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Personality, Life History and Metabolism in the Bush Karoo Rat (*Otomys unisulcatus*)

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Jingyu QIU

Personality, Life History and Metabolism in the Bush Karoo Rat (*Otomys unisulcatus*)

Résumé

Cette thèse montre un lien entre l'histoire de vie, la physiologie et le comportement chez le rat du Karoo buissonnant. Les résultats suggèrent que la personnalité individuelle, et la relation entre la personnalité et le taux métabolique au repos est influencée par l'histoire de vie. Les individus nés plus tard dans la saison de reproduction montrent une personnalité plus proactive que les individus nés plus tôt. Lorsque le moment de la naissance a été pris en compte, la corrélation directe entre les traits de personnalité et les paramètres métaboliques a disparu, mais les deux étaient indépendamment liés à la date de naissance au cours de la saison.

Comprendre la relation entre la personnalité, le métabolisme et le cycle de vie est crucial pour expliquer la variation individuelle généralisée du comportement et du métabolisme. Ces connaissances pourrons améliorer notre compréhension de la façon dont les animaux répondent aux changements environnementaux à un niveau individuel, ce qui est particulièrement précieux pour développer des stratégies de conservation efficaces face au changement climatique global, adaptées localement aux populations cibles.

Mots clés :
Phénotype comportemental, métabolisme; syndrome du rythme de vie; réponse au stress; *Otomys ; Myomorpha*

Abstract

This thesis demonstrates a link between life history, physiology and behavior in the Karoo bush rat. The results suggest that individual’s personality, and the relationship between personality and physiology traits is influenced by life history. Individuals born later in the breeding season show a more proactive personality than individuals born earlier. When time of birth was taken into account, the direct correlation between personality and metabolic traits disappeared, but both were independently related to time of birth within the season. Understanding the relationship between personality, metabolism and life history is crucial to explain widespread individual variation in behavior and metabolism. This knowledge will improve our understanding of how animals respond to environmental change at an individual level, which is particularly valuable for developing effective conservation strategies in the face of global climate change that are locally tailored to target populations.

Keywords :
Behavioral phenotype, metabolism; pace-of-life syndrome; stress response; *Otomys*; *Myomorpha*

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Communications

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Résumé

Les comportements des animaux sont divers, permettant aux individus d'interagir avec leur environnement, voire de le manipuler. Ceci est essentiel pour faire face aux changements rapides et imprévisibles de l’environnement. Bien que l'expression des comportements puisse varier considérablement entre les individus, elle présente souvent une certaine cohérence chez un même individu. Ces différences comportementales cohérentes chez les individus sont appelées "personnalité animale". Par exemple, certains individus sont constamment plus actifs et explorateurs que d'autres. Cela soulève des questions fascinantes : Pourquoi les individus diffèrent-ils en matière de personnalité, et comment cette variation contribue-t-elle à leur aptitude à survivre et à se reproduire ?

Bien que la personnalité ait une base génétique, elle peut être influencée par des facteurs environnementaux permanents, telles que les expériences précoces. Comme beaucoup de traits biologiques, le développement de la personnalité et son expression à l'âge adulte peuvent être façonnés par les expériences précoces. Par exemple, les individus ayant connu une période d'abondance de ressources au début de leur vie pourraient être mieux à même de supporter le compromis entre la survie et la reproduction. Ces individus pourraient bénéficier d'un type de personnalité "proactive" — étant plus actifs et/ou explorateurs —pourrait offrir des avantages en termes d'acquisition de ressources et de compétition avec les congénères. Comprendre ce qui définit les différences comportementales individuelles et comment elles sont liées aux traits physiologiques est crucial pour révéler la valeur adaptative des traits de personnalité et pourquoi ils persistent au sein des populations.

La personnalité chez les animaux est étroitement liée à leur dépense énergétique. Les individus proactifs, aux niveaux d'activité, d'exploration et/ou d'agressivité plus élevés, tendent à avoir des besoins énergétiques plus importants en raison de leur activité physique accrue. Outre l'influence énergétique liée à l'activité physique, les chercheurs ont également examiné la relation potentielle entre la personnalité et le taux métabolique de repos (TMR). Le TMR reflète l'énergie nécessaire pour maintenir les processus biologiques de base et constitue une part importante du budget énergétique global d'un individu. À l'échelle inter-individuelle, le TMR présente une variation considérable parmi les espèces, dont une grande partie reste inexpliquée. Comme la

personnalité est un autre trait qui varie entre les individus, elle a été suggérée comme un facteur potentiel contribuant à cette variation énergétique.

Il a été proposé que la personnalité animale puisse être intégrée dans le cadre de la théorie du rythme de vie (Pace-of-Life Theory), qui lie les traits comportementaux, physiologiques et de cycle de vie dans un continuum "rapide-lent". La théorie du rythme de vie distingue les organismes vivant à un "rythme rapide", caractérisés par une croissance rapide, une reproduction précoce et une durée de vie plus courte, et ceux à un "rythme lent", marqués par une croissance plus lente, une reproduction plus tardive et une longévité accrue. Les individus avec un rythme de vie "rapide" tendent à adopter une personnalité "proactive" — étant plus audacieux, plus actifs et/ou explorateurs — et ont un métabolisme élevé. En revanche, les individus avec un rythme de vie "lent" sont comportementalement réactifs — étant plus timides, moins actifs et/ou explorateurs — et ont un taux métabolisme plus bas. L'hypothèse a été largement soutenue par des études au niveau inter-spécifique et inter-populationnel. Cependant, lorsqu'elle est appliquée au sein d’une population, la relation semble plus complexe. Des études de terrain ont montré une absence d'association, voire une association qui contredit les prédictions de l'hypothèse.

Pour expliquer ces résultats contradictoires, Montiglio et al. (2018) ont affiné la théorie, en proposant que les changements des conditions écologiques pourraient entraîner des degrés variables d'association entre le comportement, la physiologie et le cycle de vie. Les conditions écologiques spécifiques peuvent affecter la valeur adaptative des types de personnalité. Par exemple, dans des situations de contraintes écologiques comme le manque de ressources alimentaires, le lien entre une personnalité proactive et un rythme de vie rapide peut être affaibli, car l'énergie supplémentaire dépensée pour la recherche active de nourriture pourrait ne pas conduire à un apport alimentaire suffisant pour compenser les coûts. Pour mieux comprendre comment les facteurs écologiques influencent la relation avec le rythme de vie, il est nécessaire de mener davantage d'études de terrain.

L'objectif de ma thèse est de comprendre comment les traits de personnalité interagissent avec le cycle de vie et la physiologie chez le rat de brousse du Karoo (Otomys unisulcatus), une petite espèce de rongeur vivant dans le semi-arides du Karoo succulent en Afrique du Sud. Plus précisément, j'ai étudié si les traits de personnalité sont associés à la date de naissance au sein de la saison de reproduction — un déterminant clé de la trajectoire de rythme de vie — et comment cela affecte le métabolisme. J'ai émis l'hypothèse que les individus nés plus tard dans la saison de reproduction, lorsque la densité de population augmente et que les ressources deviennent rares, adopteraient des traits de personnalité plus proactifs — comme une plus grande audace et exploration — par rapport aux individus nés plus tôt, qui ont connu une période d'abondance de ressources plus longue avant l'âge adulte.

Ensuite, j'ai étudié dans quelle mesure cela est lié à différentes mesures du métabolisme. Je m'attendais à ce que les individus proactifs aient des taux métaboliques basaux plus élevés et une réponse métabolique plus forte aux stress aigus, reflétant les exigences énergétiques de leur type de personnalité. Ma thèse se compose de trois chapitres : une étude comparative sur les rongeurs Myomorpha et deux études de terrain portant sur la personnalité, le métabolisme et le cycle de vie chez les rats de brousse du Karoo.

Dans le premier chapitre, j'ai présenté la première étude comparative contrôlée par la phylogénie sur les habitudes de nidification chez les rongeurs de type souris (Myomorpha, 1655 species), et j'ai évalué dans quelle mesure ces comportements, en particulier la construction de loges, un comportement relativement rare, sont liés à leur histoire naturelle et à des facteurs écologiques. La construction d'abris avec des plantes sèches et d'autres matériaux naturels (construction de loges) ne se retrouve que chez 3,7 % des espèces de Myomorpha. Ces espèces sont principalement herbivores, et tendent être celles présentant une plus grande taille corporelle par rapport à celles qui habitent des terriers ou des abris naturels, et sont plus susceptibles de se trouver dans des environnements arides à faible risque d'incendie. En prenant en compte la phylogénie, aucun facteur de l'histoire naturelle ou aux conditions écologiques n'a été trouvé comme étant associé à l'évolution des habitudes de construction d'abris chez les Myomorpha. Cette étude a été publiée dans le Journal of Zoology (Qiu, J. & Schradin, C. 2024. Lodge-building in rodents: relationships with ecological and natural history factors. Journal of Zoology. https://doi.org/10.1111/jzo.13207).

J'ai ensuite recentré l'étude de la modélisation phylogénétique sur l'étude de terrain d'une espèce construisant des lodges, les rats du Karoo buissonnant (Otomys unisulcatus). Dans la première partie, j'ai étudié les différences comportementales et de cycle de vie entre les individus nés plus tôt et plus tard dans la saison de reproduction. L’expérience a été répétée sur deux ans (2022-2023), fournissant des preuves de l'existence de personnalités "proactifs". J'ai également examiné comment les différences de personnalité sont influencées par le déterminant clé du cycle de vie : la date de naissance au sein de la saison.

Les résultats ont suggéré que les individus nés plus tard dans la saison, qui font face à une densité de population plus élevée et à une concurrence plus intense pour les lodges, tendent à être plus proactifs que ceux nés plus tôt. Cette découverte contredit les prédictions de la théorie du rythme de vie qui prévoit que les individus nés plus tôt dans la population, avec un cycle de vie "rapide", devraient adopter des personnalités plus proactives afin de s'investir dans une reproduction précoce. Les résultats ont mis en lumière l'influence des contraintes écologiques (une période courte et abondante en ressources, sans possibilité de reproduction et avec une disponibilité limitée de loges comme abris) dans la relation entre la personnalité et le cycle de vie. Cette étude a été soumis à la revue Behavioral Ecology and Sociobiology (Qiu, J., Pillay, N, Schradin, C., Makuya, L., H.G. Rödel. Higher proactivity in later-borns: effects of birth date on personality in a small mammal. à la revue).

Dans la deuxième partie de l'étude de terrain, j'ai examiné les relations entre le taux métabolique, la personnalité et le cycle de vie dans le cadre. L'étude a fourni des résultats sur (1) la constance des paramètres du taux métabolique, (2) l'association entre les traits de personnalité et les paramètres du taux métabolique, et (3) le rôle de la date de naissance comme facteur potentiel à l'origine de la personnalité et de la variation du taux métabolique. Les résultats suggèrent que les traits de personnalité et les paramètres métaboliques sont indépendamment influencés par la date de naissance au sein de la saison de reproduction (Qiu, J., Schradin, C., Mata, Astolfo., Pillay, N, H.G. Rödel. Associations between metabolic rate and personality are driven by date of birth. en préparation).

En résumé, mes résultats montrent un lien entre l'histoire de vie, la physiologie et le comportement chez le rat du Karoo buissonnant. Les résultats suggèrent que la relation entre la personnalité et le taux métabolique au repos est influencée par l'histoire de vie. Lorsque le moment de la naissance a été pris en compte, la corrélation directe entre les traits de personnalité et les paramètres métaboliques a disparu, mais les deux étaient indépendamment liés à la date de naissance au cours de la saison.

Comprendre la relation entre la personnalité, le métabolisme et le cycle de vie est crucial pour expliquer la variation individuelle généralisée du comportement et du métabolisme chez les espèces. Ces connaissances pourrons améliorer notre compréhension de la façon dont les animaux répondent aux changements environnementaux à un niveau individuel, ce qui est particulièrement précieux pour développer des stratégies de conservation efficaces face au changement climatique global, adaptées localement aux populations cibles.

Abstract

In the animal kingdom, diverse behaviors enable individuals to interact with and to manipulate their environment, which is essential in coping with rapid and unpredictable changes. Although the expression of behavior can be highly variable between individuals, it often shows a certain consistency within an individual. These consistent individual differences in behavior are referred to as "animal personality." For example, some individuals are consistently more active and explorative than others. This raises intriguing questions: Why do individuals differ in personality, and how does this variation contribute to their fitness?

While personality has a genetic basis, it can be permanently influenced by environmental factors, such as early-life experiences. Like many biological traits, the development of personality and its expression in adulthood can be shaped by experiences in early development. For instance, individuals experiencing resource abundant period in early life may benefit from having "proactive" personality type—been more active and/or explorative—which, although energy-demanding, may offer advantages in resource acquisition and conspecific competition. Understanding the driver of individual differences in behavior and how it is linked to physiological traits is crucial for revealing the adaptive value of personality traits and why they persist within populations.

Personality in animals is closely linked to their energy expenditure. Proactive individuals, who exhibit higher levels of activity, exploration, and/or aggression, tend to have greater energy demands due to their increased physical activity. In addition to the energetic influence associated with physical activity, researchers have also investigated the potential relationship between personality and resting metabolic rate (RMR). RMR reflects the energy required to sustain basic biological processes and constitutes a significant portion of an individual's overall energy budget. At the between-individual level, RMR shows considerable variation across species, much of which remains unexplained. As personality is another trait that varies among individuals, it has been suggested as a potential factor contributing to this energetic variation.

It has been proposed that animal personality can be integrated into the pace-of-life framework, which links behavioral, physiological, and life-history traits into a "fast-slow" continuum. This

hypothesis is rooted in the classic concept of r/K selection but extends correlations beyond life-history traits. Individuals with a “fast” pace of life tend to exhibit a “proactive” personality—being bolder, more active, and/or explorative—and have a high metabolic rate. In contrast, individuals with a “slow” pace of life are behaviorally reactive—being shy, less active and/or explorative—and have a lower metabolic rate. The pace-of-life hypothesis has been well supported by studies at the interspecific and inter-population levels. However, when applied to within-population level, the relationship appears more complex. Field studies have found no association, or even associations that contradict the predictions of the pace-of-life hypothesis.

To address these contradictory findings, Montiglio et al. (2018) revised the pace-of-life framework, proposing that changes in ecological conditions leads to varying degrees of association between behavior, physiology, and life history. Specific ecological conditions can affect the fitness value of personality types. For example, under ecological constrains situation such as lack of food sources, the link between proactive personality with fast life history maybe weaken as the additional energy spent actively foraging may not lead to sufficient food intake to offset the costs. To better understand how ecological factors influence the pace-of-life relationship, more field studies are needed.

The aim of my thesis was to understand how personality traits interact with life history and physiology in the bush Karoo rat (Otomys unisulcatus), a small rodent species that inhabits the semi-arid Succulent Karoo in South Africa. Specifically, I investigated whether personality traits are associated with time of birth within the breeding season – a key determinant of life history trajectory. I hypothesized that individuals born later in the breeding season, when population density increased and resources became rare, would adopt more proactive personality traits—such as higher boldness and exploration—compared to early-born individuals who experienced a longer period of resource abundance before reaching adulthood. Next, I studied in how far this is related to different measures of metabolism. I expected that proactive individuals will have higher RMR and a stronger metabolic response to acute stressors, reflecting the energetic demands of their personality type.

