2). PC 1 was positively related with annual temperature (eigenvector = 0.506) and within-year variation of precipitation (eigenvector = 0.449), and negatively related with within-year variation of temperature (eigenvector = −0.497) and between-year variation of temperature (eigenvector = −0.494; electronic supplementary material, table S2). High PC1 values match the tropical rainforest climate in Australia. PC2 was positively related with annual precipitation (eigenvector = 0.693) and negatively with between-year variation of precipitation (eigenvector = −0.639; electronic supplementary material, table S2). Low PC2 values match the desert climate in central Australia.

We used Bayesian generalized linear mixed-effects models (GLMMs) to control for phylogeny and estimate the associations between social organization and predictor variables [36]. The probability of each kind of social organization was modelled using a categorical likelihood, allowing gradual changes in the probability of each kind of social organization along the phylogeny; the intercept of such a model represents the phylogenetically controlled mean of extant species, and, in the absence of any directional trends, the ancestral state [36,37]. This approach corresponds to a polygenic model of trait inheritance, as opposed to alternative approaches to inferring ancestral states of categorical traits based on nucleotide substitution models [38,39]; in substitution models evolutionary change is not gradual but occurs in 'jumps' between states, which has been deemed less plausible than polygenic inheritance [36,40] (and in our opinion rightly so). Furthermore, these models often have many more free parameters, require treating the species rather than the population as the unit of observation (thus failing to account for intra-specific variation) and cannot include covariates when inferring ancestral states. We therefore prefer the quantitative genetic approach implemented by our GLMMs. This does not mean that social organization is directly genetically inherited, but simply that whatever individual-level traits contribute to social organization follow a polygenic rather than single-gene pattern of inheritance (which is widely accepted to be the case for social and behavioural traits; see e.g. [41]).

The phylogenetic history and its uncertainty were represented by a sample of 100 phylogenetic trees, downloaded from VertLife (http://vertlife.org/phylosubsets/) [42]. We created two models, the first one was to estimate the ancestral state of modern marsupials, therefore included data from all studied marsupial species: social organization (with seven categories)~species intercept + covariance for phylogeny + habitat heterogeneity + number of studies + body mass. The second model was aimed to estimate ecological (climate and habitat) effects on Australian marsupial's social organization: social organization~species intercept + covariance for phylogeny + habitat heterogeneity + number of studies + body mass + climate PC 1 + climate PC 2. Due to the limitations of climate data, this model only considered Australian marsupials. Both models were run at the population level, and included phylogeny and species as random factors (as indicated above). The number of studies per population was considered as a predictor of the occurrence of IVSO. Phylogenetic signal (λ) was calculated as the proportion of variance captured by the phylogenetic random effect [43], representing the tendency of related species to resemble each other more than species drawn at random from the same tree [44]. For analysis, the social organization of populations showing only one form of group-living was categorized as stable group. For more details on model structure, see the PDF 'Model details' on our online dataset [26].

3. Results

(a) Ancestral state of social organization of all marsupials

Out of the 65 marsupial species with data, three species were excluded from this model for lack of life-history and/or habitat heterogeneity information. Only one population of *Macropus giganteus* (the species with most data available) shows IVSO of solitary + group, and it was excluded from the analysis for lack of habitat information. In the remaining 62 species, 30.6% (19 species) were strictly solitary, 14.5% (9 species) only live in pairs, and 11.3% (7 species) were stable group-living (e.g. always MMFF [26]), 43.5% (27 species) showed IVSO, with 23 species showing two or more forms of solitary/pair-living/group-living, four species with two or more different forms of group-living (electronic supplementary material S3).

Social organization was weakly influenced by phylogenetic history ($\lambda = 0.18$, 95% CI = 0.06 – 0.31). The most probable ancestral state was solitary living (mean probability = 0.35, 95% CI = 0 – 0.88) and IVSO (SP + PG + SPG + VG; mean = 0.35), with the IVSO form of pair-living + group-living (PG) having the second highest probability (mean = 0.26, 95% CI = 0 – 0.97). The following were pair-living (mean = 0.22, 95% CI = 0 – 0.90) and group-living (mean = 0.09, 95% CI = 0 – 0.53) (figure 1; electronic supplementary material S5, table S5.1). There was no significant effect of habitat heterogeneity nor number of studies per population on social organization (electronic supplementary material, table S5.2). In addition, when the analysis was done at the species level with only the main form of social organization and no IVSO, the probability of solitary ancestor increased (mean = 0.61, 95% CI 0–1.00) (electronic supplementary material, section S7).

(b) Ancestral state of social organization and climate in Australian marsupials

For the 51 Australian marsupials, the phylogenetic signal was 0.20 (95% CI = 0.07 – 0.34). The most probable ancestral state was the IVSO form of pair-living + group-living (PG) but with high uncertainty (mean = 0.26, 95% CI = 0 – 0.97), followed by group-living (mean = 0.21, 95% CI = 0 – 0.95), solitary living (mean = 0.20, 95% CI = 0–0.79) and pair-living (mean = 0.18, 95% CI = 00.96) (figure 2; electronic supplementary material, table S6.1). All forms of IVSO combined (SP + PG + SPG + VG) had a mean probability of 0.41.

There was no significant effect of habitat heterogeneity nor number of studies per populations on social organization (electronic supplementary material, table S6.2). Climate had a significant effect on social organization (electronic supplementary material, table S6.2). PC1 showed a negative relation with the occurrence of stable group-living (mean = −0.64, 95% CI = −1.38 – 0), which indicates that species living in groups with stable composition are less common in Australian tropical rainforest. PC2 had a negative relation with the occurrence of IVSO characterised by a combination of solitary, pair and group-living (mean = −1.42, 95% CI = −2.51−−0.31), indicating such populations are more common in desert areas in Australia.

4. Discussion

Our literature review shows that marsupials are more social than previously believed. Only 31% of the 65 studied species were strictly solitary, with the remaining species living either sometimes (22%) or always (48%) in pairs or groups. Still, solitary living was the most likely ancestral state, but with high uncertainty. However, for Australian marsupials alone, solitary living was not the most likely ancestral state, and it is possible that solitary living in the South American marsupials is not an ancestral trait but an adaptation to living under competition with placentals. This means, for phylogenetic comparative studies on mammalian social evolution, one cannot assume with certainty that so far unstudied marsupials are solitary, nor that the common ancestor of modern marsupials was solitary. The result also shows that marsupials may have the ability to live in different forms of social organization, especially the mixture of pair and group-living. As was previously reported for Australian rodents [15], we found an effect of climate on sociality, indicating fewer group-living species in tropical rainforests and that species occupying harsh and unpredictable habitat like deserts are more likely to show a flexible form of social organization. Thus, our study indicates that marsupial social