My thesis consists of three chapters: one comparative study on Myomorpha rodents and two field studies focusing on personality, metabolism, and life history in bush Karoo rats. First, I presented the first phylogenetic controlled comparative study on the nesting habits in mouse-like rodents (Myomorpha, 1655 species), to test in how far lodge -building is associated with natural history and ecological factors. Lodge-building defined as constructing shelters with dry plants and other natural materials is only found in 20 (3.7% of) Myomorpha species. These species are mostly herbivorous, tend to have larger body sizes compared to those that inhabit burrows or natural shelters, and are more likely to occur in arid environments with low fire risk. This study was published in the Journal of Zoology (Qiu, J. & Schradin, C. 2024. Lodge-building in rodents: relationships with ecological and natural history factors. Journal of Zoology. https://doi.org/10.1111/jzo.13207).

I then moved the focus from phylogenetic modelling to field studies on a lodge-building species, the bush Karoo rat (Otomys unisulcatus). First, I I found evidence on the existence of personality and “proactive” behavioral syndromes. I then examined how personality differences are influenced by birth date within the season, the key life history factor.

The results showed that individuals born later in the season, who face higher population densities and more intense competition for stick lodges, were more proactive than those born earlier. This finding contradicts the prediction the pace-of-life theory, that early born individuals in a population with a "fast" life history should adopt more proactive personalities for investment into early breeding, supporting the revised hypothesis that ecological constraints (short resource abundant period with no option for breeding and limited availability of lodges as shelter) can modify the relationship between personality and life history along the fast-slow continuum. The results highlighted the influence of ecological constrains, in this study the constrain of lodge availability, in shaping the relationship between personality and life history. This study is currently under review (Qiu, J., Pillay, N, Schradin, C., Makuya, L., Rödel, H.G. Higher proactivity in later-borns: effects of birth date on personality in a small mammal. under review).

In the second part of the field study, I examined the relationships between metabolic rate, personality, and life history under the pace-of-life framework. The study investigated (1) the consistency of metabolic rate parameters, (2) the association between personality traits and metabolic rate parameters, and (3) the role of birth timing as a potential driver of both personality and variation in metabolic rate. The findings suggest that in bush Karoo rats, personality traits and metabolic parameters are both but independently from each other influenced by the date of birth within the breeding season. (Qiu, J., Schradin, C., Mata, Astolfo., Pillay, N, Rödel, H.G. Associations between metabolic rate and personality are driven by date of birth. in prep)

In sum, my thesis provides evidence for the link between life history, physiology, and behavior in a lodge-building species, the bush Karoo rat. The results suggest that the relationship between personality and resting metabolic rate is mediated by life history. When birth timing was added as a factor, the direct correlation between personality traits and metabolic parameters disappeared, but both were independently linked to date of birth within the season.

Understanding the relationship between personality, life history, and metabolism is crucial for explaining the widespread individual variation in behavior and metabolism across species. This knowledge can enhance our understanding of how animals respond to environmental changes at the individual level, which is particularly valuable for developing effective conservation strategies in the context of global environmental change.

General Introduction

Animal personality is an intriguing concept that describes consistent between individual variation in behavior (Stamps and Groothuis, 2010). For instance, some individuals are always more active than others. Personality universally occurred across a wide range of taxa from vertebrates to invertebrates (Lucon-Xiccato et al., 2023; Golab et al., 2021; Sih et al., 2004a; Stamps and Groothuis, 2010), Individuals in the same population, even from the same litter or genetic clones can differ in their personalities (Freund et al., 2013). Understanding animal personality is crucial for understanding how individuals behaviorally respond to prevailing environmental conditions and how behavior covariates with other individual characteristic, such as life history and physiology traits.

Box I.1. Definition of animal personality and behavioral syndromes

Human shows consistent individual differences in how they behave. Many words have been used to describe this behavioral pattern, such as friendly, aggressive in general language, and openness, conscientiousness, extraversion, agreeableness and neuroticism in psychology (Zimbardo, 1992). Similar terms have been used to describe this difference in animals, such as “personality”, “coping style” or “behavior syndrome”. In this thesis, only “animal personality” or “personality” is used to refer to these behavioral differences, defined as consistent differences in behavior between individuals across time and contexts (Réale et al., 2007).

In biology, "syndrome" is used to describe a set of correlated characteristics or features. The term “behavioral syndrome” describes a suit of correlated behaviors across situations within population or species, the expression of behavior syndrome in an individual is referred to as behavioral/personality type. For example, aggressive syndromes have been observed in several species (Riechert and Hedrick, 1993; Jandt et al., 2014), where some individuals are generally more aggressive than others (“aggressive” type).

I.1 Animal personality

Over the past few decades, the field of animal behavior has increasingly interested in the consistent individual differences in behavior, how it’s developed and influences individual fitness (Dingemanse and Réale, 2005; Rödel et al., 2015; Smith and Blumstein, 2008). This phenomenon has been referred to variously as coping styles (Koolhaas et al., 1999), temperament (Réale et al.,

2000) or animal personality (Réale and Dingemanse, 2012; Schuett et al., 2010). I will use the term "personality", which refers to an individual's behavioral tendencies of being different from other conspecifics but consistent in its behavior over time and across situations (Box I.1; Réale and Dingemanse, 2012).

I.1.1 Personality traits

Five axes of behavioral traits have been widely used in the description of animal personality: shyness-boldness, exploration-avoidance, activity, aggressiveness and sociability (Réale et al. 2007; Figure I.1). In the shyness-boldness axis, individuals differ in their behavioral responses to risky situations, such as being in the presence of predators (e.g. in a predator stimulus test, Carter et al., 2012). Activity refers to the general level of activity and is one of the most commonly measured axes in personality research, where the quality and quantity of active behavior (usually locomotion) are assessed in controlled settings (e.g. open field test; Gould et al., 2009). Exploration-avoidance can be measured by an individual's reaction to a novel environment (e.g. open field test or novel environment test; Huang et al., 2016) or novel objects (e.g. novel object test; Heyser and Chemero, 2012). Sociability and aggressiveness are both related to interactions in a social context. Sociability refers to individual's reaction (apart from aggressive behavior) to the presence or absence of conspecifics. This can be measured in separation tests by recording an individual's reaction to being separated from its group (Faure and Mills, 2014). Aggressiveness refers to individual's agonistic reaction; for example, the "mirror test" has been used for the measurement of conspecific aggression (Balzarini et al., 2014). Studies also included the agonistic reaction to other species, such as prey animals, as an aspect of aggressiveness (Riechert and Hedrick, 1993). The proper measurement for personality traits can vary between species. Thus, the experimental setting often requires adjustment to acquire biological meaningful data of the focal species, such as using a visual stimulus for more visually dependent animals, or an odor stimulus for more olfactory-dependent animals.

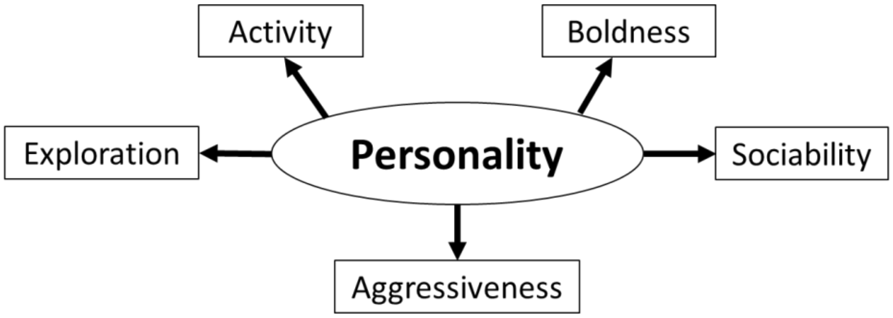

Figure I.1. Methodological framework proposing 5 axes for the ecological study of temperament/personality. Derived from Réale et al. 2007.

I.1.2. Behavioral syndromes

Personality traits are not independent from each other. Instead, they seem to be different expressions of the same phenotype in various contexts (Sih et al., 2004a). The correlation of behavioral traits is referred to as behavioral syndromes, a suite of correlated behaviors across situations within/across populations (Box I.1; Sih et al., 2004a; Sih et al., 2004b). This can involve several behavioral variables that are correlated under different contexts, for example female funnel-web spiders (*Agelenopsis aperta*) that show high aggression towards conspecifics are also more aggressive to their prey (Riechert and Hedrick, 1993); or the correlation between different behavior traits under the same/different contexts, such as bent-wing bats (*Miniopterus fuliginosus*) that show mutually positively correlated personality traits of boldness, activity and exploration, described by the authors as "proactive" behaviors (Kuo et al., 2024).

Having behavioral syndromes can bring potential benefits. In Largespring mosquitofish (*Gambusia geiseri*), an individual's behavioral type remains stable in the absence or presence of a predator, such that mosquitofishes with a higher score in active/explorative axis are more likely to escape from a novel predator species (Blake and Gabor, 2014). However, correlations between traits sometimes set limits to behavioral flexibility, so that when considered in isolation, some traits appear to be non-adaptive (Sih et al., 2004). A typical example is high level of activity in prey animals, which increases their predation risk when predators are present (Brodin and Johansson, 2004; Sih et al., 1988).

If having behavioral syndromes can be maladaptive under some situations, it raises the question why behavioral syndrome exists across taxa. From mammals to birds, laboratory studies found genetic correlations underlying these behavioral traits, which directly affect behavioral patterns and the common neuroendocrine system that regulates a suite of behaviors (Boissy, 1995; Bućan and Abel, 2002; Friedrich, 2022; Øverli et al., 2005). Common genetic bases can make it difficult to decouple suites of correlated behaviors, even when some of them are maladaptive under certain scenarios. In spiders, a taxon known for aggression towards conspecifics (Pruitt and Avilés 2018), high aggressiveness can be associated with several non-adaptive behaviors: aggressive funnel web spiders (*Agelenopsis aperta*) initiate attacks quicker, both on prey and on conspecific intruders (Riechert and Hedrick 1993) and show more overkilling predation (kill but do not completely consume; Maupin and Riechert 2001). Although overkilling behavior is considered maladaptive, it may be selected as a by-product of aggressive behavioral syndromes, which in other contexts brings advantages, such as territory competition and predation success (Sih et al., 2004).

Behavioral syndromes have a genetic basis, thus the related behavioral traits are often heritable (Sih et al., 2004). Quantitative genetic studies in various species have provided evidence that behavioral traits such as boldness, aggressiveness and exploration are genetically based (Drosophila: Sokolowski, 2001; mice: Sluyter et al., 1995; birds: Dingemanse et al., 2002). Exploration and boldness traits are genetically correlated and can be selected for in great tits (Dingemanse et al., 2002; van Oers et al., 2004). The genetic correlation underlying behavioral traits can lead to evolutionary constraints but has the potential to evolve, allowing the emergence of new syndromes for the population to better cope with changing environments (Sih et al., 2004). Three-spined stickleback (*Gasterosteus aculeatus*) populations from large ponds with presence of predators exhibited a set of correlated aggressiveness, activity and exploration behaviors. Although this behavioral syndrome may bring more risk of predation, it can be the optimal trait combinations under this environment (Dingemanse et al., 2007).

The association between behaviors can be species- or population-specific, depending on local environmental conditions, behavioral syndromes found in one population may be absent or different in another (Sih et al., 2004). From the same study of three-spined sticklebacks, another population from a smaller pond with an absence of predators showed no correlation between aggressiveness, activity and exploration behavioral traits as their neighboring population of the larger pond (Dingemanse et al., 2007). Aggressiveness towards conspecific and heterospecific individuals can co-evolve in solitary species, but the association may be weakened in group-living species or populations that experience more socially complex environments (Katzir, 1981; Schoepf and Schradin, 2012). It therefore appears that the selection for behavioral syndromes is environment-depended, combining multiple behavioral traits that interact to enhance individual overall fitness under specific ecological conditions.

I.1.3. Personality development and maintenance

Although animal personality has a genetic basis (Friedrich, 2022) and is mostly stable across time and context, it is still under the influence of other biological factors such as age (Cabrera et al., 2021; Class and Brommer, 2016; Zablocki-Thomas et al., 2018) and early life conditions (Zablocki-Thomas et al., 2018). The experiences early in life, including competition for the access to resources, exposure to stress and social interactions, can permanently influences the development of individual physical growth and phenotype, which ultimately affect their future fitness (Monaghan, 2007). Heavier European rabbit (*Oryctolagus cuniculus*) pups were more exploratory and showed lower levels of anxiety than lighter pups (Rödel and Monclús, 2011). In seasonal changing environments, resource availability and competition can vary greatly over time, and thus the timing of birth can significantly impact an individual’s early life experience and the development of life history strategies (Montiglio et al., 2014). New-born individuals must cope with the environmental conditions in which they are born. For example, in seasonally breeding species, resources may be constrained for those individuals born during the later breeding season, due to the naturally decrease of resources and increasing population density along the season. From physical development (Vaiserman and Koliada, 2017) to behaviors, challenging conditions can trigger a set of long-lasting outcomes that can last until adulthood. For example, European starlings (*Sturnus vulgaris*) that went through a period of food deprivation become faster foragers (Andrews et al., 2015). Similarly, in house mice (*Mus musculus*), inadequate nutrition of pups promotes competition for access to nipples and predisposes the development of active and aggressive behavioral traits (Mendl and Paul, 1991). Early-life condition can also have a long-lasting influence on personality in adulthood (Dingemanse et al., 2010, Rödel et al., 2011). Early-life stress experienced as an embryo can lead to more active, explorative and bolder personality in birds, which gain fitness benefits in later stressful environments (Dingemanse et al., 2004; Smith and Blumstein, 2008). Similarly, early postnatal development had a long-term effect on the personality type of European rabbits, where pups with higher body mass were more explorative and showed less predator anxiety as adults (Rödel et al. 2011).

Maternal effects can have a direct influence on the development of offspring's behavior (Sachser et al., 2011; Braastad, 1998; Weinstock, 2001; Coutellier et al., 2008; Curley et al., 2008; Eriksen et al., 2011). The levels of stress hormones in females fluctuate throughout the breeding period. For instance, elevated stress hormone concentrations can affect the behavioral traits of offspring during the prenatal period. (Weinstock, 2008; Sachser et al., 2011; Hinde, et al. 2015). It has been found in European rabbit (*Oryctolagus cuniculus*) and domesticated pigs that increased maternal in glucocorticoid levels have negative effect on offspring survival (Benedek et al., 2021; Stanton and Carroll, 1974). Within-litter competition contributes to these differences (Innes and Millar 1993; Koivula et al. 2003; Eccard and Rödel 2011). In several rodent species, competition for milk and the warmer centre of the huddle leads to behavioral differences among siblings. Lighter individuals experience negative feedback loops that prime them to adopt a more proactive behavioral style, such as repeatedly climbing toward the centre of the huddle where they were consistently pushed back (Hudson et al., 2011). These early-life adversities can have lasting effects, promoting a more proactive behavioral type later in life compared to their siblings.

Other fundamental resources, such as food, not only vary significantly between seasons, but also induce competition within the season. As population density increases rapidly during the food abundant period, individual could face more intense competition for other limited resources. Resource limitation related to date of birth can continuously influence individual behavior type at older age, as individuals becomes independent and collect resources (internally or externally) for later survival and reproduciton. Generally, early-life adversity decreases activity and exploration, and has negative effects on survival and long-term fitness (Rödel et al., 2008; Burns et al., 2012; Lehto Hürlimann et al., 2014; Marasco, Smith and Angelier, 2022; Patterson, Strum and Silk, 2022).

Relatively few studies have investigated to what extent personality can be affected by life experiences after maturity. In adult European mink (*Mustela lutreola*), personality can be influenced by the prevailing situation and context: the levels of boldness and exploration vary between breeding seasons (Haage et al. 2013). Similarly, common voles (*Microtus arvalis*) show a decrease in boldness during winter, when the environment becomes harsh (Gracceva et al., 2014). Due to the difficulty of capturing wild animals repeatedly in their early life stage, most studies on early-life influence were done in captive colonies or animals housed in a semi-natural enclosure. Studies on how the influence of early life on personality influences later-life stages, especially in the wild, are still limited. Investigating species under their natural environments will help to expand our understanding of early and later life influences on the development and maintenance of personality differences.

I.2. Behavior and energy expenditure

The expression of behavior is often supported by physical activity and thus energy demanding (Brown et al., 2004). The energy cost can vary widely depending on an individual's activity level, which is closely related to personality traits (e.g., activity). For example, "proactive" individuals with higher levels of activity, exploration and aggression can be expected to spend more energy on physical activity than "reactive" ones.

I.2.1. Metabolic rate

Individual's energy budget broadly includes energy required in maintaining basal biological functions, energy allocated to thermoregulation, growth, maintenance of a functional immune system, heat generation through digestion and physical activity (Blaxter, 1989; Speakman and Selman, 2003). Energy spent on basic biological process is an important part of the total energy expenditure (Soares and Müller, 2018; DeLany and Lovejoy, 1996), and any influences on this energy expenditure will impact the total energy budget. The rate at which an animal oxidizes food to produce energy is defined as the metabolic rate (MR), which is one of the most widely measured physiological traits. Basal metabolic rate (BMR) is defined as the rate of energy expenditure to maintain necessary biological processes by endothermic animals (McNab, 1997). Measurements of BMR require highly standardized conditions: the animal should be post absorptive, nonactive, non-reproductively active adult, and remain fasted and at complete rest during the measurement. The testing environment should be within the animal's thermoneutral zone (McNab, 1988). These requirements can be difficult to meet, especially under field conditions. Thus, as an approximate approach, resting metabolic rate (RMR), has often been used as a substitute for BMR when studying energy budget in animals (Agnani et al., 2020; Speakman et al., 2004). RMR measurement requires less rigorous conditions, allowing individual been measured in a more broadly basal state, but still requires the animal remaining in a resting stage and measured within its thermoneutral zone. Resting metabolic rate includes the basal metabolic rate (BMR) and the thermic effect of food (Blaxter, 1989). The difference between RMR and BMR is generally small, thus they are often used synonymously in the literature (Careau et al., 2008).

The literature indicates an increase of the physical activity level typically results in an increase in RMR during the resting state (Speakman and Selman, 2003). Because RMR often constitutes a substantial, and sometimes the largest, portion of an individual's daily energy budget (Clarke et al., 2010), the influence of behavior on resting metabolic rate (RMR) may be more significant than the direct energetic costs of the physical activity required to perform the behavior itself (Speakman and Selman, 2003).

RMR also shows high intra-specific variation. However, attempts for explaining this intra-specific RMR differences are not as conclusive as explanations for inter-specific variation in RMR. Even after accounting for body mass, ambient temperature and other environmental and natural history factors, such as age, sex, social rank, mate choice and parasite load, a considerable variation between individuals remains unexplained (Burton et al., 2011; Metcalfe et al., 1995; McNab, 2002; Steyermark et al., 2005).

I.2.2. Personality and energetic consequences

Many studies have investigated the relationship between metabolic rate and personality, focusing on basal metabolic rate (BMR) or resting metabolic rate (RMR), but the findings were inconclusive (Mathot and Dingemanse, 2015). Some of them report a positive association between resting metabolic rate and proactive personality types (Behrens et al., 2020; Careau et al., 2011; Šíchová et al., 2014), suggesting proactive individuals tend to have higher RMR. Individual personality type can have energetic consequences: maintaining a high activity level requires more energy devoted to physical activity. Thus, more explorative individuals need to spend additional energy in exploring new environments, and more aggressive individuals are likely to engage in intense physical confrontations, which are often energy-costly (Ros et al., 2006). The positive association found in these studies indicates a generally higher energy budget in maintaining basic biological process and these energy costly traits. However, numerous studies reported alternative associations (Behrens et al., 2020; Careau et al., 2011; Careau et al., 2015; Šíchová et al., 2014), where individual personality types were not associated with their RMR, or energy costly personalities were associated with lower RMR, implying no energetic association, or energy-costly personality and RMR constrains each other under a fixed energy budget . As the variation in this association apparently exists across contexts and species, further investigation is needed to understand how context-specific factors and species differences shape the relationship between personality and RMR.

Personality is also associated with variations in stress response (Baugh et al., 2013a; Xin et al., 2017). Birds with more proactive personalities show relatively lower increases in corticosteroid levels (Arlettaz et al., 2015; Cockrem, 2007), a class of steroid hormones involved in regulating the physiological stress response (hypothalamic-pituitary-adrenal axis activity) in various taxa (rodents: Gong et al., 2015; reptiles: Moore and Jessop, 2003; birds: Baugh et al., 2013b). Blanca et al (2018) proposed that variation in corticosteroid levels can be interpreted by response of energy metabolism to stress. They found that psychological stressors, such as noise exposure, lead to an increase in metabolic rate, which is reflected in elevated corticosteroid levels. This study provided evidence that acute stress can increase metabolic rate and may, therefore, be associated with personality as part of its influence on energy metabolism.

Personality also influences energy intake. For example, more explorative great tits (*Parus major*) are more competitive when accessing food and have a higher food intake (Cole and Quinn, 2011). Although being active, bolder and more explorative require more energy, individuals with such personality traits can afford this cost by increasing access to food sources, which not only supports the energetic costs of proactive behaviors but may also allow for a generally higher overall energy budget.

Three energy management models have been proposed to study the link between behavior and metabolism (Figure I.2, Mathot and Dingemanse, 2015): The allocation model assumes that the total energy budget is fixed and the energy available for metabolism is constrained by energy spent on behavior. This model predicts that individuals with an energy costly “proactive” personality type should have lower BMR. The independent model assumes that the energy budget for basic metabolism is independent of individual behaviors, suggesting no impact of personality type on metabolic rate. Finally, the performance model assumes that higher metabolic rate is associated with energetically costly behaviors, which provide a net energy gain, predicting an increase of BMR associated with “proactive” personality type. The relationship between personality, behavior and energy metabolism remain unclear, highlighting the need for further investigation of personality and metabolic traits, in particular in free-living populations (Jäger et al., 2017).

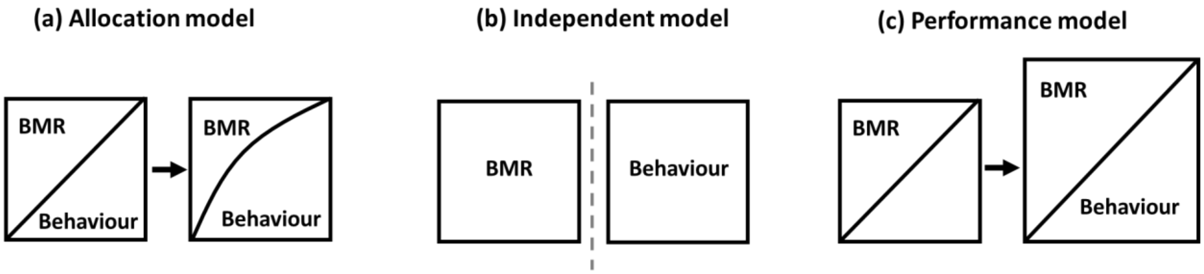

Figure I.2. Illustration of three energy management models for the relationship between energy available for behavior and BMR. Figure adapted from Mathot and Dingemanse, 2015.

I.3. Pace of life: continuum of personality, metabolism and life history

Increasing evidence supports the correlation between traits beyond behavioral characteristics, forming a syndrome of behavioral, life history, and physiology. The pace-of-life syndrome hypothesis suggests that closely related species should differ in a suite of physiological (e.g. metabolic, hormonal, immunity) and behavioral traits that have coevolved with their particular life-history, offering a framework that integrates behavioral and physiological traits with life history (Biro and Stamps, 2008; Careau et al., 2008; Wolf et al., 2007). Closely related species or populations can differ in pace-of-life depending on the given ecological conditions that favor a particular combination of traits. This concept was later extended to the concept of pace-of-life continuum (Réale et al. 2010). Rooted in the classic concept of r/K selection (MacArthur and Wilson, 1967; Pianka, 1970), it integrates life history, physiology and behavior along a “fast-slow” axis (Figure I.3). At the inter-specific and interpopulation levels, pace-of-life theory has been well supported by field studies: For example, tropical birds have a slow pace-of-life related to their temperature zone, with long life span, late maturity and fewer offspring produced (Wikelski et al., 2003; Wiersma et al., 2007). The pace-of-life of Trinidadian guppies (*Poecilia reticulata*) depends on predation pressure: populations living upstream under low predation rick have “slow” pace-of-life, characterized by slower development and later maturity, while populations downstream with high predation risk mature earlier and exhibit more proactive behaviors (Fraser and Gilliam, 1987; Reznick et al., 1996). In recent years, personality was included in testing the pace-of-life hypothesis: bolder marine gastropods grew faster and had higher resting metabolic rates (Cornwell et al., 2020). Even under artificial selection, domestic dog breeds that were shy had a longer life span and lower energy needs than aggressive breeds, supporting the interdependence of personality, metabolism and life-history traits (Careau et al., 2010).

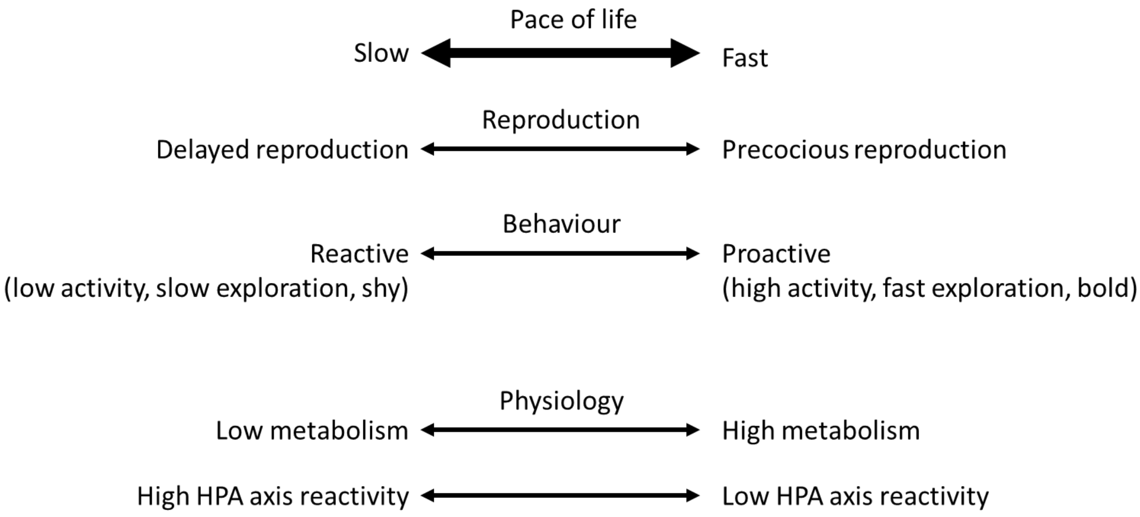

Figure I.3. Potential integration of life history, behavior and physiology traits long a pace-of-life continuum. Figure adapted from Réale et al., 2010.

When studying behavior under the pace-of-life framework, one interesting question that can be addressed is whether physiology and life history traits contribute to (or are associated with) individual variation in behavior. The pace-of-life syndrome predicts that behavioral traits such as high boldness, exploration or activity levels that increase resource acquisition at an expense of survival should be linked to a “fast” pace-of-life, as it increases the ability to compete for reproduction opportunities or reproductive resources (Montiglio et al. 2018; Réale et al. 2010). Several studies have found support for this hypothesis: In bighorn sheep (*Ovis canadensis*), bolder and more proactive rams had higher reproductive success but lower survival rates, consistent with a fast pace-of-life. Docile individuals, in contrast, exhibited delayed reproduction and greater longevity, exemplifying a slower pace-of-life (Réale et al., 2009). Superb fairy-wrens (*Malurus cyaneus*) showed a risk-taking behavioral syndrome: fast-exploring individuals were less likely to be present in the population after the age of 12 months (Hall et al., 2015). Finally, a meta-analysis on the intrinsic state and personality revealed that aggressive, bold explorative and active individuals have relatively high metabolic rates and body masses (Niemelä and Dingemanse, 2018).

However, the pace-of-life relationship within populations was not as well supported as between-population or species. Studies have found non-significant, even negative association contrary to what the pace-of-life hypothesis predicts. In a wild population of multimammate mice (*Mastomys natalensis*), exploration behaviors were not associated with survival; stress sensitivity was linked with decrease in survival, but only during food scared periods (Vanden Broecke et al., 2021). In Trinidadian guppies (*Poecilia reticulata*), metabolic rate, personality and growth rate showed individual variation, but were not associated with each other under challenging ecological situations, such as when food sources are limited and homogeneously distributed, the energy intake from actively foraging may not cover the energy cost in maintaining a proactive personality. Thus, the link between proactive personality with life history traits can be diminished, because it is generally maladaptive under these conditions. Another explanation for the absence of pace-of-life syndrome could be the occurrence of methodological biases. That is, behaviors that reflects personality traits are highly dependent on species characteristics, for example, exploration can be measured as hopping and flights between branches for birds (Dingemanse et al., 2003), or individual's visit to novel compartments in a maze test for rodents (Korpela et al., 2011). Behavioral differences between species makes it challenging to determine whether the measured behavioral variables can reliably detect individual personality type, or which aspect of personality it is actually reflects (Montiglio et al., 2018). One way to achieve more biologically meaningful behavioral measurements could be to use correlated variables that form behavioral syndromes, which provide a more integrated and reliable way of quantifying personality.