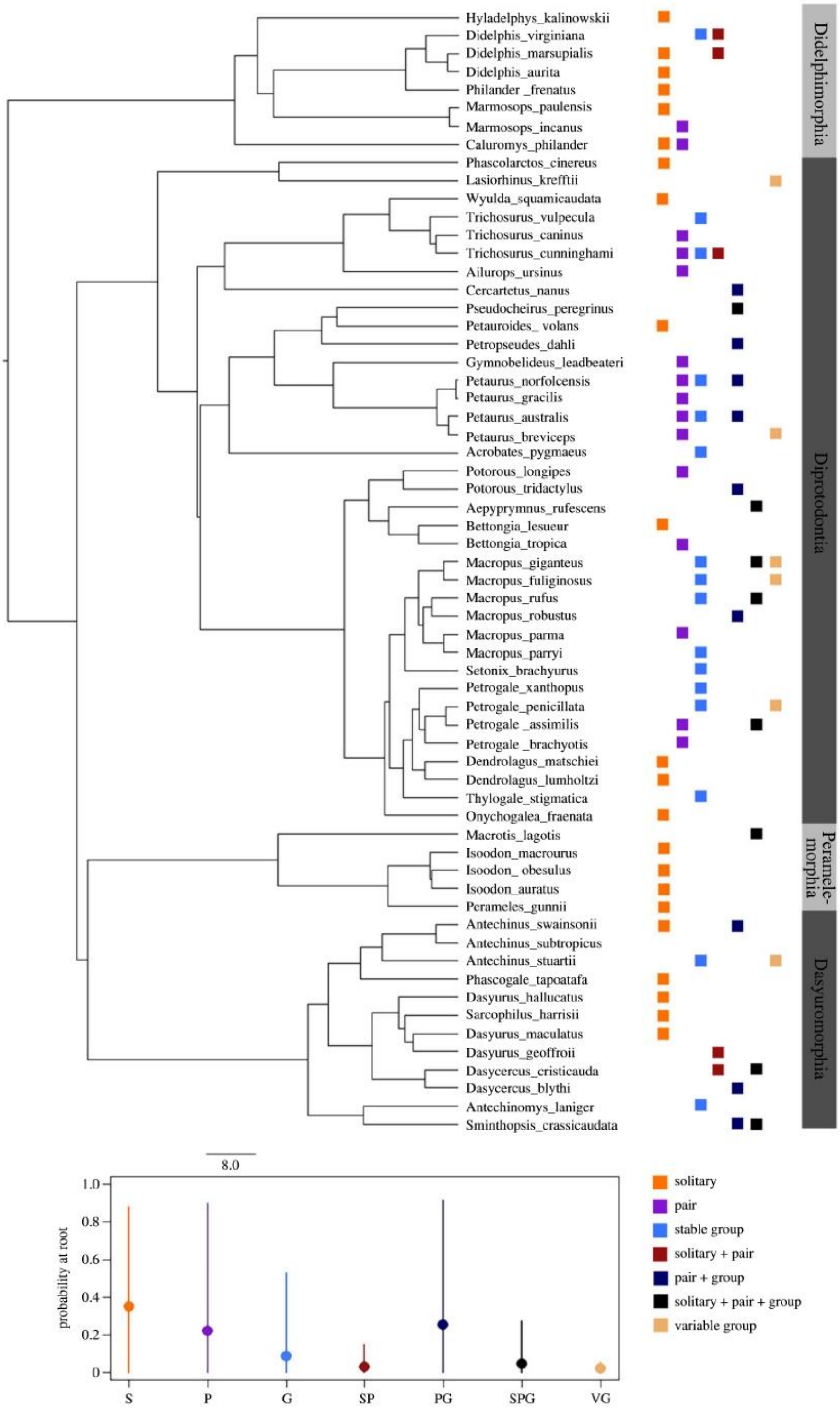

Figure 1. Phylogeny of 62 marsupial species with available data and the probability of each kind of social organization at the root of the phylogeny (i.e. the last common ancestor of all marsupials). The different forms of social organization recorded for each species at the population level are shown on the right, using the colour indicated in the legend. (Online version in colour.)

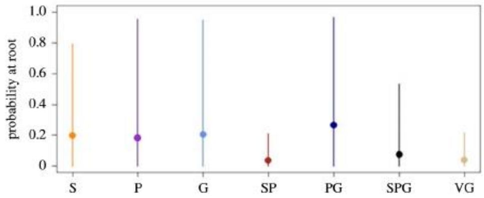

Figure 2. The probability of different kinds of social organization for the last common ancestor of Australian marsupials. S: solitary, P: pair, G: stable group, SP: solitary + pair, PG: pair + group, VG: variable group. (Online version in colour.)

organization is not at primitive solitary default stage but represents complex and variable adaptations to climate.

While Russell in 1984 regarded marsupials as being pre-dominantly solitary living, he also pointed out that the variability in social organization within species has been overlooked and that field data for most species were lacking [21]. With more observations on marsupial social organization having been published in recent decades, we found that most studied species can form social units of two or more individuals. Important to note is that nearly every other species showed variation in social organization, which often included solitary living. Our study indicates that previous assumptions about marsupial social organization have been outdated by the addition of more field studies. This new understanding must be considered when conducting comparative studies on mammalian social organization.

To our knowledge, we did the first statistical model to estimate the ancestral social organization of marsupials, which so far were assumed to have evolved from a solitary ancestor [21]. While solitary living had the highest probability, this was associated with a very wide confidence interval, and only a minority of species (31%) was strictly solitary living. In other words, the ancestral state cannot be accurately estimated with the current information we have and leaves the possibility that the ancestor was more sociable than previously believed. This is also supported by fossils found in Bolivia indicating a gregarious lifestyle for marsupials 60 Ma [45]. In sum, our study does not support nor reject the assumption that the ancestor of all marsupials was solitary living; a more sociable ancestral state was virtually just as likely.

Ecological factors can shape sociality in macropods: large, diurnal generalist grass-feeding species living in open habitat are more social than cryptic, nocturnal, selectively browsing fruit and fungus feeders [25]. In our study, we did not find support for the prediction that habitat heterogeneity is associated with social organization. Like in artiodactyls [10], more habitats occupied per species/population didn't increase the occurrence of IVSO, suggesting that IVSO did not evolve as an adaptation to habitat heterogeneity in the two taxa. The number of papers published per species/population also had no effect, i.e. IVSO was not more commonly reported for better studied populations. However, climate had a significant effect. Harsh environments characterized by low rainfall, high ambient temperature and high variation in these climate factors favour sociality in a variety of taxa [5,15,17]. Australia is a continent of environmental extremes and contrasts, with significant variation of precipitation and temperatures. We found group-living to be less common under the climate condition of tropical rainforest, which are home to many solitary species [46,47]. For Australian rodents, it was previously reported that sociality evolved in harsh environments [15]. Our independent study in the same environments with other mammalian taxa partly supports this result. We did not find a direct relationship between group-living and harshness, but a negative relationship between group-living and benign environments. Our criteria for determining social organization was more restricted and clearer than the definition of 'sociality' by Firman, which for example excluded territorial species from social species [15]. In sum, our study which strictly focussed on the composition of social units as a measure of social organization adds to previous studies showing that climate is related to sociality.

Instead of only considering the main social organization at the species level, we took variation within and between populations into account. We found IVSO to be more common in climates with low and highly unpredictable precipitation (variation between-years), which in Australia is characteristic of central deserts. Here, populations that have (and thus probably can switch between) multiple forms of social organization among solitary, pair and group-living were more common than in other climate situations. IVSO might offer a buffer against environmental unpredictability. Many kangaroos are a prime example for this, as depending on food availability, a function of previous rainfall and bush fires, they can forage solitarily, in small or large groups [48]. While for Australian rodents [15], mammals in general [5] and birds [8], it was found that sociality evolved under harsh climatic conditions, our study indicates that having a flexible social organization might also be an adaptation to harshness.

Evolutionary change needs variation in traits. This is why intra-specific variation is important for understanding social evolution. Unfortunately, many papers we found failed to present their field data in a way that they could be included into our database [27]. Often no data but only a general statement about the assumed main form of social organization was reported, especially in mainly solitary species such as the Tasmanian devil or the koala. Ignoring such studies might lead to an underestimation of solitary living, but including such studies might lead to an underestimation of IVSO. For example, koalas are generally believed to be solitary living, but possible deviation (pairs) has been reported, unfortunately in a way that it could not be incorporated in our database, as it was not clear how many pairs were observed and whether these were stable or not [49]. An alternative analysis, which included studies only reporting the main form of social organization found, as one would predict, stronger support for solitary living as the ancestral state (electronic supplementary material, section S8) than our model considering IVSO. We believe that overgeneralizations, like assuming that most species of a taxon are solitary living, can lead to conclusions that are in contrast with the existing data [11] which might then bias comparative studies [50]. In sum, we need more field studies [50] that report data in a way they can be used in comparative analyses [27].

5. Conclusion

Our study estimated the ancestral social organization of marsupials using Bayesian phylogenetic mixed-effect models based on a new and accurate database accounting for variation within and between populations. Our analysis demonstrates that the previous assumption of a solitary marsupial ancestor has low confidence, and many modern species are found to be more sociable than was believed. In summary, the ancestral form of social organization of marsupials and as such of all mammals demands further investigation, for which more field data from more species are needed. While previous studies found arid environments with low and unpredictable rainfall to be positively correlated with the care system in birds [17] and mammals [5], our study suggests that when studying the influence of variable and unpredictable climate on sociality, one should also consider variation in sociality.

Data accessibility. The data are provided in electronic supplementary material [51]. R code and dataset are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.jwstqjqd8 [26].

Authors' contributions. J.Q.: data curation, formal analysis, investigation, methodology, software, validation, visualization and writing—original draft; C.A.O.: formal analysis, methodology, software, validation and writing—review and editing; A.V.J.: methodology, validation and writing—review and editing; C.S.: conceptualization, investigation, methodology, project administration, resources, supervision, validation and writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare that we have no competing interests.