The pace-of-life hypothesis assumes that metabolism is the driver of individual behavior and life history (Careau et al. 2008; Biro and Stamps 2010; Réale et al. 2010, Montiglio et al., 2018). The prediction is consistent with the energy performance model; specifically, there should be a positive association between being proactive, high metabolic rate and a fast life history (Careau et al., 2008, Biro and Stamps 2010). However, studies testing this association within populations have so far provided inconsistent results. For example, in a study on common lizards (*Zootoca vivipara*), correlations between behavioral and metabolism parameters were weak, and expressed a marginally significant, positive correlation at the age of one year (Le Galliard et al., 2013). In wild-caught field crickets (*Gryllus pennsylvanicus*), bold individuals had a lower standard metabolic rate than shy individuals (Careau et al., 2019), supporting the energy allocation model, which contradicts to what the pace-of-life hypothesis suggests. In adult male guppies, the study population showed "proactive" syndromes, but it was not significantly correlated with resting metabolic rate (Godin et al., 2022). In response to these inconsistent results, Salzman et al. (2018) proposed that the pace-of-life syndromes may not always be obvious. That is, the correlation between life history, behaviors and energy metabolism could be flipped around under some ecologically constrained situations.

I.4. Desert rodent adaptations

The order Rodentia comprises more than 2,000 species that inhabit a wide range of terrestrial environments globally (Musser and Carleton, 2005). Rodents exhibit significant inter-specific variation in phenotypic traits in response to a variety of unpredictable environmental conditions. Examples of such an adaptation to ecological challenges occur in desert/semi-desert rodents, where the environmental conditions are generally harsh, with highly variable temperature and rainfall, and relatively short food abundant periods during the year. Such environments are especially challenging for small mammals because their small body size limits their ability to store energy and makes them less resistant to thermal stress (Klockmann et al., 2017). To compensate for these phenotypic limitations, desert rodents show a series of physiological adaptations, such as reducing urination, decreased metabolism and reducing energy expenditure by shrinking the size of non-essential organs (Rymer et al., 2016). Desert rodents have also developed a range of behavioral adaptations, including nocturnal or crepuscular activity patterns (Randall, 1993), burrowing or constructing above-ground shelters to avoid extreme thermal conditions (Jackson et al., 2002). Unlike physiological traits, behavioral adaptations allow direct interaction with, and even modification of, the current environment, enabling a more flexible response to rapid and unpredictable environmental changes (Lynn and Brown, 2009). The adaptive value of personality in such environments could be context specific: individuals with a proactive personality may have an advantage in competing for resources and reproduction during the resource abundant period (breeding season), while reactive individuals may more likely to survive the prolonged, resource-scarce periods.

I.5. The study species: *Otomys unisulcatus*

My study species is the bush Karoo rat (*Otomys unisulcatus*), a rodent endemic to arid environments in South Africa (Wolhuter et al., 2022). The bush Karoo rat is a diurnal, small (adult body mass 60 - 160 g) solitary rodent living in semi-arid habitats in the Succulent Karoo, South Africa. The species is breeding seasonally and has a short life expectancy of less than 2 years in the wild (Wolhuter et al. 2022). The species' breeding activity depends on rainfall (Wilson et al. 2017). In the study site, the Succulent Karoo, the breeding season is in the moist winter/spring (around July to November), followed by the non-breeding season in hot and dry summer (December to March) and autumn (April-June). Due to limited breeding opportunities and high mortality during the dry season, bush Karoo rat densities vary significantly between seasons; the population density is usually at its lowest point at the end of the dry season, then gradually increases as reproduction starts, typically reaching its maximum during the late breeding season.

Bush Karoo rats reach sexual maturity earliest between 5 - 6 weeks old in lab, and the reproductive period in the field spans over 3 - 4 months per year (Vermeulen, 1988; Wolhuter et al., 2022). In the field, new-born individuals usually have to survive through the following dry season and have their first reproductive activity in the next year, but those born early in the breeding season were able to reach sexual maturity within the same season of birth, thus have the chance to reproduce before the dry season arrives, reducing the risk of dying without leaving any offspring. Therefore, adopting a "fast" pace of life—trading off current survival for additional reproductive opportunities—seems advantageous for individuals born early in the season.

In contrast, individuals born later in the season needs to survive through the non-breeding season before having their first chance of reproduction. In addition, they also face greater survival challenges during their own development. During breeding season, population density continually increases while resource available for everyone decreases over time. Individuals born later were exposed to higher population densities and more intense competition for resources, such as food and other resources critical for survival. Adopting a "slow" pace of life can reduce energy cost and predation risk during resource-constrained period (dry season), thus have greater change to survive until the next breeding season. But the intense resource competition during the late breeding season, especially for limited resources, may also drive competitive behavioral and physiological traits in later-born individuals. Thus, early and late-born individuals differ in their access to resources, later-borns face more intense competition due to the increase of population density along the season (Figure I.4). In bush Karoo rats, limitation for scarce resources can be reflected in the availability of shelter, a critical resource for the survival of bush Karoo rats in this harsh desert environment (Wolhuter et al., 2022). In sum, the reproduction and survival differences induced by the date of birth within breeding season makes bush Karoo rats an ideal study species to investigate the relationship with behavior and physiology linked to life history.

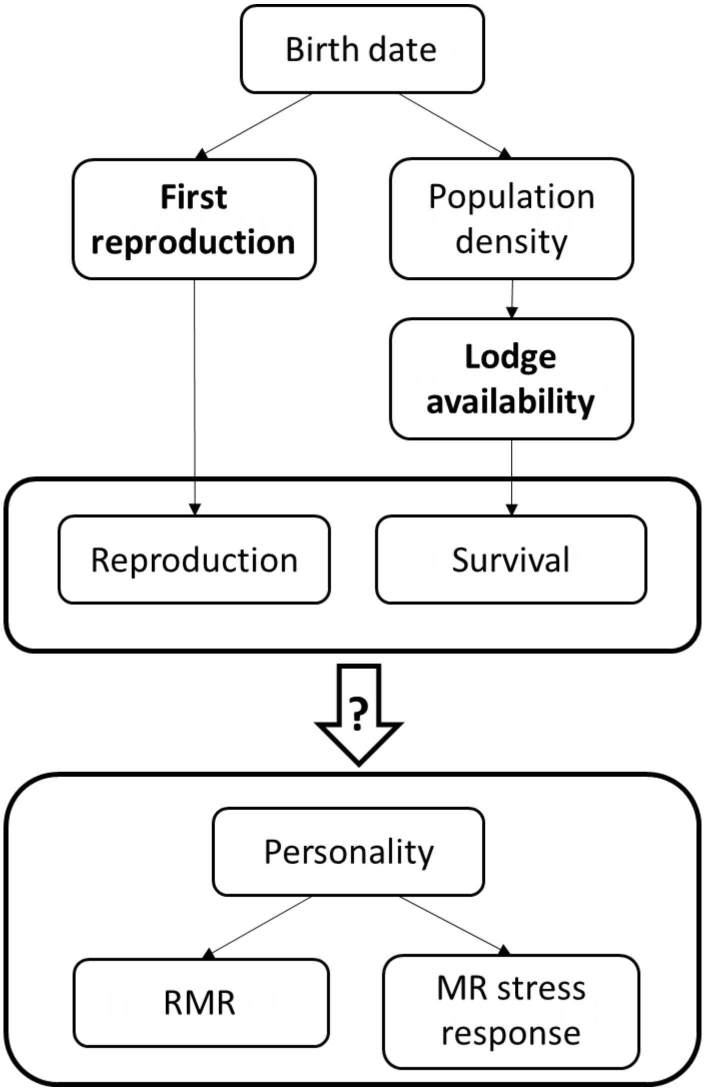

Figure I.4. Schematic representation of the mechanisms under study. (1) The influence of life history (birth date) on individual behavior (personality) and physiology (RMR: resting metabolic rate; MR stress response: metabolic rate response to acute stress), and (2) the association between personality and metabolic rate variables in bush Karoo rats.

Bush Karoo rats build unique construction of above-ground shelters, called "stick lodges". Lodges are strong structures consisted of interlaced stick and twigs, usually supported by a living shrub (Vermeulen, 1988). These observable structures (parabolic shape, mean volume 0.41 m^3) usually sheltered by one rat at a time, occupancy can be easily determined by the existence of fresh droppings and green plant materials left near the lodge entrances (Vermeulen, 1988).

The construction of stick lodges is a typical example of how behavior and its consequences extend beyond the individual's physical form, a concept known as the extended phenotype (Dawkins, 2016; Woods et al., 2021). As a typical way of manipulating the environment, extended phenotype of shelter construction can be found in many taxa (Hölldobler & Wilson, 2009; Barber, 2013; Kinlaw, 1999). Individuals interact and modify their external environments by creating architectures, most commonly as protective shelter, trapping/foraging tools or for interaction with other individuals (Hansell 2005). Depending on ecological characteristics, shelters can be built in a variety of ways. For example, bats can shelter in modified bird nest, ant/termite mound or make “tents” by modifying leaves (Page and Dechmann 2022). Many species of rodents dig extensive burrowing systems (Kinlaw, 1999). Such underground tunnels offer a mild micro environment for nesting and protection from large predators (Erlinge et al., 1983; Leahy et al., 2016). Underground foragers such as moles also use tunnels to search for insects or tubers (Kinlaw, 1999, Zhang, Zhang and Liu, 2003). Although less common, rodents are also architects above ground, constructing “lodges”, “mounds”, “houses” or “middens” with a variety of useable materials such as sticks, twigs, stones and even urine and feces (Figure 1.5). The stick lodges built by bush Karoo rats offers critical protection from the ambient environment, not only protecting them from predators, but also creates a micro-climate with relatively high humidity and mild temperature from the hot dry summer day to cold winter night (Brown and Willan, 1991; du Plessis and Kerley, 1991). As a complex animal architecture, the stick lodges are costly to construct, but are long-lasting structures that can be re-used by other individuals, and therefore represents an essential and valuable resource throughout individual lifetime. Existing stick lodges can be inherited and continually maintained, offering shelter for other conspecifics after the original builder disappears (Vermeulen and Nel, 1988; Onley et al., 2022).

Figure I.5. Sheltering behaviors in Myomorpha rodents. From left to right: using natural shelters, burrowing and lodge building.

From massive beaver dams to bush Karoo rat lodges, these above-ground structures are energetically expensive to build and maintain. They are usually critical resources for the survival of the building species but they can be vulnerable to unpredictable natural events: for example, packrat (*Neotoma* spp.) middens made from dry plant materials can persist for millennia, but can be easily destroyed by wildfire (Howard et al., 1959). Similar situations can be expected for other species that build their shelters with flammable materials such as dry sticks and twigs. The distribution of these building species may be constrained to areas where their shelter can persist over a long period with low risk of being destroyed by unpredictable events, such as areas of low fire risk (Kerley and Erasmus, 1992).

I.6. Study objectives and organizational layout

In this thesis, I am interested in the link between life history, physiology and behavior in a lodge-building species, the bush Karoo rat. My thesis includes one phylogenetic comparative study on the sheltering behavior of mouse-like rodents (Myomorpha), and two research chapters focusing on a wild population of bush Karoo rats (Figure I.6). The main aim was to investigate whether personality traits are influenced by an individual's birth date during the breeding season—a critical life history determination factor—and how these traits relate to physiology. I hypothesized that individuals born later in the season would adopt a more active, bold and explorative ('proactive') personality type, as a behavioral adaptation to the decrease of critical resources in the late breeding season. Additionally, I hypothesized that certain personality trait expressions would have energetic consequences, with proactive individuals exhibiting higher resting energy expenditure, and reactive individuals would be more sensitive to a stressful stimulus, reflected in metabolism as having higher metabolic rate increase after exposed to acute stressor.

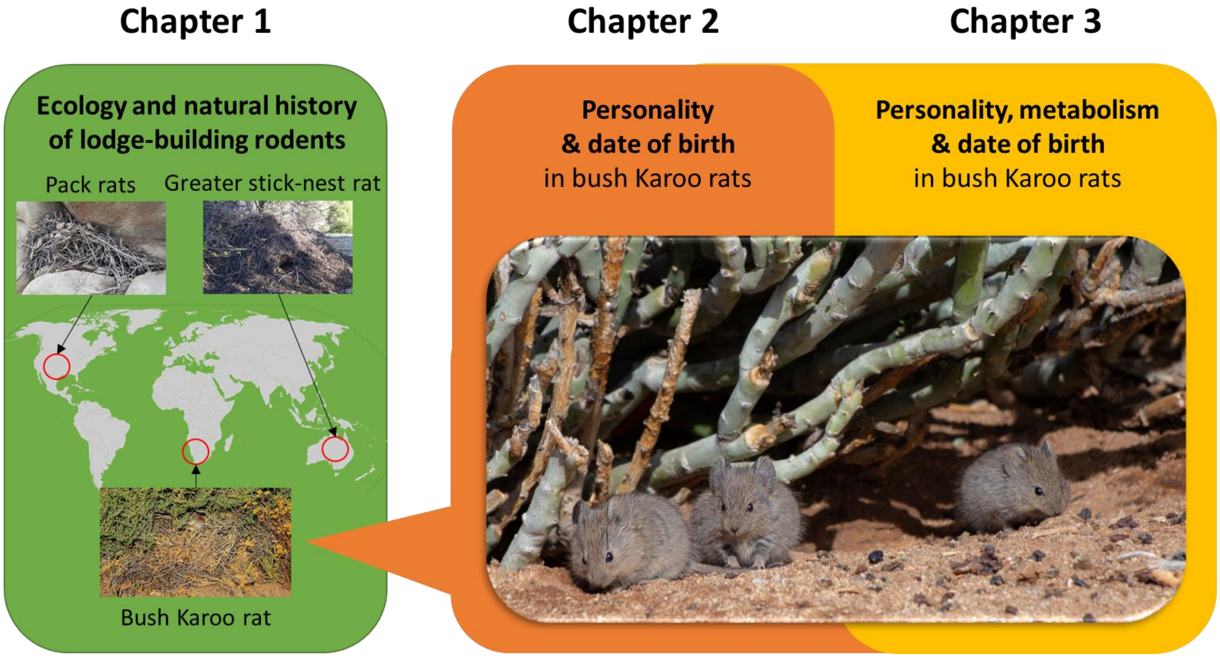

Figure I.6. Schematic representation of the structural framework used in this thesis. Chapter 1 covers questions on ecology and natural history of lodge-building in Myomorpha rodents. Chapters 2 and 3 focusses on the lodge-building bush Karoo rats. Chapter 2 explores the link between personality and life history and Chapter 3 focuses on the association between metabolism, personality and life history.

Chapter 1 − Ecological and natural history factors of lodge-building in Myomorpha

In the first part of my PhD, I conducted a phylogenetic comparative study of sheltering behavior to investigate the association with phylogeny and life history as well as ecological factors in mouse-like rodents. This study was done while I was waiting for my residence permit in France before I could obtain a visa for field work in South Africa. The aim of this study was to investigate which environmental and life history factors are linked to the evolution of sheltering behavior, especially the unique lodge-building, and to what extent it is affected by phylogeny. The results suggest that lodge-building species are more likely to inhabit arid areas with low fire risk, with a moderate to high phylogenetic signal. This chapter relates to the next two experimental chapters, because my study species is one of the rare lodge-building rodents, and lodges are a vital resource throughout its life cycle, with lodge availability possibly influencing personality.

Chapter 2 − Effects of birth date on personality in a small mammal: higher proactivity in later-borns

In my second chapter, I conducted a field study on individual differences in behavior of free-living bush Karoo rats. I investigated the behavioral and life history differences in earlier/later-born individuals, providing results on (1) the personality (behavioral consistency within individual), (2) the existence of “proactive/ reactive” behavioral syndromes and (3) personality differences depending on an individual’s date of birth. Although the pace-of-life hypothesis suggests that later-born individuals should adopt a “slow” pace-of-life and thus a “reactive” personality type because they do not have the opportunity to reproduce within the same breeding season of their birth, the results of my study provide evidence of the opposite association between personality and time of birth. Together with the evidence of increasing competition for of stick lodges as the breeding season progresses, the expression of pace-of-life syndromes may be altered by ecological constrains.

Chapter 3 − Associations between metabolic rate and personality are driven by date of birth

In the second empirical chapter, I investigated how individual metabolic rate, personality and life history are related to each other under the pace-of-life framework, testing about the (1) consistency in metabolic rate parameters, (2) association between personality and metabolic rate parameters and (3) time of birth as a potential driver for both personality and variation in metabolic rate. This study suggests that personality traits and metabolic parameters are independently linked to the date of birth within the breeding season, and further highlights the importance of considering metabolic stress response as a biologically relevant parameter.

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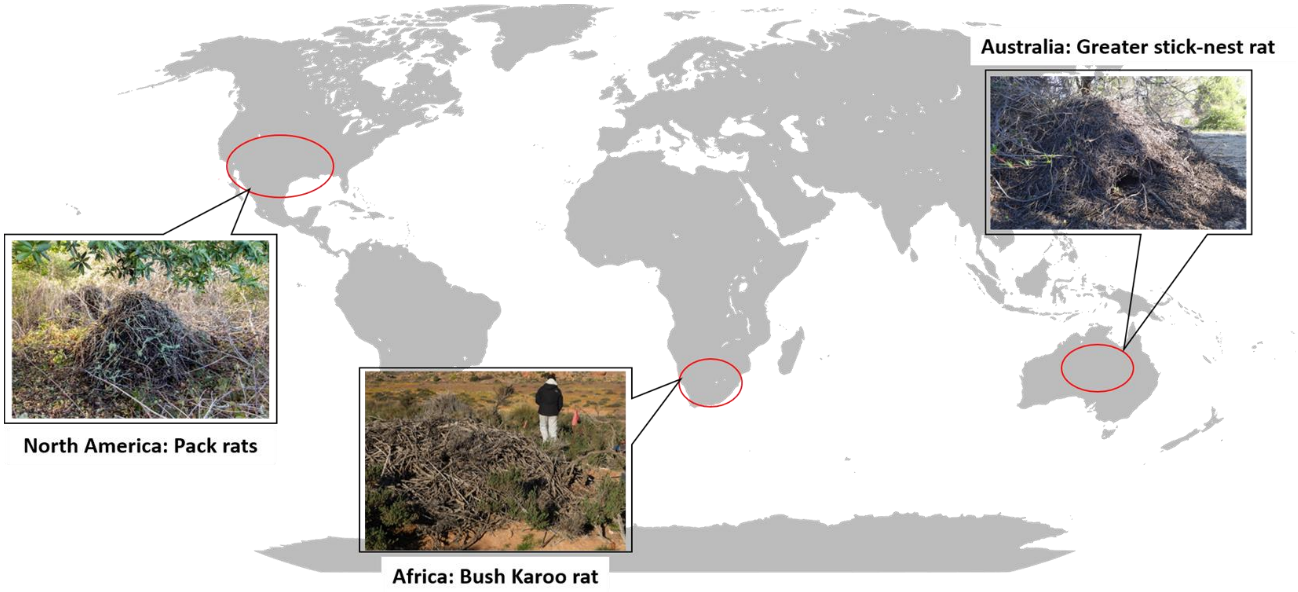
Chapter 1


Australia: Greater stick-nest rat
North America: Pack rats
Africa: Bush Karoo rat

Lodge-building in rodents: relationships with ecological and natural history factors

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II.1. Abstract

Mouse-like rodents often take cover in natural shelters or burrow underground where they build simple nests. A few species build extensive shelters above ground, called lodges, mounds or houses. Here we present the first phylogenetically controlled comparative study on the ecological factors of habitat heterogeneity, environmental aridity and fire risk related to nesting habits in mouse-like rodents (Myomorpha, 326 genera). 20 species from 7 genera were found to build lodges, and they mainly occur in arid environments with low fire risk. Most lodge-building species (14 out of 20) belong to the packrats (genus *Neotoma*), which in phylogeny only represent one event of evolution of lodge building and therefore limit the statistical power of the phylogenetically controlled analysis. The Bayesian phylogenetic mixed-effects models show a phylogenetic signal of 0.43 for 515 Myomorpha species. Under this moderate to strong phylogenetic relatedness, we did not find specific factors being associated to the evolution of sheltering habit in Myomorpha. We suggest studying the importance of aridity combined with low fire risk for lodge building on the species level, for example by studying the limits of species distribution ranges depending on these factors.

Keywords:

Myomorpha; lodge; shelter; phylogenetic; aridity; fire

II.2. Introduction

Many animals construct external structures as an adaption against the harshness of the local environment. Such structures extend beyond the individuals` body and are thus one example of extended phenotypes (Dawkins, 2016; Woods et al., 2021). Eusocial insects such as termites, ants and bees build nests that offer protection for hundreds to millions of individuals (Lüscher, 1961; Korb, 2003; Hölldobler & Wilson, 2009), many fish and bird species construct nests during the breeding season to incubate and raise their offspring (Barber, 2013). Among mammals, apes build leaf nests for sleeping (Prasetyo et al., 2009), bears prepare dens for hibernation (Diedrich, 2011), and rodents are famous for constructing burrow systems (Kinlaw, 1999, Hayes, Chesh & Ebensperger, 2007). The protective nature of external structures could be especially important for small animals as they often face high predation risk (Erlinge et al., 1983; Lima et al., 2001; Leahy et al., 2016, Deeming, 2023) and are prone to thermal stress (Blanckenhorn, 2000; Klockmann, Günter & Fischer, 2017).

As the largest order in mammals, rodents show a high diversity in ecological niches occupied and in shelter usage. Some use natural shelters such as tree holes and rock crevices, in which they build simple nests, or create their own architecture, most commonly underground burrows (Frank & Layne, 1992, Zhang, Zhang & Liu, 2003, Hayes, Chesh & Ebensperger, 2007), or/and relatively rare aboveground shelters (Whitford & Steinberger, 2010). Burrows offer protection for their nest, and for some species below ground foraging opportunities (Kinlaw, 1999, Zhang, Zhang & Liu, 2003). Fewer species build shelters above ground, which are called houses (Birkenholz, 1963), middens (Campos, Boeing & Throop, 2019) or lodges (Vermeulen, 1988, Wolhuter et al., 2022). Lodge building in rodents is rare and could represent an adaptation to specific environments.

Lodges are structures built above ground, usually made of plant material, offering protection for the nest which lays inside (Jackso et al., 2002). Beavers (*Castor spp.*) are famous for building extensive lodges inside ponds they create with beaver dams (Baker & Hill, 2003). North American packrats (*Neotoma spp.*) use urine, plant and animal materials to build middens above ground, which are extremely sturdy and can last for thousands of years after being abandoned (Betancourt, Devender & Martin, 2021). Bush Karoo rats (*Otomys unisulcatus*) from South Africa and greater stick-nest rats (*Leporillus conditor*) from Australia build extensive stick lodges which offer protection against the arid and hot climate (Vermeulen et al., 1988; Copley, 1999; Moseby & Bice, 2004; Robinson, 1975). For small rodents, lodges are energetically expensive to build but can offer protection for generations (Vermeulen & Nel, 1988; Onley et al., 2022).

Specific climate conditions can make the investment of lodge building adaptive. For example, the temperature inside the lodges of bush Karoo rats from semi-deserts in South Africa varies less than ambient environment: the temperature inside is higher than outside in cold winter nights, and lower in hot summer days (Du Plessis, Kerley & Winter, 1992). Water vapor pressure inside lodges is 64-74% in summer and 56-83% in winter, both varies less and is always higher than in the outside arid environment (Du Plessis et al., 1992). If lodges generally offer a favourable micro-climate, they may be especially adaptive in environments with extreme temperatures and aridity. Lodges built in arid and hot habitats may offer protection against the harsh ambient conditions, but the high temperatures and lack of rainfall can create low fuel moisture in such habitats. The dry plant material used to build these lodges is highly flammable and therefore vulnerable to wildfires (Kerley & Erasmus, 1992, Jackson, Bennett & Spinks, 2004). If lodges burn, then instead of offering protection they might represent a deadly trap. This leads to the prediction that lodges occur mainly in arid environments with low fire risk.

Ecological factors and natural history shape evolution, but how they influence and interplay with the evolution of lodge-building behavior is less clear. Ecological factors that can influence the evolution of lodge building include fire risk, aridity, and habitat heterogeneity. As sheltering habit may evolve as an adaptation to specific habitats, species that occur in multiple types of habitats may develop either a consistent sheltering habit that is universally adaptive to all the habitats they live in or the ability to show multiple sheltering habits depending on the local environment. Regarding natural history factors, the protective nature of lodges could be especially important for animals with small body sizes, as they are more sensitive to thermal stress (Blanckenhorn, 2000; Klockmann, Günter & Fischer, 2017), or alternatively, a larger body size may bring advantages in carrying building materials and in defending their precious lodges against competitors. Considering the overlap of food sources and building materials, plant-based diet can be expected to facilitate lodge building and maintenance, animals feeding on green plant materials may be more efficient in collecting sticks, and the food remains can contribute as building materials (Betancourt, Devender & Martin, 2021). Lodges may offer protection against the heat during the day for nocturnal species, or offer protection against predators for diurnal species

(Betancourt, Devender & Martin, 2021). In sum, the natural history factors of body size, diet and activity pattern might influence the evolution of lodge building. Despite these potential influences, how this distinct trait in sheltering habit may differentiate these lodge-building species from their relatives in ecological and natural history remains unknown.

We conducted a comparative study focusing on sheltering habits for mouse-like rodents (suborder Myomorpha) to determine what ecological and natural history factors were associated to lodge building. The extreme arid environment where the lodge building may be adaptive often associated with high climate fire risk, which puts the flammable lodges at risk. Specifically, we predicted that (1) lodge building is more common in arid environments as an adaption to highly variable or extreme ambient temperature/humidity and (2) lodge building is more common in areas with low fire risk.

II.3. Materials and Methods

II.3.1. Database on shelter use

We established a database on shelter use for mouse-like rodents (suborder Myomorpha). We searched for information of 1655 species of Myomorpha (classified by IUCN 2022) in the "*Handbook of the Mammals of the World*. Vol. 7. Rodents II" (Wilson et al., 2017) and found information on shelter use for 532 species (seven families, 201 genera). For 11 species, the description in the book was not clear enough to determine sheltering type (e.g., it was stated they use shelters without stating the type of shelter, or it was not stated whether they constructed shelters or used shelters constructed by other species), such that we searched for additional information online (publications, photos of the shelters), allowing us to add seven additional species into the database (included in the 532 species). Shelter type was categorized as natural shelter (nests inside dense vegetation, rock crevices, tree holes, or shelters build by other species), burrows, and lodges (shelters above ground constructed by sticks and other materials). Because some species can use more than one types of shelter, we classified shelter use into seven categories: lodge, burrow, natural, lodge + burrow, lodge + natural, burrow + natural, lodge + burrow + natural.

II.3.2. Natural history variables

As important natural history variables that may affect preferred sheltering types and the ability of shelter construction (see introduction), we recorded body mass and length, diet and activity patterns from the "*Handbook of the Mammals of the World.* Vol. 7. Rodents II" (Wilson et al., 2017). Habitat type was obtained from the species description in the IUCN Red List of Threatened Species. Habitat heterogeneity was then calculated as the total number of habitats occupied per species (Olivier et al., 2022, Qiu et al., 2022). Table 1 summarises the categories of these variables.

II.3.3. Aridity

Aridity was estimated based on the Koppen-Geiger climate classification map (Beck et al., 2018), which presents global climate classification maps from 1980 to 2016. Based on threshold values and seasonality of monthly air temperature and precipitation, the Koppen-Geiger system classifies global climate into five main classes: tropical, arid, temperate, cold and polar (Beck et al, 2018). To focus on aridity, we coded the arid areas as one and non-arid areas as zero. By comparing this map with species distribution polygons, we could determine how much of the species distribution area falls into the arid climate classification. The levels of aridity for each species was then calculated by the percentage of arid area in each species distribution polygon, ranging from zero (no distribution in arid climate) to one (totally distributed in arid climate).

Species distribution information was obtained from the IUCN Red List of Threatened Species, based on definitions of presence, areas coded as "extant", "probably extant", "possibly extant" were considered as the distribution area of the species. From the 516 species included in the phylogenetic model, the distribution of 12 species contained areas where the species were introduced (category "Extant & Introduced" in the IUCN). Only three species had considerable introduced area (Polynesian rat, *Rattus exulans*; House rat, *Rattus rattus*; Oriental house rat, *Rattus tanezumi*).),We included these areas in this study because (1) the species would not be able to become resident in introduced area if they are not pre-adapted to the local environments and (2) origin and introduced area were sometimes difficult to distinguish, and natural dispersal may be involved, especially for globally spread species such as the house mouse (*Mus musculus*), for which the IUCN Red List of Threatened Species gives no information about their native origin.

II.3.4. Fire risk

We were interested to know if species building lodges do not occur in areas that frequently burnt (high fire risk). Thus, we calculated fire risk by the proportion of historically burnt area in this study**.** The data was produced by a data mining process using MODIS burnt area product Collection 6 (MCD64A1, https://lpdaac.usgs.gov/products/mcd64a1v006/). The entire product is available under the umbrella of the Global Wildfire Information System (GWIS, Boschetti et al, 2022), which provides numerous data services to report and forecast the global activity of wildfire. With this global burnt area map, we used all data available from 2001 to 2020, information was given by tile (smallest special unit that sum up the fire event and burnt area of each fire, 0.25*0.25 degree). Burnt area was acquired daily with accuracy of one hectare, overlapping in the same area was counted separately (see Artés et al. 2019 for more details).

By comparing the species distribution ranges with this fire dataset, we were able to obtain the cumulated burnt area from 2001 to 2020 (km^2, cumulated data of 20 years) in each species distribution range. Specifically, for each species, the tiles from the fire map that had its centroid intersect located within the species distribution polygon were selected to add up to the burnt area, multiple fires events from the same tile of the 20 years were included. This value was then divided by species distribution range (km^2) to get a comparable fire risk between species. (For detailed calculation, see SM II.A in Suppl. Materials).