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Appendix D

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ETHOLOGICAL METHODS

Field studies need to report essential information on social organisation – independent of the study focus

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Abstract

Comparative studies on social evolution are ideally based on large datasets to ensure high statistical power, but their scientific validity also relies on the quality of the data. However, even though social organisation, that is the composition of social units, is measured in many field studies testing specific hypotheses, these data are often not adequately reported. Here, we summarise which data on social organisation should always be reported regardless of the study focus to make them available for comparative studies. As an example, we report data from a literature survey on one of the four superorders of placental mammals, the Xenarthra from South America (armadillos, anteaters and sloths), of which all 30 species are generally assumed to be solitary living. In total, we found 4510 articles. The titles and abstracts of 61 publications indicated that data on social organisation were collected, but only 12 publications contained sufficient information for us to determine the social organisation. We found reliable information on nine species, of which seven were strictly solitary. Two species showed a combination of solitary-living and pair-living with one including female groups. This review therefore indicates that Xenarthra may not be exclusively solitary. Our literature survey further shows that valuable data are often not reported even though it can be assumed that these data had been collected. We report examples from 23 additional studies on monotremes, marsupials and two other placental superorders showing similar issues in reporting data. It is important to make authors aware that this information would be valuable for comparative studies. In sum, we recommend including data on the composition of social units, sex of individuals, occupancy of sleeping sites, frequency of observations and trapping events, home range overlap and the proportion of the individuals in the study area, independent of the study question in all publications.

KEYWORDS
comparative study, field data, intra-specific variation, social organisation, social structure, social system

1 | INTRODUCTION

Comparative studies yield significant insight into the evolution of social systems (Chak et al., 2017; Cornwallis et al., 2017; Firman et al., 2020; Griesser et al., 2017; Lukas & Clutton-Brock, 2013). The quality of such comparisons has increased over the last decades due to significant improvements in statistical methods that correct for phylogeny and enable us to include ecological and life-history factors (Garamszegi, 2014). However, the quality of comparative studies also depends on the quality of the used database (Schradin, 2017). Many researchers focused on getting a large, instead of an accurate, database, for example by using phylogenetic inferences to add species that had not been studied (birds: Cockburn, 2006; used also by Gonzalez et al., 2013; Jetz & Rubenstein, 2011; mammals: Lukas & Clutton-Brock, 2013). There are now statistically sound methods to infer missing phylogenetic data points (for example see Callaghan et al. (2021)). This can be important to include species into the database for which information on the social system is missing, but for which important life-history and ecological data are available. However, such inference should only be done if the social data are missing from just a few but not the majority of species (Schradin, 2017). Furthermore, information assuming the social system from anecdotal observations or expert opinion published in secondary and tertiary sources has often been included for species that have never been studied in the field (Schradin, 2017). This has been criticised and a more careful approach has been recommended (Griesser & Suzuki, 2016; Huck et al., 2020), that is to only use data from studies where animals have been studied in their natural environment (Schradin, 2017). However, while the number of field studies has increased over the last decades (Schradin & Hayes, 2017), basic data on social systems are often not reported in a way that makes them useable for comparative studies.

In the field of Behavioural Ecology, the focus on field studies is on theory-driven research and not on describing the social system of species (Clutton-Brock & Janson, 2012). Social organisation, which means the sex and the composition of social units, is one of the four key components of social systems (Kappeler & van Schaik, 2002). Social organisation is easier to observe and to record than the three other components of the social system (Schradin et al., 2018), which are the mating system (who reproduces with whom), the social structure (social interactions; social networks) and the parental care system (who takes care of the offspring) (Kappeler, 2019). While field researchers often record the composition of study groups, details of such basic data are often not reported in the arising publications that test specific hypotheses.

The conclusions from hypothesis-driven research are important to test and develop theory; however; conclusions can change and the main values of each study are the data that were recorded. It is as important to include these data and the conclusions drawn from them. The availability of published data has been recognised as being of crucial importance (Ramachandran et al., 2021; Reichman et al., 2011). For comparative studies and for meta-analyses, data are more valuable than interpretations. This is demonstrated by the example of intra-specific variation in social systems (Lott, 1984; Schradin et al., 2018). For example, if a study population is reported to be pair-living because most animals live in pairs but some individuals also live solitarily or in groups, then biologically meaningful variation might be missed. We have been building a database on mammalian social evolution since 2015 (Agnani et al., 2018; Valomy et al., 2015). For this, we have searched more than ten thousand peer-reviewed articles for information about the composition of social units, focusing on data reported in the methods and results sections. We noticed that many field studies that presumably collected such data did not report them, but instead assigned a general form of social organisation to the study population in the introduction and/or discussion.

The aim of this paper was to identify which data are often missing from publications even though they probably had been collected and could have been used to accurately assign social organisation, including its variation. For this, we surveyed the literature on one mammalian superorder as an example, the Xenarthra (armadillos, sloths and ant-eaters), and added more examples from other mammalian taxa. We chose this superorder as it is small, containing only 30 species. Our aims were to (1) provide an overview of what is known regarding the social organisation of Xenarthra, (2) identify which information is missing in published field studies on Xenarthra to correctly characterise their social organisation, (3) report additional examples from other mammalian taxa and finally (4) provide a template for field researchers on which data to provide in every published paper so that they are available for comparative studies of social evolution.

2 | METHODS

2.1 | Xenarthra social organisation

Xenarthra (armadillos, sloths and anteaters) is one of four superorders within the placentals; with the other three being Afrotheria (elephants, sea cows and elephant-shrews), Euarchontaglires (primates and rodents) and Laurasiatheria (bats, carnivores and ungulates) (Wildman et al., 2007). Xenarthra mainly occur in South America, with one species ranging to North America. They consist of 30 species of which 20 belong to the order Cingulata (armadillos) and 10 to the order Pilosa (six species of sloths and four species of anteaters). Xenarthra are typically considered to be solitary living (Lukas and Clutton-Brock (2013) categorised all 24 Xenarthrans in their database as solitary living), though it has been acknowledged that small groups might occur (Nowak & Wilson, 1999; Wilson & Mittermeier, 2018). Determining the social organisation of species in this superorder is important for comparative studies regarding mammalian social evolution.

2.2 | Data collection and literature review Xenarthra

Literature research was done from July 27, 2020 until June 30, 2021. During this period, a species list of the extant members of the superorder Xenarthra was compiled using the IUCN Red List of Threatened Species (www.iucnredlist.org). Using this list, a search was conducted on the primary literature on social organisation in Web of Science and Google Scholar. The search string used to assemble this information consisted initially of the term social in conjunction with the species scientific name or common name. For example, the search string used for the Northern long-nosed armadillo *Dasypus sabanicola* was ("*Dasypus sabanicola*" OR "Northern long-nosed armadillo" AND "*social*"). If no records were found with the initial search string, then a second search string was used that consisted only of the scientific species name (e.g. "*Dasypus sabanicola*"). If the second search string still yielded no results, then the final search string used was just the genus name and the term social (e.g. "*Dasypus*" AND social). Within the search results from Web of Science, the following research areas were selected to refine the results—"*zoology,*" "*behavioural science*" and "*environmental science/ecology*"—and the document type—"*article.*" All publication titles that were not applicable to the topic were removed from the generated database. From the remaining articles, the abstracts were read and reviews not reporting primary data or studies done on captive animals were excluded from the database. The PDFs of the remaining publications were then obtained and searched for the following terms related to social organisation: "*social,*" "*group,*" "*territorial,*" "*solitary,*" "*bachelor,*" "*plural,*" "*aggregation,*" *gregarious,*" "pair" and "*singular.*" The figures, tables and supplementary materials were also checked for information that may not have been recorded in the main text. The same process was applied in Google scholar to search for additional articles.

The social organisation described in the primary literature for each of the species was recorded according to the following categories (for details see (Agnani et al., 2018; Valomy et al., 2015)): "*solitary,*" "*pair,*" "*one male multiple females,*" "*one female multiple males,*" "*multiple males* and *multiple females.*"

2.3 | Data from other mammalian taxa

We are in the process of building a database on mammalian social organisation reported from field studies using the same methods as described above. In addition to the detailed case study on Xenarthra, we also reported examples from several other mammalian taxa, but without the claim to cover all species in these taxa.

2.4 | Data analysis

The following variables were calculated from the information provided from the literature. The total number of social units observed per population and per species was summed up. Then the main social organisation was determined by the most commonly observed social organisation. Following this, the percentage of main social organisation was calculated by dividing the number of social units of the main social organisation by the total number of social units multiplied by 100. Finally, intra-specific variation in social organisation (IVSO) was determined as within population when variation occurred only within a population, among populations when variation occurred among populations only, both if variation occurred within and among populations and none if there was no variation reported.