II.3.5. Statistical analysis

Phylogenetic comparative analyses were conducted in R v.3.6.1, using the R packages brms (Bürkner. 2017; Bürkner. 2018), RStan (Stan Development Team. 2020) and Rethinking (McElreath. 2020). The modelling and R code were adapted from Jaeggi et al 2020 and Qiu et al 2022. Habitat heterogeneity, aridity and fire risk were included in the Bayesian phylogenetic mixed-effects model to estimate whether they have an influence on the evolution of shelter use. Aridity was weakly correlated with fire risk (Pearson's $r = -0.02$), we therefore included them as independent variables in the model. We conducted an alternative model to test for the potential interaction between aridity and fire risk, which did not give any significance differences; therefore, we excluded the interaction from the main model. The phylogenetic relationships and their uncertainty were represented by a sample of 100 phylogenetic trees, downloaded from the phylogeny subsets of online database VertLife (http://vertlife.org/phylosubsets/), which produce distributions of trees with subsets of taxa (Jetz et al., 2012).) Phylogenetic signal (ʎ) was calculated as the proportion of random factors variance captured by the phylogenetic random effects, representing the tendency of related species to resemble each other more than species drawn at random from the same tree. The model employs a categorical error distribution, fitted with two Markov Chain Monte Carlo (MCMC) chains, undergoing a total of 2000 iterations each, with the first 1000 iterations in each chain designated as burn-in to allow for parameter convergence. The shelter categories were combined to simplify the model and increase statistical power: For, the main analysis, we used three categories: natural shelter (natural), burrows (burrow, burrows + natural) and lodge (lodge, lodge + burrow, lodge + natural). As some lodge-building species also dig burrows, we ran an additional phylogenetic analysis with four categories: natural shelter (natural), burrows (burrow, burrows + natural), lodge (lodge, lodge + natural), burrow + lodge.

II.4. Results

II.4.1. Shelter usage

Out of the 532 species of Myomorpha with available data, 145 species use natural shelters, 320 species dig burrows and 14 species construct lodges, with the remaining 53 species having more than one form of shelter use: 47 species use natural shelters and dig burrows, one species construct lodges and use natural shelters, five species construct lodges and dig burrows. No species use three types of shelters at the same time, reducing the shelter usage categories to six for statistical analysis (Figure II.1). In total we found 20 species that build lodges. Of these, three species (Round-tailed muskrat, *Neofiber alleni;* Common muskrat, *Ondatra zibethicus;* Water mouse, *Xeromys myoides*) are semi-aquatic and construct lodges upon or nearby water, the other 17 species are terrestrial and construct dry lodges on the ground. 14 of 20 lodge building species belongs to the packrat (*Neotoma*), a lodge-building genus. One exception in this genus is *N. mexicana*, which generally does not build lodges and was thus recorded as non-lodge building in our data source. However, it’s important to note that they can use lodges build by other species and were reported to be capable of building lodges inside naturals shelters such as rock cracks (Cornely & Baker, 1986).

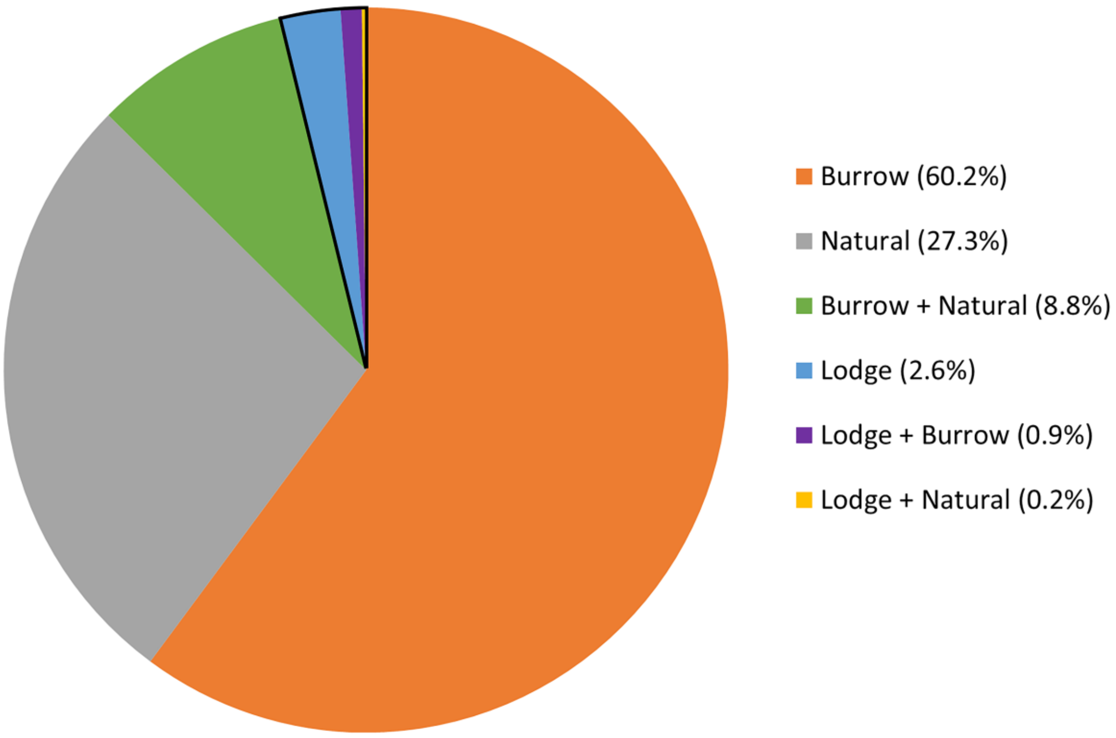

Figure II.1. 532 Myomorpha species with available information on shelter use. Burrow: only construct burrows; Natural: only use natural shelters; Burrow + Natural: construct burrows and use natural shelters; Lodge: only construct lodges; Lodge + Burrow: construct lodges and burrows; Lodge + Natural: construct lodges and use natural shelters. The 20 species that build lodges are framed by black line.

II.4.2. Description of natural history and ecological factors

The majority species were herbivorous, and this was more pronounced in lodge-building species (Figure II.A in Suppl. Materials; lodge 89%, burrow 54%, natural 56%). Most species were nocturnal independent of shelter use (Figure II.B in Suppl. Materials). The most common habitat was forest (270 species), followed by shrubland (240 species), grassland (216 species) and artificial (191 species). Mean habitat heterogeneity was two and did not differ significantly between the species with different sheltering habit (Figure II.C in Suppl. Materials). There also no significant differences in body length and body mass (Figure II.D in Suppl. Materials), but lodge-building species had a lower body length/mass ratio than others (Table II.A in in Suppl. Materials; lodge: 1.2 ± 1.07; burrow 2.4 ± 1.5; natural 2.2 ± 1.39).

The mean aridity of lodge-building species was higher than species that dig burrows or live in natural shelters (lodge: 0.566 ± 0.416; burrow: 0.426 ± 0.406; natural: 0.158 ± 0.260; Figure II.2, Table II.A in in Suppl. Materials). Fire risk was lowest where lodge-builders occur (lodge: 0.210 ± 0.324, burrow: 0.725 ± 2.231; natural: 0.720 ± 1.345; Figure I.2, Table II.A in Suppl. Materials).

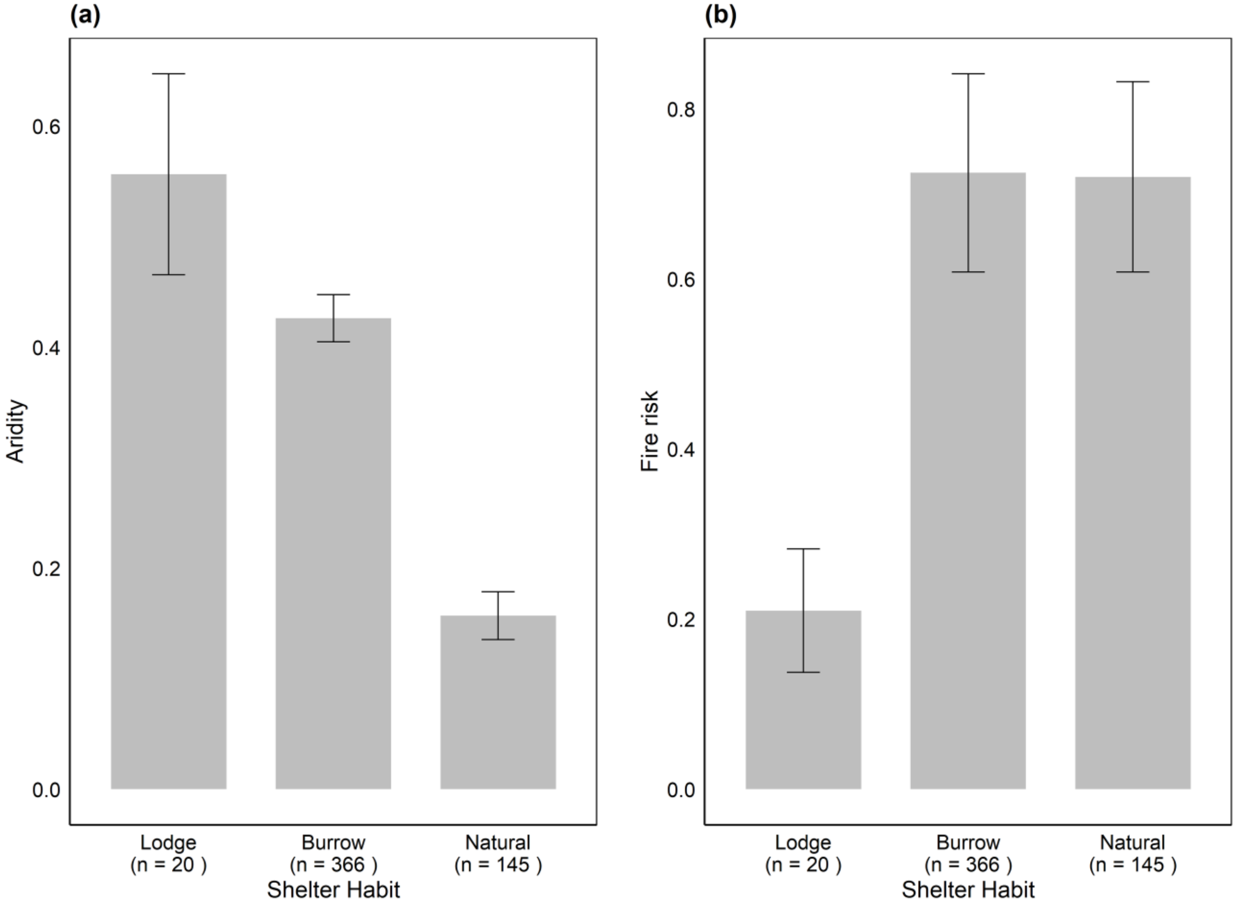

Figure II.2. The association of sheltering habit with (a) aridity, range from 0 (no distribution in arid habitat) to 1(totally distributed in arid habitat) and (b) fire risk, total area burnt during 20 years within the species distribution range (km^2)/species distribution range (km^2), both as mean ± SE. Data available for 531 Myomorpha species.

II.4.3. Phylogenetic comparative analyses

The phylogenetic signal (ʎ=0.43) was moderate to high for the 515 Myomorpha species in the model. Phylogenetic distribution showed six independent evolutionary origins of lodge building behavior (Figure II.3). In the phylogenetically controlled analysis the associations of lodge building with ecological factors (habitat heterogeneity, aridity and fire risk) were non-significant (Figure II.4). The additional model with 4 categories gave similar results (Figure II.E in Suppl. Materials).

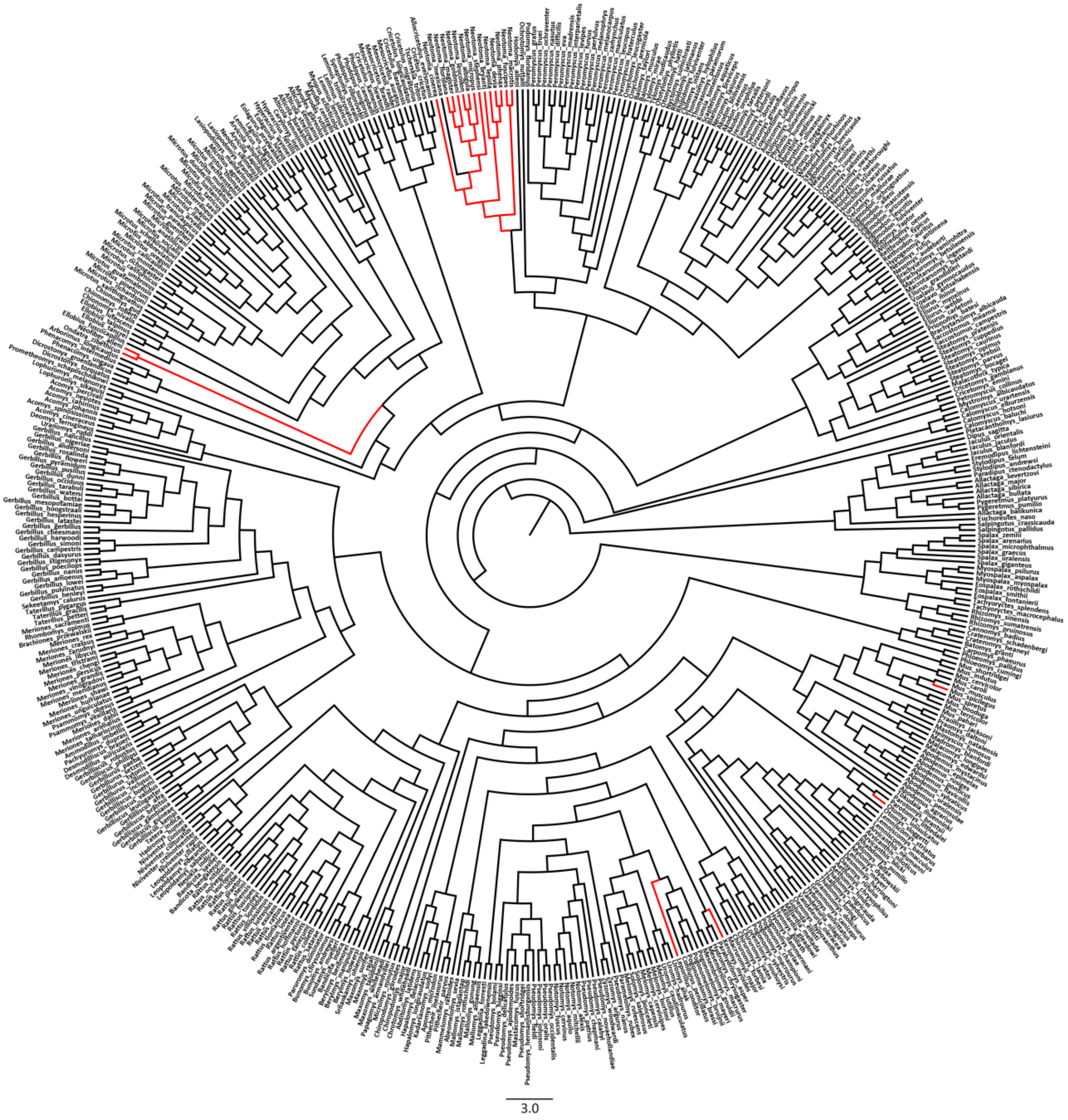

Figure II.3. Phylogeny of 532 Myomorpha species and the occurrence of lodge building. Red branches represent the lodge-building species.