3 | RESULTS

3.1 | Xenarthra

We found 4510 articles (1801 for Pilosa and 2709 for Cingulata). The titles from 61 articles (30 for Pilosa and 31 for Cingulata) indicated that information on social organisation was collected. These articles were searched in detail for information. Twelve publications provided information on social organisation for 15 populations of nine of the 30 Xenarthran species. From these nine species, the following seven species were reported to be exclusively solitary: southern naked-tailed armadillo, *Cabassous unicinctus* (Desbiez et al., 2018), giant armadillo, *Priodontes maximus* (Desbiez et al., 2019), nine-banded armadillo, *Dasypus novemcinctus*, (McDonough, 2000), maned three-toed sloth, *Bradypus torquatus* (Falconi et al., 2015), Hoffmann's two-toed sloth, *Choloepus hoffmanni* (Vaughan et al., 2007), southern tamandua, *Tamandua tetradactyla* (Rodrigues et al., 2001) and giant anteater, *Myrmecophaga tridactyla* (Di Blanco et al., 2017; Medri & Mourão, 2005; Shaw et al., 1987). Two Pilosa species showed intra-specific variation in social organisation. In the pale-throated three-toed sloth, *Bradypus tridactylus* (Taube et al., 1999), solitary living (of both sexes), pair-living and multi-female groups were reported. In the brown-throated sloth, *Bradypus variegatus*, solitary living (of both sexes) and pair-living was reported (Garcés-Restrepo et al., 2017; Pauli & Perry, 2012).

While the title and abstract of 61 publications indicated that data on social organisation was collected, only 12 publications contained useable information. Most of the 49 remaining studies focussed on population dynamics ($N = 14$), habitat use ($N = 12$), or other ecological aspects such as conservation, spatial ecology or monitoring via camera traps (see ESM 1). Most studies could not be used to correctly determine social organisation because they either did not report the sex of individuals or state the composition of the social units they observed (for example they observed/trapped/tracked individuals but did not present data whether they were solitary or not; Table 1). Studies using radio-tracking often failed to report whether or not individuals shared home ranges and sleeping sites (Table 1). One study had information we could use for our database for one species (*Bradypus tridactylus*) and missing information for the other species (*Choloepus didactylus*) (Taube et al., 1999).

3.2 | Other mammalian taxa

Examples from other mammalian taxa show that the same information to determine social organisation is often missing, just as for Xenarthra (Table 1; ESM 2). For example, in Perissodactyla, groups have been observed in onagers (*Equus hemionus*) and kiangs (*E. kiang*) without the sex of the individuals being reported (ESM 2), which would be essential to determine the sex composition of the social units, that is whether it is one male with several females, multi-male multi-female groups or all male and all female groups. The same problem occurred in several species of kangaroos (ESM 2). In

TABLE 1 Reasons why field studies could not be used to determine the social organisation of the study population

Missing information to determine social organisation	Total number of field studies on Xenarthra (ESM1)	Examples from other mammalian taxa (ESM2)
Composition of social units not stated.	29	Carnivora: 1 Chiroptera: 2 Marsupialia: 1 Monotremes: 3
Sex of individuals not stated.	24	Perissodactyla: 6 Carnivora: 2 Chiroptera: 2 Rodents: 2 Marsupialia: 4 Monotremes: 1
Occupancy of sleeping sites.	6	Monotremes: 1
Home range overlap not stated.	3	Monotremes: 1
Frequency of trapping events not stated.	2	Monotremes: 1
Not stated what proportion of the population was studied.	1	

Note: For Xenarthra, data from a detailed literature survey trying to identify all published field studies are reported. Additional examples from other mammalian taxa are also reported.

platypus (*Ornithorhynchus anatinus*), which are typically regarded to be solitary living (Wilson & Mittermeier, 2015), den sharing has been reported repeatedly, but not whether the same individuals permanently share one den and home range, or whether such associations were short-lived, representing random aggregations at preferred resting sites (ESM 2).

4 | DISCUSSION

It is mandatory to have access to reliable field data of animal social systems if one wants to do comparative studies on social evolution (Schradin, 2017). Conducting field studies is costly in time and funding (Clutton-Brock & Sheldon, 2010; Schradin & Hayes, 2017). It is, therefore, both surprising and frustrating when such valuable data are collected but not reported. Here, we report in detail for one superorder of placentals, the Xenarthra, that most conducted field studies do not report data essential to accurately determine social organisation. We further add examples from other mammalian taxa indicating similar problems. Data on social organisation are valuable and difficult to collect; therefore, we give advice on how to report such data in the future, independent of the study focus.

So far, Xenarthrans, which represents sloths, anteaters and armadillos, have been believed to live solitarily (Wilson & Mittermeier, 2018). This might be the reason why most field studies on Xenarthrans did not report the composition of social units: possibly the authors were assuming that it is clear that they are solitary. However, in our literature survey we found some indication that some species of Xenarthrans show intra-specific variation in social organisation, including pair-living and female groups. The Xenarthra represent one of four mammalian superorders, such that the social organisation of these species might have a significant impact on comparative studies regarding mammalian social evolution. From our point of view, while solitary living is the most common form of social organisation in Xenarthra, ignoring other possible forms of social organisation in this taxon could lead to mistakes in comparative studies of mammals. To prevent such mistakes from occurring, field data from long-term monitoring of natural populations are essential; however, these data are often missing.

In another database, all Xenarthra were classified as solitary living (Lukas & Clutton-Brock, 2013). It is important to note that there is agreement that comparative studies need clear definitions (Lukas & Clutton-Brock, 2017; Schradin, 2017). For example, Lukas and Clutton-Brock (2013) had a more stringent definition to classify species as pair-living than we had: pairs had to be together for more than one breeding season (Lukas & Clutton-Brock, 2013). Whereas we recorded pairs in pale-throated three-toed sloths (*Bradypus tridactylus*; Taube et al. (1999)) even though it was unknown for which time they stayed together. In contrast, using radio-tracking in brown-throated sloths (*Bradypus variegatus*), the authors indicate mate fidelity of one female remaining in the home range of one male for 3 years (Fig 3a in Garcés-Restrepo et al. (2017)), and the female mated only with this male, such that it can be regarded as a pair (Garcés-Restrepo et al., 2017). We did not consider observed pairs in nine-banded armadillos (*Dasypus novemcinctus*) as indication for pair-living, because pairs were only present during courtship and mating, indicating a solitary form of social organisation (McDonough, 2000). The secondary literature also reports some degree of sociality for some Xenarthra, for example female groups in Hoffmann's two-toed sloth (*Choloepus hoffmanni*; Nowak and Wilson (1999)), groups in pale-throated three-toed sloths (*Bradypus tridactylus*, Wilson and Mittermeier (2018)) and groups of adult offspring staying together in nine-banded armadillos (*Dasypus novemcinctus*, Nowak and Wilson (1999)). In sum, some data from the primary literature (Garcés-Restrepo et al., 2017; McDonough, 2000; Taube et al., 1999) and reports from secondary literature (Nowak & Wilson, 1999; Wilson & Mittermeier, 2018) indicate that Xenarthra might be less asocial than generally assumed. Whether to score these species as solitary, variable in their social organisation or excluding them due to uncertainties from further comparative analysis will have to depend on the specific study objective.

A similar problem as in Xenarthra exists for monotremes, which are all generally believed to be solitary living (Wilson & Mittermeier, 2015). However, numerous reports of den sharing in the platypus (*Ornithorhynchus anatinus*), covering decades of studies (Grant et al., 1992; Serena 1994; Serena et al., 1998 and older reports cited within), indicate that this general assumption might not cover the full range of social organisation occurring in this species.

In Xenarthra and monotremes, the general assumption that they live solitarily might explain why researchers are reluctant to report data on social organisation. In group-living species, we found that the correct group composition could often not be determined as no information about the sexes was given such as in Perissodactyla, Carnivora, Rodentia and Marsupialia. However, whether the social organisation consists of one male with multiple females or multiple males and multiple females, has significant influences on other aspects of the social system, for example the mating system and the social structure (Kappeler, 2019). In sum, we found throughout the mammalian taxa examples of field studies that likely collected data on social organisation without reporting it. This can lead to the misclassification and ignorance of important variation (Schradin et al., 2018), therefore affecting the outcome of comparative studies (Schradin, 2017).

To compensate for missing data, others solved this by using phylogenetic interferences (assuming closely related species have the same social system), included data from captive studies and expert opinions, with the risk of coming to wrong conclusions (Schradin et al., 2018). Here, we argue for field researchers to report life-history data in a precise way, making it possible to accurately determine the social organisation and especially the composition of social units, one of the key components of social systems (Kappeler, 2019). Sometimes, it is impossible for researchers to give the correct information about the sex composition of social units, especially in species forming large herds (Moehlman 1998; Rudman 1998) or when individuals are not captured, sexed and individually marked. However, when such information is routinely collected, it should also be reported. In Xenarthra, this problem exists for studies published during the last 4 decades and was even dominant during the last decade (ESM 1); indicating that it is not a problem of research methodology, but of publishing culture. We argue that in future, it is important to report such data even if the study focus is on a different topic.

Kappeler (2019) defined the social organisation as the composition of social units, which was inferred by previous comparative studies from direct observations (Jaeggi et al., 2020), trapping data (Valomy et al., 2015) and from sleeping sites (Agnani et al., 2018). Table 1 states the information which every study on wild living animals should report in their methods and results section, to make information about the social organisation of the study population available for comparative studies, even when the study focus is on something else. While Table 1 lists this information in the order of missing information, in any publication it should typically be reported as: (1) proportion of individuals within the study area trapped, marked, radio-tracked and observed, (2) frequency of trapping/observation event, (3) sex of individuals studied, (4) composition of social units, (5) in studies using radio-tracking the home range overlap with all individuals should be stated and (6) which individuals shared nesting/sleeping/resting sites and how regularly. It is very important that all of this information is also reported for species which are believed to live solitarily, because as demonstrated here for Xenarthra, important deviation from this main form of social organisation might occur. Furthermore, it has been empirically demonstrated that many species that were believed to be solitary living in fact live in pairs or groups (Agnani et al., 2018; Valomy et al., 2015).

Similar considerations as for reporting data on social organisation may also apply to the three other components of the social system. For the mating system, it is now common that the number of extra-pair paternities are reported, how many offspring each male sired in a group, and the frequency of multiple paternities, which can then be used in comparative studies (Dobson et al., 2018). For the social structure, different measures of the social networks must be reported in a way that they can be used for comparative studies (see https://github.com/bansallab/asnr). For the parental care system, it is important to report not only whether maternal, paternal and alloparental care by breeders and non-breeders occurs, but also how commonly this behaviour is shown by the different group members, and how many social units show which category of parental care system (Griesser et al., 2017; Griesser & Suzuki, 2016). Therefore, our demand to accurately report data on social organisation can be extended to the other components of the social system.

5 | CONCLUSIONS

During the process of building a database on mammalian social organisation, we came across several peer-reviewed publications that indicated that they had collected data we could use for the database, but this information was not presented in a way that we could reliably determine the composition of social units. Here, we argue for field researchers to always report life-history data, making it possible to accurately determine the social organisation; especially to report the proportion of population studied, frequency of trapping/observation events, sex of individuals studied, the composition of social units and sharing of home ranges and sleeping sites. These recommendations are not only important for mammals but also for databases in other taxa, such as fish (Tanaka et al., 2018) and birds (Griesser & Suzuki, 2016).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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Appendix E

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ORIGINAL ARTICLE

Geographic intra-specific variation in social organization is driven by population density

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Abstract

Social flexibility enables individuals to switch between group and solitary living and is suggested to be an adaptation to varying environments. Several previous studies on different species compared two populations and hypothesized that observed differences in the social organization were due to differences in population density but lacked the necessary sample size to test this prediction. In a previous 8-year long-term study, we showed that one population of African striped mice (*Rhabdomys pumilio*) displayed temporal social flexibility, living solitarily in years when population density was low but in groups in years when population density was high. Building on this temporal variation, we now tested whether geographic variation reveals the same pattern. We studied 6 populations in discrete geographical locations simultaneously, predicting more solitary living in populations with lower population density. Population density correlated significantly with the percentage of striped mice living in groups whereas other (environmental) factors were not significant. Moreover, some individuals dispersed over unoccupied habitats between these populations, switching from group to solitary living. Geographic variation in population density could make social flexibility adaptive because it allows individuals to respond quickly to the prevailing conditions they experience post dispersal. Our results suggest that geographic variation drives the evolution of social flexibility in our metapopulation of striped mice, causing intra-specific variation in its social organization, which might also be important in other species, especially in species with a fast life history.

Significance statement

Populations of the same species can differ in their social organization. It has often been assumed that this is due to differences in population density. We studied 6 populations of the African striped mice, showing that more mice were solitary living when population density was low. Thus, we demonstrated that population differences in social organization were due to differences in population density.

Keywords Group living · Intra-specific variation · Social evolution · Social system · Social organization · Solitary living

Introduction

Animal species show an interesting variety of social systems, such as solitary living, group living, and even eusociality. Social systems consist of several subsystems that should be studied independently. These include social organization (the composition of groups), social structure (social interactions), mating system, and care system (who takes care of dependent offspring) (Kappeler and Schaik 2002; Kappeler et al. 2019). Most of the available data concern social organization, since group composition is easy to measure. Social organization can be solitary living, pair living, or living in groups of different compositions (Kappeler and Schaik 2002; Schradin et al.

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2018). Variation in social organization is obvious between different species.

Typically, only one form of social organization has been described for each species. However, we have long known that many species can have several forms of social organization (Lott 1984, 1991; Maher and Burger 2011; Schradin et al. 2018). While different mechanisms can theoretically lead to intra-specific variation in social organization (Schradin 2013), the most common one is social flexibility (Schradin et al. 2018). Social flexibility is a case of phenotypic plasticity, where individuals of both sexes adapt their social tactics in response to the prevailing environmental conditions, enabling them to switch between different forms of social organization (Schradin et al. 2012). For example, burying beetles (*Nicrophorus vespilloides*) can form pairs or groups consisting of one male and two females, depending on carrion size (Eggert and Müller 2000; Müller et al. 2006). In house mice (*Mus musculus*), food availability influences whether they live solitarily, in pairs, or in communal groups (Latham and Mason 2004; Berry et al. 2008). Social flexibility can be an adaptation to an environment varying in time but could also be an adaptation to other forms of variation.

In most species, social flexibility occurs due to changes in the severity of competition, for example, due to changes in population density or resource availability (reviewed by Maher and Burger 2011; Schradin 2013). Dispersing individuals that migrate into a population where environmental conditions differ from their natal population will benefit if they can adapt their social tactics to prevailing conditions. Thus, social flexibility would be adaptive for dispersing individuals if geographically isolated populations vary in ecological conditions, influencing which social tactic yields the highest fitness. While geographic variation could lead to the evolution of social flexibility, this is challenging to study, as multiple populations would have to be monitored simultaneously.

It is well known that different populations of the same species can have different forms of social organization (Lott 1991; Agnani et al. 2018; Schradin et al. 2018). Multiple studies have compared two populations of one species (reviewed in Lott 1991; Maher and Burger 2011; Strier 2017). For example, pied kingfishers (*Ceryle rudis*) can form pairs in or family groups in areas with a high abundance of high-quality nesting sites but can form in polygynous groups in areas where good nesting sites are rare (Reyer 1980, 1984). The comparison of two populations of European badgers (*Meles meles*) in Spain lead to the hypothesis that differences in population density and landscape structure might influence social organization (Molina-Vacas et al. 2009). Population density has also been hypothesized to explain intra-specific variation between two populations of the mountain brushtail possum (*Trichosurus cunninghami*) (Martin and Martin 2007) and two populations of the African striped mouse (*Rhabdomys spp.*) (Schradin 2005; Schradin and Pillay 2005). A study of four populations of kiwis (*Apteryx* spp.) differing in population density showed that all populations had pair living as social organization, although pairs were less stable in the population with the lowest density (Taborsky and Taborsky 1999). Whereas all these studies are interesting, they lack the requisite sample size to show statistically that the observed differences between two (or four) populations are due to the proposed differences in population density. An early study comparing 23 populations of langurs (*Presbytis entellus*) showed that the relationship between population density and group composition is complex and can be revealed only with a sufficiently large number of populations (Moore 1999). Thus, many previous studies comparing two populations discussed the possibility that differences in population density results in variation in social organization, but this was a prediction, not a conclusion, of these studies. To our knowledge, no study has compared a sufficient number of populations for statistical comparisons, as has been proposed by (Maher and Burger 2011).

Intra-specific variation in social organization between populations of the same species could be due to genetic differences caused by local adaptation of isolated populations, or due to social flexibility caused by individuals changing their social tactics when immigrating into a different environment (Schradin 2013). Studying whether social flexibility occurs in a geographically heterogeneous habitat could best be achieved in a small animal species that have a metapopulation consisting of populations connected by dispersing individuals (also called sub-populations or demes (van Nouhuys 2016)). Our study population of African striped mice (*Rhabdomys pumilio*) inhabits areas around seasonal riverbeds that are dry for most of the time and carry water for only a few days every couple of years after high rainfall. These populations are separated from each other by dry sandy flats, hills, and mountains, but individuals disperse over these unoccupied areas from population to population (Solmsen et al. 2011), forming one large metapopulation (van Nouhuys 2016).