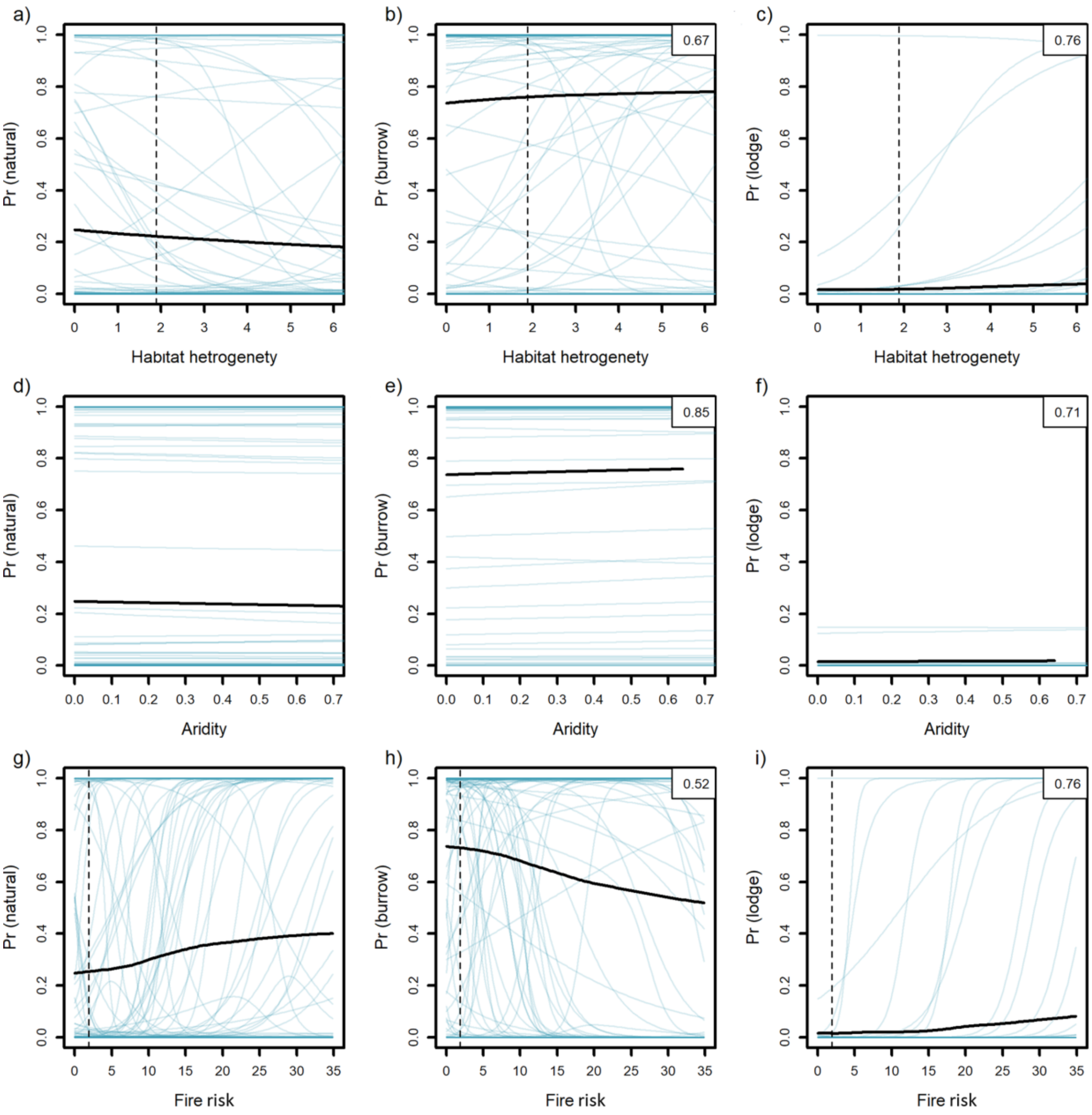

Figure II.4. Illustrating evolutionary transitions in sheltering habit as a function of the predictors. Columns show (from left to right) the probability of natural shelter, burrows, lodge, while rows show (from top to bottom) predicted changes in those probabilities as a function of number of habitat (a–c), aridity (d–f) and fire risk (g–i). The numbers in the legends are the posterior probabilities (PP), i.e. the proportion of the posterior distribution that supports a given association; these were not available for natural shelter, as this was the reference category. Within each row, all other predictors were held at their baseline value. Solid black lines are the predicted means, thin coloured lines are 100 random samples drawn from the posterior to illustrate uncertainty.

II.5. Discussion

We studied whether lodge building rodents occur especially in harsh arid areas with low fire risk, which would benefit them with a mild micro-climate within the lodge without the risk that their lodge becomes a deadly burning trap. Our descriptive results correspond with this hypothesis: lodge building species occur in arid areas with low fire risk. Lodge building is a conspicuous behavior, but worldwide only 20 myomorph rodent species (4% of studied species) have been reported to build lodges. However, when controlling for phylogeny, neither aridity nor fire severity remained as a significant predictor for the evolution of lodge building. This is probably due to the fact that most lodge species belong to one single genus, the packrats (*Neotoma* spp.), reducing the number of independent evolutionary origins to only six. Two evolutional pathways for lodge building did not associate with low aridity, which were species building lodges nearby water, as is also known for several species of another rodent suborder, the Castorimorpha (Beavers, Baker & Hill, 2003).

Wildfires directly threaten the survival of a variety of animals (Jolly et al., 2022). Small mammals cannot run away from wildfires but seek protection in shelters (Ford *et al.*, 1999). Observations suggest that not many rodents can escape from wildfires unless protected by underground burrows (Howard, Fenner & Childs, 1959). Wildfires can kill rodents directly and reduce their survival probability after fires. As fire destroy above ground shelters, they additionally increase predation risk (Pastro, 2013). Lodges are usually made of dry plant material in environment with low humidity and are thus vulnerable to fire. Fire vulnerability has been observed in packrats (*Neotoma* spp.), which are reluctant to vacate their lodges and likely die under fire event (Howard et al., 1959; Simons, 1991). Although some lodge-building species can dig burrows underneath their lodges, this cannot protect their expensive and flammable lodges from being burnt down. A burning lodge would likely kill the rodent hiding in it, and even if it survives, it would loss its protecting shelter.

Our study points to two strategies for lodge-building species to avoid fire. Three semi-aquatic species build lodges near water, making fire unlikely to ignite their wet lodges. Similar tactics are observed in non-myomorph rodents such as the two species of beavers (*Castor spec*.), which construct lodges near waters with sticks and branches (Baker & Hill, 2003). Most lodge-building species (17 of 20) in Myomorpha habituated in arid environments, based on the hot weather with low humidity, they face a relatively high theoretical fire sensitivity. However, the actual fire risk was very low for lodge building species, probably because their arid environments had little fuel available to support wildfires. Many arid environments are associated with low plant productivity (Turner & Randall, 1989; Miranda et al., 2009; Yue et al., 2020), which does not provide a lot of natural shelters but also makes fires unlikely to spread: if a fire starts, it simply runs out due to patches without any burnable material (McLaughlin & Bowers, 1982; Pausas & Keeley, 2021). For example, the bush Karoo rat (*Otomys unisulcatus*) occurs in the arid and hot Succulent Karoo of South Africa, where wildfires cannot spread as there is not sufficient plant material, but it does not occur in South African savannah habitat, where wildfires occur regularly (Kruger et al., 2006).

The dataset we used to calculate fire risk was based on daily observed fires with threshold 100×100m (by hectare) for a period of 20 years, such that fires that occur in intervals longer than 20 years were not represented. The dataset does allow for the detection of relatively small fires, however, fires with burnt areas smaller than 1ha were not represented. Even in areas with a high fire risk, there might be pocket areas that were less burnt, and in areas with low fire risk, small fires might occur in patches with sufficient fuel., Whether such local environmental characteristics influence species distribution would be interesting to study, especially to understand the variation in distribution of a species within its distribution range.

Our descriptive results agree with the hypothesis that lodge-building species are more likely distributed in arid environments with low fire risk, but these effects were not significant when controlled for phylogeny. Phylogenetically controlled models take the evolutionary relatedness of species into account (Hadfield & Nakagawa, 2010), and the 20 lodge-building species fall into seven genera (two of them closely related) of two (seven in total) myomorph families. Most (14 of 20) of the lodge-building species are packrats (*Neotoma* spp.), such that their data are phylogenetically dependent, representing only one independent evolutionary transition. While only approximately 1/3 of myomorph species had data on shelter usage, the use of lodges is very conspicuous and our data source has probably reported for most species that do build lodges. Thus, it is unlikely increase the statistical power of our analysis by including more species that build lodges. In summary, our result suggests lodge-building species often distribute in areas characterized by low fire risk, during evolutional processes, they may have persisted in areas with less incidence of large and intense fires, possibly due to low fuel loads.

Two evolutionary transitions to lodge building occurred in species living in wetlands and along waterways. These species (*Neofiber alleni, Ondatra zibethicus, Xeromys myoides*) live in regions with an overall three times higher fire risk compared to the other lodge-building species (0.63 *vs.* 0.21). However, within these habitats they choose aquatic niches for lodge building which significantly reduces the likelihood of their lodges being burnt down. Therefore, these species suggest another possibility for the evolution of lodge building. The vulnerability of lodges to fire could be reduced by either (i) the environment being too wet to allow lodges to ignite, or (ii) the environment has low primary productivity and does not produce sufficient fuel to maintain fires.

Based on the result of this study, we suggest future studies on lodge-building rodents should focus on specific species to test whether aridity combined with low fire risk is associated with the limitation of their distribution range, for example, this would predict that the range of lodge-building species ends where fire risk increases, or that in these areas they use different shelters than lodges. In addition, studies on specific species also help capturing the effect of short and patched fires with smaller spatial and time scales, which are likely underestimated in studies conducted in global scale. Most lodge-building species are folivores (*Otomys*, *Leporillus*, many species of *Neotoma*), some eat seeds and fruits (*Mus spicilegus*, *Neotoma phenax*) and one even eats invertebrates (*Xeromys myoides*). The mainly folivores diet is consistent with their sheltering habit as lodges are mainly constructed with plant material and thus also offer a food source directly at the shelter. Our descriptive results suggested that lodge-building species have larger body size (body mass/length ratio) than those living in natural shelters or burrows, which may bring advantages for them to construct and defend their lodge against other rodents (Schradin & Pillay, 2005; Schradin, 2005). As these descriptive results are not controlled by phylogeny, we cannot determine to what extent the association is biased by their phylogenetic relatedness. It would be interesting to have further investigation on the natural history traits commonly shared by lodge builders and the potential interaction with ecological factors, for example if lodge-builders becomes larger when faces high interspecific competition for their lodges. Therefore, studies comparing the body size between lodge-building species with sympatric non-lodge building rodent species would be useful to test this potential association.

Conclusions

Our study investigated possible associations between ecology, natural history and sheltering habits in mouse-like (myomorph) rodents. The descriptive result suggests that lodge-building species are mostly herbivorous, tend to have larger body size than those who live in burrows or natural shelters, and are more likely to occur in arid environment with low fire risk. However, lodge-building remains a rare sheltering strategy for mouse-like rodents (3.7% of species), and the high relatedness between those species makes it difficult to test these associations in phylogenetically controlled studies. In sum, the associations found in our study should be tested rather on a species than comparative level. For example, a previous study on bush Karoo rats suggested that their distribution was limited by wildfire (Kerley & Erasmus, 1992). We suggest to study lodge building rodents such as the South African bush Karoo rat or the Australian stick-lodge rat toto test the predictions: (1) lodge builder are larger than other sympatric rodents, and (2) lodge builders have a species distribution range restricted by aridity (species distribution more arid than area around it) and (3) fire risk.

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II.6. Supplementary Material

SM II.A. Calculation of fire risk

- Formula

The fire risk (R_i) for species *i* was calculated as:

$$R_i = \frac{A_{\text{burnt},i}}{A_{\text{distribution},i}}$$

$A_{\text{burned}, i}$ is obtained by cumulating the burnt areas within the distribution range of species *i*, including multiple fire events over the 20 years.

$A_{\text{distribution, i}}$ is the total geographical area covered by the distribution of species *i*.

- Data source

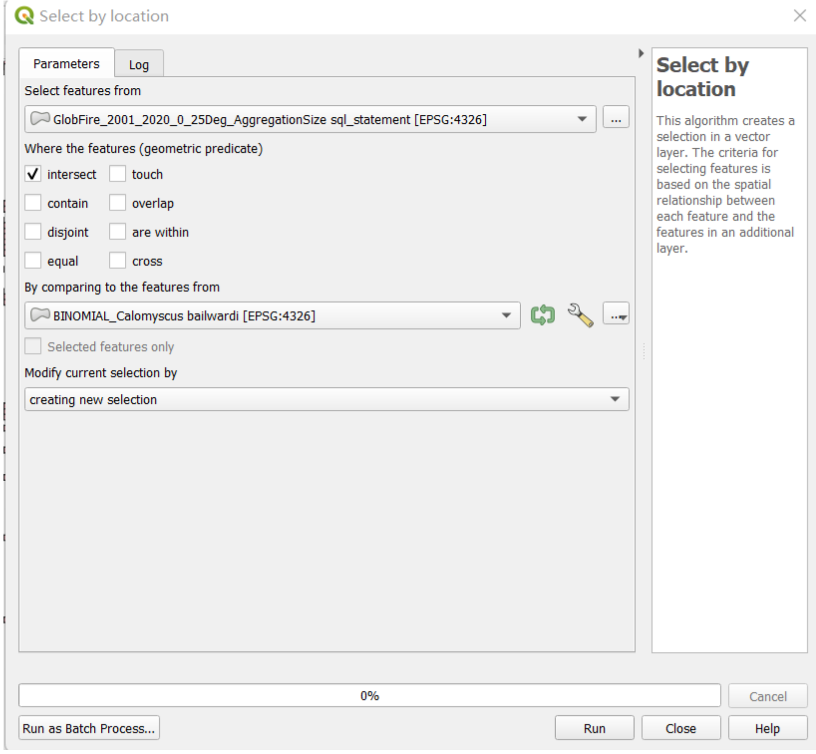
The global burnt area map was produced by a data mining process using MODIS burnt area product Collection 6 (MCD64A1, https://lpdaac.usgs.gov/products/mcd64a1v006/), available under the umbrella of the Global Wildfire Information System.