Striped mice show social flexibility, allowing them to live solitarily or in groups of up to 30 adult individuals of both sexes (Schradin et al. 2010a). A correlative field study conducted for 8 years on one population showed that within this population, social organization depended on reproductive competition and population density (Schradin et al. 2010a). Outside the breeding season, when reproductive competition is absent, striped mice always formed groups independent of population density, but within the breeding season, social organization was density-dependent (Schradin et al. 2010a; Schoepf and Schradin 2012). To avoid reproductive competition in the form of female infanticide, females became solitary breeding when territories became available, but remained in communally breeding groups when population density was high (Schradin et al. 2010a; Schoepf and Schradin 2012; Hill et al. 2015). Male social tactics followed females' tactics:

more males became solitary roamers when fewer groups of communally breeding females were available to be defended; instead, they visited solitary breeding females for mating (Schradin et al. 2010a; Schradin and Lindholm 2011). Thus, temporal variation in population density explained why in this population, many striped mice lived solitarily in some years, while in other years, nearly all lived in groups. The striped mouse offers an ideal system to study whether social flexibility could also be an adaptation to geographic (spatial) variation.

Here, we tested whether geographic variation in population density is related to social organization in striped mice. Thus, we tested whether the relationship described between population density and the likelihood of group living that was previously described for 8 study years (Schradin et al. 2010a) could be replicated in a one year study of 8 populations. We predicted that more striped mice would be group living in a population with higher local population density, replicating the relationship between population density and sociality reported previously. In addition, we recorded any individuals dispersing between populations and whether they changed their social tactics, since dispersal could make social flexibility adaptive. Social flexibility would allow immigrants to follow the best alternative reproductive tactic depending on the prevailing environmental conditions of the population into which they immigrated.

Methods

Study area and study period

The study was conducted from January to October 2018 in an area covering 5540 ha of the Goegap Nature Reserve in South Africa (S 29 41.56, E 18 1.60). Goegap lies within the semi-desert biome of the Succulent Karoo, which is characterized by cold and moist winters followed by high food abundance in spring and hot dry summers with low food abundance. The landscape is dominated by short-living ephemerals (in spring) and perennial succulent shrubs. The breeding season of striped mice is in spring (August–November), when population density starts at its minimum.

Data were collected on 8 different sites (Fig. 1). All field sites were located along dry riverbeds with perennial succulent shrubs providing a suitable habitat for striped mice. These included our main field site where we have continuously monitored the striped mouse population since 2001 (Schradin et al. 2012), a field site where an experimental PhD study was done from 2007 to 2010 (Schoepf and Schradin 2012) (Klein Goegap), and 6 field sites where striped mice had been trapped for a population genetics study in 2008, and which found dispersal among these populations (Solmsen et al. 2011). Thus, these populations form one metapopulation that could be viewed as 8 sub-populations or 8 demes. We retain the term "population" for each site, as there was no direct contact between them, and all were isolated from each other by habitat not inhabited by striped mice (Fig. 1).

Trapping

Each population was trapped 4 times. Trapping during January (onset of the dry season, no breeding), April (middle of the dry season, no breeding), and July (end of dry season, no breeding) was done to ensure we have viable populations for our study during the breeding season and to monitor potential dispersal between populations. The gate population became locally extinct in July and the Highlands population by September, leaving us with 6 populations in spring for study (Fig. 1). Extinction might have been associated with the very dry conditions of the years 2015 to 2018, which experienced less rain than the average of 151 mm/year since 2005 (2015: 65 mm; 2016: 85 mm; 2017: 41 mm; 2018: 71 mm).

Data collection regarding social organization was done during the breeding season (September and October). Before trapping, field sites were pre-baited for 2 days by casting bait around trapping stations. In January, trapping was done for 3 days at 6 sites but for 5 days at the field sites with lower trap success, i.e., gate and office. During all subsequent trapping periods, all field sites were trapped for 5 days.

At each population, we trapped along transects of 580 m consisting of 30 trapping stations, one every 20 m under shrubs providing sufficient shelter or where signs of striped mice activity were apparent (feces, tracks). Two traps were set at each trapping station (60 traps in total for each field site). In the morning, we set traps 20 min before the sunlight was incident on the field site because the activity of striped mice is dependent on the onset of direct sunlight (Schradin et al. 2007). Traps were checked twice, first 30 min after the sun started shining on the first stations and again approx. 40 min later. Traps were then unset (locked open) for the hot period of the day. In the evening, we set traps 45 min before sundown and checked traps once after the sunlight was no longer incident on the field site. Striped mice never spent more than one hour in traps. Trapped striped mice were weighed, sexed, and permanently marked with ear tags (National Band and Tag Co., USA) (Schradin and Pillay 2004; Schradin 2006). Striped mice were also temporarily marked with hair dye (Inecto Rapido, Pinetown, South Africa) only during the breeding season in September/October to allow for individual identification during direct observations at their sleeping sites (Schradin and Pillay 2004).

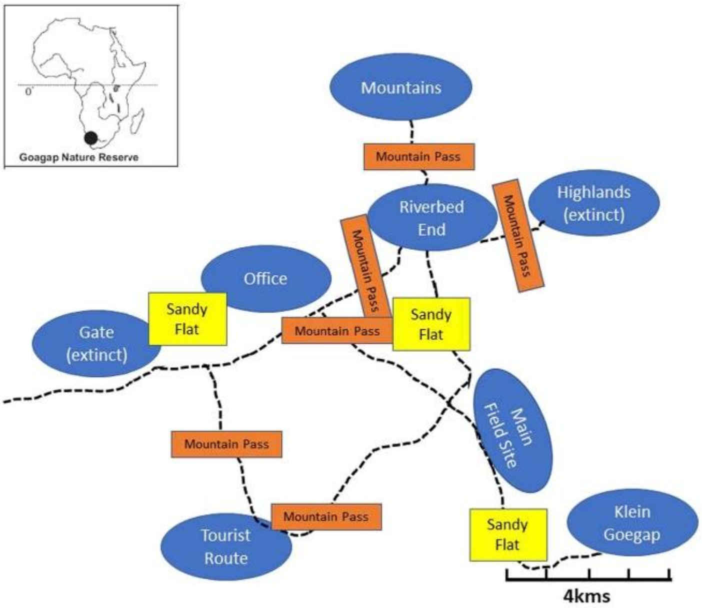

Fig. 1 Schematic representation of the 8 populations studied in Goegap Nature Reserve, South Africa. Dashed lines represent roads and tracks, which are often along dry riverbeds. All populations were separated by areas not inhabited by striped mice such as sandy flats or mountain passes. While striped mice were trapped at all localities in April, the gate population had become locally extinct by July and the highlands population by September

Determination of social tactic

It was not possible to record data blind because our study involved focal animals in the field. The social tactic was determined during the breeding season in September/October to establish whether individuals were living solitarily or in groups. For this, each trapped individual weighing ≥ 30 g received a radio-transmitter (MD-2C transmitters from Holohil, Canada) weighing 2.0 to 3.5 g. We radio-tracked striped mice using an AOR 8000 wide-range receiver once during their activity period in the afternoon before trapping and a second time at night to determine sleeping sites.

Radio-tracking started on the same day the radio-collar was fitted. The sleeping site was determined at night and we also placed 4 to 6 traps at the nesting site and started trapping there the next morning for the rest of the study. Any additional striped mice trapped were marked and received a radio-collar; trapping at nesting sites continued, with more traps being set if necessary. Some sleeping sites were also observed during mornings and afternoons to determine whether striped mice not carrying transmitters were present. We rather observed sleeping sites where one mouse was radio-tracked than sleeping sites where several mice were radio-tracked (known to be group living) to verify that an individual was solitary. If after the original 5 days of trapping, the social organization was not apparent for every individual, radio-tracking, trapping, and observations continued for up to another seven days. We did not have to spend any extra days at the main field site, since we knew the social tactics of all trapped mice there, nor on the two field sites where no striped mice were trapped within 5 days (regarded as extinct: gate and highland). In total, we spent 6 days at office, 10 days at tourist road, 11 days at riverbed end and Klein Goegap, and 12 days at mountains. We determined group versus solitary living by using the following definitions from our previous studies (Schradin et al. 2009; Schradin and Yuen 2011).

1. Group living: two or more adult mice sleep together in the same nest for a minimum of three consecutive nights. Groups consisted either only of adult females, a pair, or adults of both sexes.
2. Solitary living female (with or without pups): a female sleeps alone for a minimum of three consecutive nights and we either trapped no other adult individual at the same nest(s) for at least 3 days, or other adult individuals trapped there were radio-tracked at night at another nest.
3. Solitary living male (roamer): a male sleeps alone for a minimum of three consecutive nights and we either trapped no other adult individual at the same nest(s) for at least 3 days, or other adult individuals trapped there were radio-tracked at night at another nest.

Altogether we determined the social tactics of 39 males and 48 females (sex ratio: 0.81).

Population density

Population density was estimated for the breeding season only. The habitat in Goegap is heterogeneous and many areas are not inhabited by striped mice, as they do not provide the necessary resources, such as food and shelter (Schradin and Pillay 2006; Solmsen et al. 2011). While we chose our trapping transects in areas suitable for striped mice, the long transects often also included unoccupied areas, especially sandy areas without vegetation providing food and cover. To calculate population density as an indicator of competition for scarce resources, we thus only included the areas used by striped mice. For this, we used the GPS points of all sleeping sites, all trapping sites where striped mice were trapped, and of all radio-tracking data collected during afternoons. Using the minimum polygon method, we then determined the size of the area in hectares using the software QGIS 3.6. For individual home ranges of striped mice, convex polygons correlated highly and significantly with Kernel estimates (Schradin and Pillay 2006; Schradin et al. 2010b), but as Kernel contours would be more affected by single individuals with small home ranges, we used convex polygons. Visual inspection of the polygons did not indicate any outliers having a huge impact on field site estimates. For each population, population density was then calculated as the number of adult striped mice (body mass $\geq$ 30 g) per hectare.

Statistical analyses

Data were analyzed using R v. 3.6.1 (the R foundation for statistical computing, http://www.r-project.org/), GraphPad InStat 3.05, and CurveExpert 1.4. Data are reported as means ± standard deviation. Because we had data from only 6 populations, restricting the statistical power of our analysis, we could not include co-variates into the statistical analysis and we thus focused on population density, the variable of interest in our study. However, we measured food availability, rainfall, and the percentage of cover and report that they had no influence on sociality with the given sample size (see electronic supplement). Population density was log-transformed for statistical analysis since the relationship with sociality was non-linear.

Results

Due to extremely dry conditions during the years 2015–2018, population density was generally low, and two populations had become extinct by the onset of the study. For the remaining 6 populations, population density ranged from 1.1 striped mice/ha to 22.4 mice/ha, with a mean of 5.1 ± 8.5 (SD) mice/ha (Fig. 2). In one population (riverbed end), no striped mice lived in groups, while in another population (office), all striped mice lived in groups.

There was a significant regression between the percentage of striped mice living in groups and log-transformed population density ($r^2 = 0.821$, $p = 0.01$; Fig. 2a). At lower population density in a population, more striped mice lived solitarily.

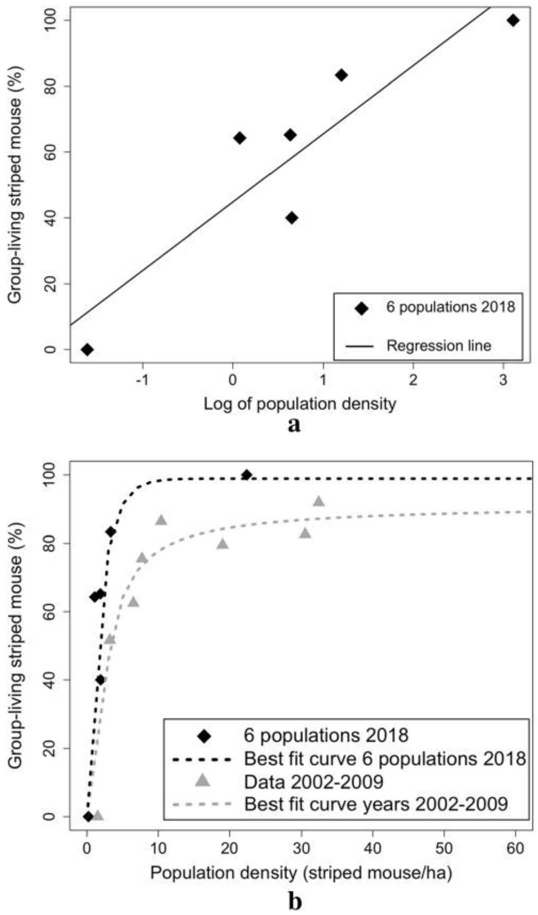

Fig. 2 a Relationship between log population density and the percentage of striped mice living in groups. **b** Raw data. Black: data from 6 populations studied simultaneously in 2018 at 6 distinct geographic locations. Gray: published data from 8 different years in the population main field site (Schradin et al. 2010a), which provided the predictions for the current study. Best-fit curves on the raw data were fitted using CurveExpert

For females alone, the regression was also significant ($r^2 = 0.73$, $p = 0.03$), and also for males ($r^2 = 0.91$, $p = 0.004$). Significantly more females (66.5 ± 36.8%) than males (50.0 ± 33.9%) lived in groups (paired $t_5 = 2.75$, $p = 0.04$).

Using CurveExpert, the relationship was best described by a non-linear regression with the formula $y = 98.89 \text{ x } (1 - (\exp(-0.516x))$, with y representing the percentage of group-living striped mice in the population, and x the population density in striped mice/ha (Fig. 2b). The correlation coefficient was 0.942 (SE = 14.74) indicating a very high model fit. For females and males alone, the best-fit curves were very similar (females: $y = 97.77 \text{ x } (1 - (\exp(-0.76x)))$, SE = 15.91, correlation coefficient = 0.938; males: $y = 97.87 \text{ x } (1 - (\exp(-$

$0.34x$))), SE = 11.14, correlation coefficient = 0.960). In comparison, the best-fit model from the data published in 2010 was $y = 91.3 - (136/x)$ and the correlation coefficient was 0.984 (SE = 5.82) (Schradin et al. 2010a; inserted in Fig. 2b for comparison). Our small sample size did not allow us to include additional environmental co-factors into the analysis; in any case, from the start of the project planning, we focused on the effect of population density as the main effect. In the electronic supplement, we show that all regressions between the dependent variable (% group-living striped mice) and several environmental co-factors (number of food plants, plant cover and rainfall) were non-significant, indicating that population density, the a priori chosen main factor, was the most important.

During the entire study, we observed seven individuals (five males and two females) originating from main field site that immigrated into three other populations (Table 1). Of those, three dispersal events occurred during the breeding season (last trapped on main field site after 1 July and trapped on new field site in September; Table 1). For three males that dispersed during the breeding season, we established that they had changed their social tactic from group-living philopatric males at main field site to solitary living roamer at the new population (Table 1).

Discussion

Social flexibility has been interpreted as an adaptation to changing environments. Change occurs not only in time but also in space. Here, we showed for the first time that geographic variation in population density is significantly related to social flexibility, a prediction that emerged from many field studies on multiple species where differences between two populations were observed (Schradin and Pillay 2005; Martin and Martin 2007; Molina-Vacas et al. 2009). We showed that 6 populations of a larger metapopulation differed in their degree of sociality, depending on population density. Thus, within this metapopulation, individuals being able to switch from group to solitary living and back might benefit from this flexibility not only when the environment changes over time (Schradin et al. 2010a) but also when they disperse over space.

Dispersal is adaptive when there is a chance that a dispersing individual ends up in an environment which differs sufficiently from its original environment to generate higher fitness. A previous study using molecular markers showed that striped mice disperse several kilometers over unoccupied habitats between populations (Solmsen et al. 2011). When populations of the same species differ in social organization, this can either be due to them being isolated and having evolved different social tactics fixed between populations or due to social flexibility of individuals (Schradin 2013). Genetic studies (Solmsen et al. 2011) and our limited observations indicate that dispersal between populations occurs and that dispersing striped mice changed their social tactics, indicating that population differences in social organization are due to social flexibility rather than genetic differentiation. We found dispersal throughout the year, with most events in July, which corresponds to previous findings of the same population using a large sample size (Vuarin et al. 2019). While more exhaustive studies are needed to understand the fitness consequences of dispersal, here, we demonstrate dispersal of individuals over several kilometers between populations that differed in population density and social organization and associated reproductive tactic change in some dispersers.

Striped mice are well known for their social flexibility, i.e., individuals being able to switch from group to solitary living and back to group living (Schradin et al. 2012). This has been demonstrated first with long-term data collected during 8 years from our field site, where more striped mice were group living at a higher population density (Schradin et al. 2010a), in agreement with the habitat saturation hypothesis (Koenig and Pitelka 1981; Emlen 1982; Komdeur 1992). Female tactics drive male sociality, since for males, it is beneficial to join groups of communally breeding females and defend them as

Table 1 Individual striped mice that dispersed from main field site to a different population

Sex	Last trapped on main field site	New population	First trapped at new population	Last trapped at new population	Social tactic at main field site	Social tactic at new population
Male	27.03.2018	Klein Goegap	25.04.2018	25.04.2018	Group living	Tactics not determined in April
Female	11.04.2018	Klein Goegap	27.04.2018	27.04.2018	Group living	Tactics not determined in April
Male	09.06.2018	Mountain	18.07.2018	10.09.2018	Group living	Solitary living
Male	02.02.2018	Riverbed end	07.09.2018	13.09.2018	Group living	Solitary living
Female	18.07.2018	Riverbed end	14.09.2018	14.09.2018	Group living	Not determined because it was trapped on last day
Male	27.07.2018	Klein Goegap	24.09.2018	03.10.2018	Group living	Solitary living
Male	08.09.2018	Klein Goegap	05.10.2018	05.10.2018	Floater? (Only trapped once)	Floater? (Only trapped once at each site)

the only breeding male against other males. However, when many females live solitarily, solitary living males visiting several single females can also have high reproductive success (Schradin and Lindholm 2011). Importantly, single breeding females have much larger home ranges than communal groups, making it impossible for single males to defend the home ranges of multiple solitary females (Schradin et al. 2010b). Reproductive competition between males is high, and single males defending groups of communally breeding females can explain why we found more solitary males than females in every population. Our current study extends our previous findings, demonstrating that striped mice of different populations can either live solitarily (one population), in groups (one population), or that within an area both solitary and group living can occur (4 populations). Thus, social flexibility is a key characteristic of striped mice in both time and space.

Here, we showed that 6 populations of a metapopulation of striped mice differed both in population density and sociality. The relationship between population density and sociality causing intra-specific variation in social organization has been hypothesized by comparing two populations in several different species (e.g., brushtail possums (Martin and Martin 2007) and Europeans badgers (Molina-Vacas et al. 2009)), including striped mice (Schradin and Pillay 2005). However, comparing only two populations ($N = 2$) reduces statistical validity. Thus, such studies are useful to make predictions, but not to draw conclusions, and it has been suggested that more populations need to be studied (Maher and Burger 2011). We found within the metapopulation studied that the lower the population density, the more likely striped mice were solitary. Our six populations were studied within 1.5 months in the same nature reserve and under similar ecological conditions (electronic supplement 1). The relationship was not linear, indicating that solitary living is favored at very low population density, but then group living becomes more quickly common and reaches a plateau at which nearly all striped mice are living in groups (Fig. 2). Our study indicates that some female striped mice prefer to breed solitarily when free territories are available and that more males follow a solitary roaming tactic when more solitary females can be visited. Female striped mice in communal groups suffer from reproductive competition in the form of female-female aggression and female infanticide (Schradin et al. 2010a). In this context, solitary living is a beneficial alternative tactic (Hill et al. 2015). Social flexibility thus allows striped mice to respond to prevailing conditions. These studies help us to understand the reasons for animals living solitarily, a point often missed in behavioral research that normally focuses on the contrary point of why animals live in groups (Krause and Ruxton 2002; Hill et al. 2015; Kappeler 2019).

Experimental manipulation of population density has resulted in changes in social organization in the cichlid *Neolamprologus pulcher* in captivity (Bergmüller et al. 2005), prairie voles (*Microtus ochrogaster*) kept in enclosures (Lucia et al. 2008), and free-living populations of striped mice (Schoepf and Schradin 2012) and Seychelles warblers (*Acrocephalus sechellensis*) (Komdeur 1992, 1994). Whereas these studies focused on one population, a multitude of previous studies comparing two populations showed that intra-specific variation in social organization between populations is widespread (Taborsky and Taborsky 1999; Martin and Martin 2007; Molina-Vacas et al. 2009) and can be related to population density (Schradin 2013), for example in prairie voles (Streatfeild et al. 2011). Variation in social organization between two populations has typically been discussed to be adaptive, but these studies lacked statistical power to test this assumption, creating hypotheses but not reaching conclusions. In caviomorph rodents, intra-specific variation in social systems is common and apparently related to ecological factors (but in degus, at least, it is not related to population density (Ebensperger et al. 2011)). However, most studies on caviomorphs were purely observational, suffering from low sample size and short study periods, such that conclusions could not be drawn with confidence, again leading to predictions rather than conclusions (Maher and Burger 2011). Maher and Burger (2011) recommended comparing several populations of the same species, which is what we have done here. Thus, multiple previous studies suggested that IVSO between populations is related to population density, and here, we showed this for the first time statistically.

In many primate species, individual flexibility in social behavior stabilizes the social organization, for example by changing dominance hierarchies and coalitions, such that the main form of social organization can be maintained (Schradin et al. 2018). In comparison, some other species, such as striped mice, cannot respond to conflict by adjusting their social hierarchy and groups might instead break up, leading to intra-specific variation in social organization (Schradin et al. 2018). Nevertheless, variation in social organization is also common in primates (Strier 2017; Agnani et al. 2018) and explained by socio-ecological models focusing on resource abundance (Dunbar 1988; Kappeler and Schaik 2002; Kappeler et al. 2013, 2017; Koenig et al. 2013) and demography (Moore 1999; Strier 2017). Comparing multiple populations of the same species helped to understand the adaptive significance of infanticide in langurs (Moore 1999). For primates, it has been suggested that intra-specific variation must be taken into account in comparative studies (Sandel et al. 2016) because it significantly changes our understanding of primate social evolution (Kappeler and Fichtel 2016). Similar claims have been made in the studies regarding cooperative breeding in birds, where the importance of variation within species has been ignored (Griesser and Suzuki 2016).

Individuals of both sexes changing their social tactics (individual trait) can change the social system of an entire population, which is called social flexibility (observed at the population level; Schradin et al. 2012). It has been hypothesized that the variation in social organization observed between two populations of a species might be due to differences in population density (Taborsky and Taborsky 1999; Schradin and Pillay 2005; Martin and Martin 2007; Molina-Vacas et al. 2009) but more populations must be studied simultaneously to test this hypothesis (Maher and Burger 2011). To date, this phenomenon had been studied in relation to environmental change over time in one population (Schradin et al. 2018, 2019). Here, we showed that, for the metapopulation studied, intra-specific variation in social organization can be related to geographic variation in population density. Thus, social organization can differ at different localities simultaneously in time depending on population density. How individual dispersal tactics and associated changes in social tactics benefit individual fitness will require further studies. Our study emphasizes the importance of considering intra-specific variation in social tactics in both a spatial and temporal context.

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Data availability All data generated or analyzed during this study are included in the supplementary information files of this published article.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All animal experimentation met the ABS/ASAB guidelines for the ethical treatment of animals. Animal ethics clearance was provided by the University of the Witwatersrand (AESC 2007/40/01), following the guidelines for the use and care of animals in teaching and research of the University of the Witwatersrand which complies with the University's ethical and legal practices and with the National Code.

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Charlotte-Anaïs OLIVIER
Évolution de l'organisation sociale et sa variabilité chez les mammifères

Résumé

Expliquer l'évolution de l'organisation sociale a été fondamental pour comprendre la socialité humaine et plus largement l'évolution sociale. Dans le passé, on pensait que chaque espèce avait une organisation sociale spécifique. Cependant, la variation intra-spécifique de l'organisation sociale (IVSO) a été constatée chez de nombreux taxons. Cette thèse vise à comprendre l'évolution de l'organisation sociale des mammifères et offre une nouvelle perspective en se concentrant uniquement sur les espèces étudiées dans leur environnement naturel, en utilisant de nouvelles méthodes de statistiques Bayésiennes à effets mixtes et en considérant pour la première fois l'IVSO comme variable continue. Mes études montrent que 1) l'IVSO existe chez 51,12 % des espèces de mammifères étudiées sur le terrain ; 2) Les facteurs liés à l'histoire de vie, en particulier la masse corporelle et les rythmes d'activité, ont des effets importants sur l'organisation sociale des primates et des mammifères ; et 3) en considérant l'IVSO, l'organisation sociale ancestrale de tous les mammifères était variable, la vie en couple étant l'organisation sociale la plus courante.

Mots clés : évolution; organisation sociale; système social; mammifères; primates; macroscelidea; variation intra-spécifique

Résumé en anglais

Explaining the evolution of social organization has been fundamental to understanding human sociality and social evolution more widely. In the past, it was thought that each species had a specific social organization. However, intra-specific variation in social organization (IVSO) has been found in many taxa. This thesis aims to understand the evolution of mammalian social organization and provides a new perspective by focusing only on species studied in their natural environment, using new mixed-effect Bayesian statistical methods and considering for the first time IVSO as a continuous variable. My studies show that 1) IVSO exists in 51.12% of mammalian species studied in the field; 2) life history factors, especially body mass and activity rhythms, have important effects on primate and mammalian social organization; and 3) considering IVSO, the ancestral social organization of all mammals was variable with pair-living as the most common social organization.

Keywords: evolution; social organization; social system; mammals; primates; macroscelidea; intra-specific variation