The map uses tiles as area measurement unit:
Tile: 0.25*0.25 degree tile, 770 km^2, 1 tile can have multiple Fid
Fid: months when fire occurred, a fid can have multiple events (number of fire) including fire range (burnt area) of each event

- Calculation in QGIS

Select tiles that overlap with species distribution polygon

1. Load the global burnt area map in QGIS
2. Load polygon of the species needs to be calculated in QGIS
3. Open “Select by location” function
4. Select features from the **map layer**, select “**Intersect”**. select “**the species polygon”**. for “by comparing to the features from”. Hit **Run**.
5. Right click the map layer, Export – Save selected features as – Format XLSX OR CSV



Select by location

Select features from: GlobFire_2001_2020_0_25Deg_AggregationSize sql_statement [EPSG:4326]

Where the features (geometric predicate): ☑ intersect ☐ touch ☐ contain ☐ overlap ☐ disjoint ☐ are within ☐ equal ☐ cross

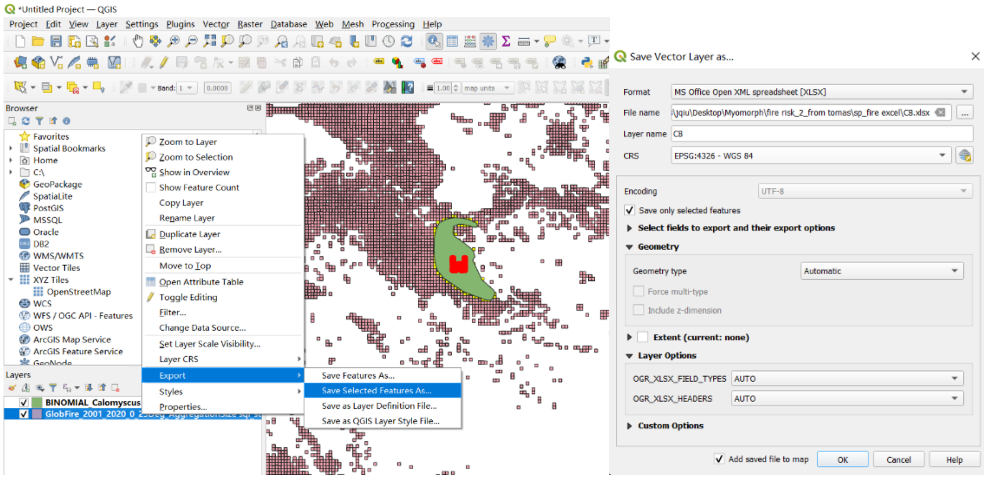
By comparing to the features from: BINOMIAL_Calomyscus bailwardi [EPSG:4326]

☐ Selected features only

Modify current selection by: creating new selection

Select by location

This algorithm creates a selection in a vector layer. The criteria for selecting features is based on the spatial relationship between each feature and the features in an additional layer.



Layers: ☑ BINOMIAL_Calomyscus; ☑ GlobFire_2001_2020_0_25Deg_AggregationSize_sql_st…

Export → Save Selected Features As...

Save Vector Layer as...

Format: MS Office Open XML spreadsheet [XLSX]

File name: :\jqiu\Desktop\Myomorph\fire risk_2_from tomas\sp_fire excel\CB.xlsx

Layer name: CB

CRS: EPSG:4326 - WGS 84

Encoding: UTF-8

☑ Save only selected features

Geometry type: Automatic

☐ Force multi-type

☐ Include z-dimension

☐ Extent (current: none)

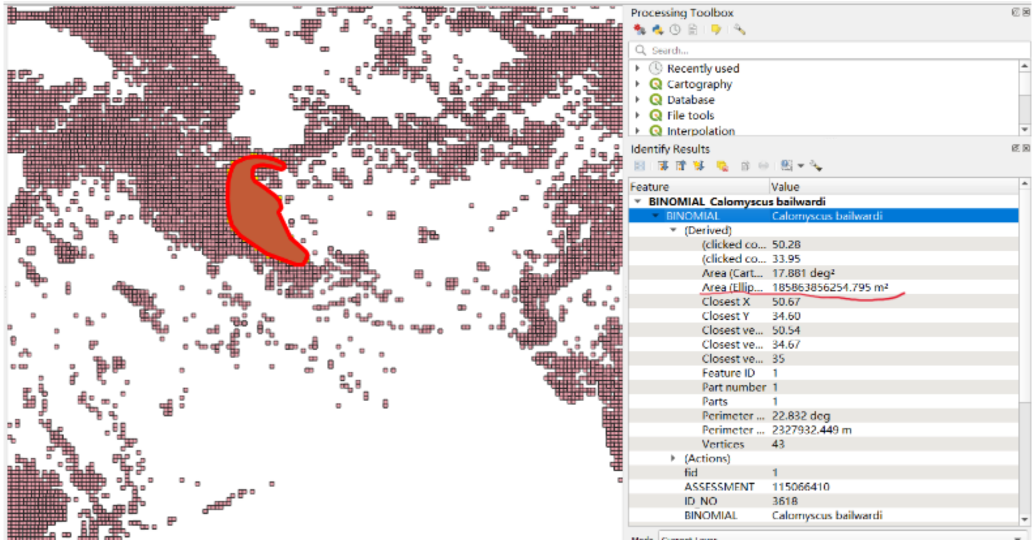
OGR_XLSX_FIELD_TYPES: AUTO

OGR_XLSX_HEADERS: AUTO

☑ Add saved file to map

Number of fire events per km^2

1. Open EXCEL file
2. Convert m^2 to km^2: Record “species polygon *0.000001” in **I1**
3. Calculate sum of number of fire **=SUM(G:G) in I2**
4. Number of fire event per hectare **= I2/I1**



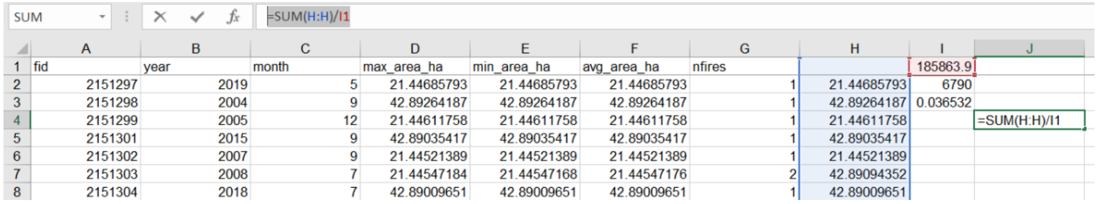
Feature	Value
BINOMIAL_Calomyscus bailwardi	
BINOMIAL	Calomyscus bailwardi
(Derived)	
(clicked co...	50.28
(clicked co...	33.95
Area (Cart...	17.881 deg²
Area (Ellip...	185863856254.795 m²
Closest X	50.67
Closest Y	34.60
Closest ve...	50.54
Closest ve...	34.67
Closest ve...	35
Feature ID	1
Part number	1
Parts	1
Perimeter ...	22.832 deg
Perimeter ...	2327932.449 m
Vertices	43
(Actions)	
fid	1
ASSESSMENT	115066410
ID_NO	3618
BINOMIAL	Calomyscus bailwardi

Total burnt area in 20 years/species distribution area

1. Calculate total burnt area for each fid

   F * G*0.01 in H for the entire column

2. **=SUM(H:H)/I1**



=SUM(H:H)/I1

	A	B	C	D	E	F	G	H	I	J
1	fid	year	month	max_area_ha	min_area_ha	avg_area_ha	nfires		185863.9	
2	2151297	2019	5	21.44685793	21.44685793	21.44685793	1	21.44685793	6790	
3	2151298	2004	9	42.89264187	42.89264187	42.89264187	1	42.89264187	0.036532	
4	2151299	2005	12	21.44611758	21.44611758	21.44611758	1	21.44611758		=SUM(H:H)/I1
5	2151301	2015	9	42.89035417	42.89035417	42.89035417	1	42.89035417		
6	2151302	2007	9	21.44521389	21.44521389	21.44521389	1	21.44521389		
7	2151303	2008	7	21.44547184	21.44547168	21.44547176	2	42.89094352		
8	2151304	2018	7	42.89009651	42.89009651	42.89009651	1	42.89009651		

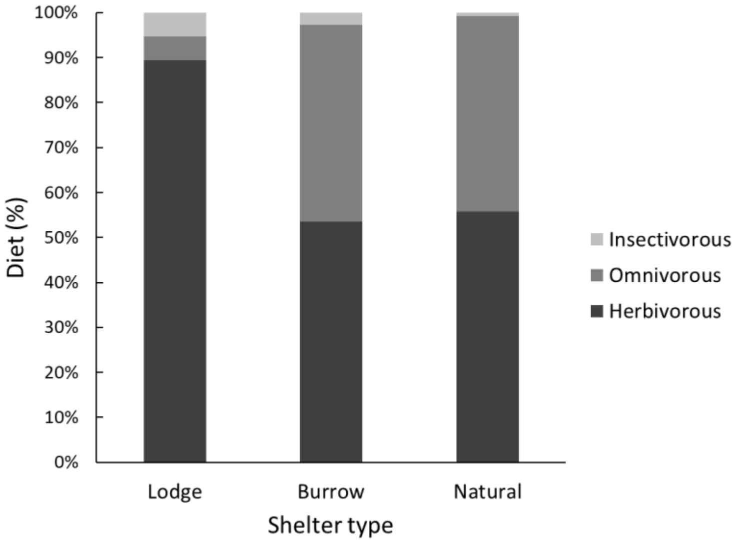


Figure II.A. Diet of myomorph rodents with different shelter habits. Lodge: species that construct lodges (may in addition use natural shelters or dig burrows); Burrow: species that dig burrows (may use natural shelters but do not construct lodges); Natural: species that only use natural shelters. Data available for 327 burrowing species, 19 lodge-building species, and 131 natural sheltering species.

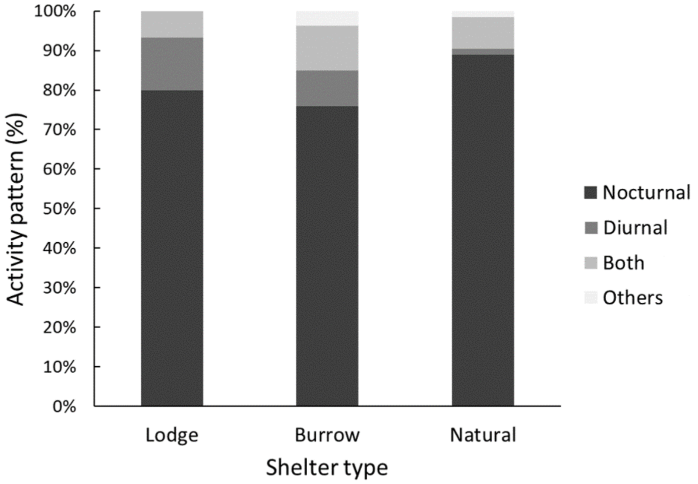


Figure II.B. Activity pattern of myomorph rodents with different shelter habits. Lodge: species that construct lodges (may use natural shelters or dig burrows); Burrow: species that dig burrows (may use natural shelters but do not construct lodges); Natural: species that only use natural shelters. Data available for 325 burrowing species, 15 lodge-building species, and 126 natural sheltering species.

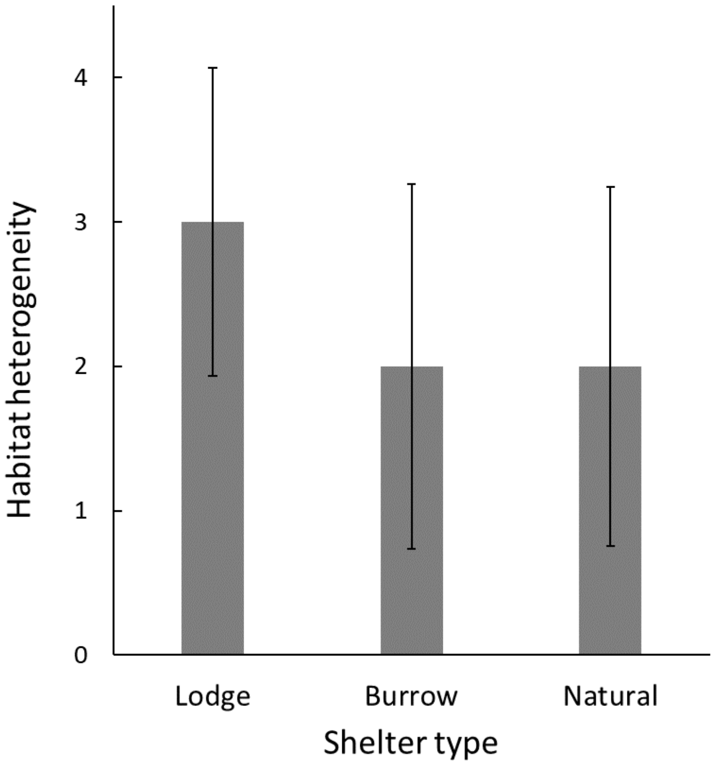


Figure II.C. Habitat heterogeneity of myomorph rodents with different shelter habits, mean ± SD. Lodge: species that construct lodges (may use natural shelters or dig burrows); Burrow: species that dig burrows (may use natural shelters but do not construct lodges); Natural: species that only use natural shelters. Data available for 367 burrowing species, 20 lodge-building species and 145 natural sheltering species.

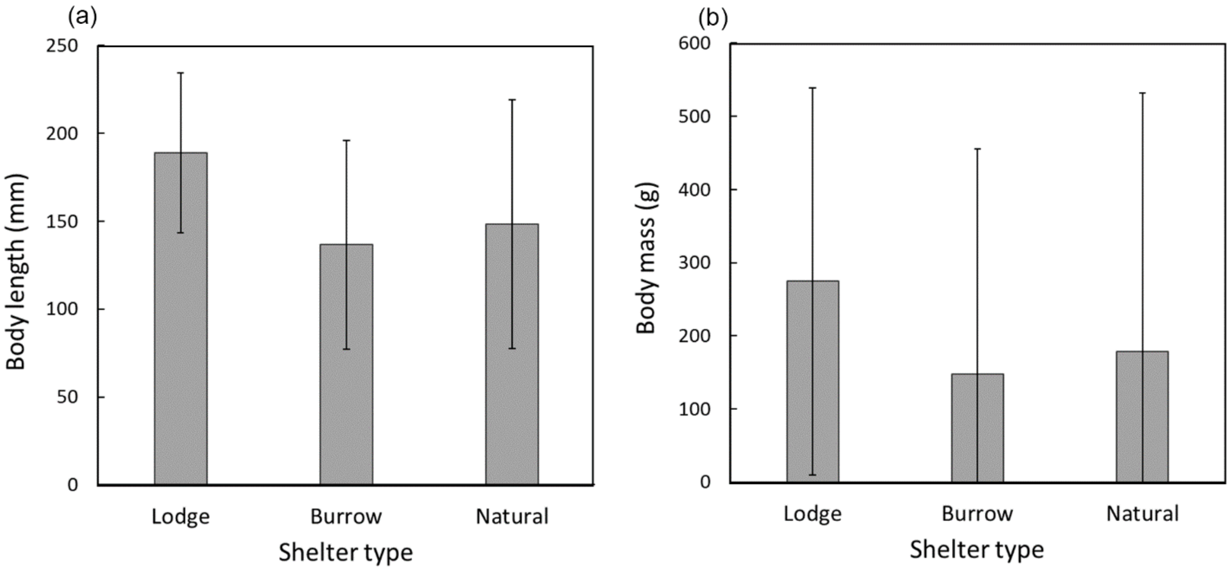


Figure II.D. Body mass and body length of myomorph rodents with different shelter habits, mean ± SD. Lodge: species that construct lodges (may use natural shelters or dig burrows); Burrow: species that dig burrows (may use natural shelters but do not construct lodges); Natural: species that only use natural shelters. Data available for 332 burrowing species, 18 lodge-building species and 133 natural sheltering species.

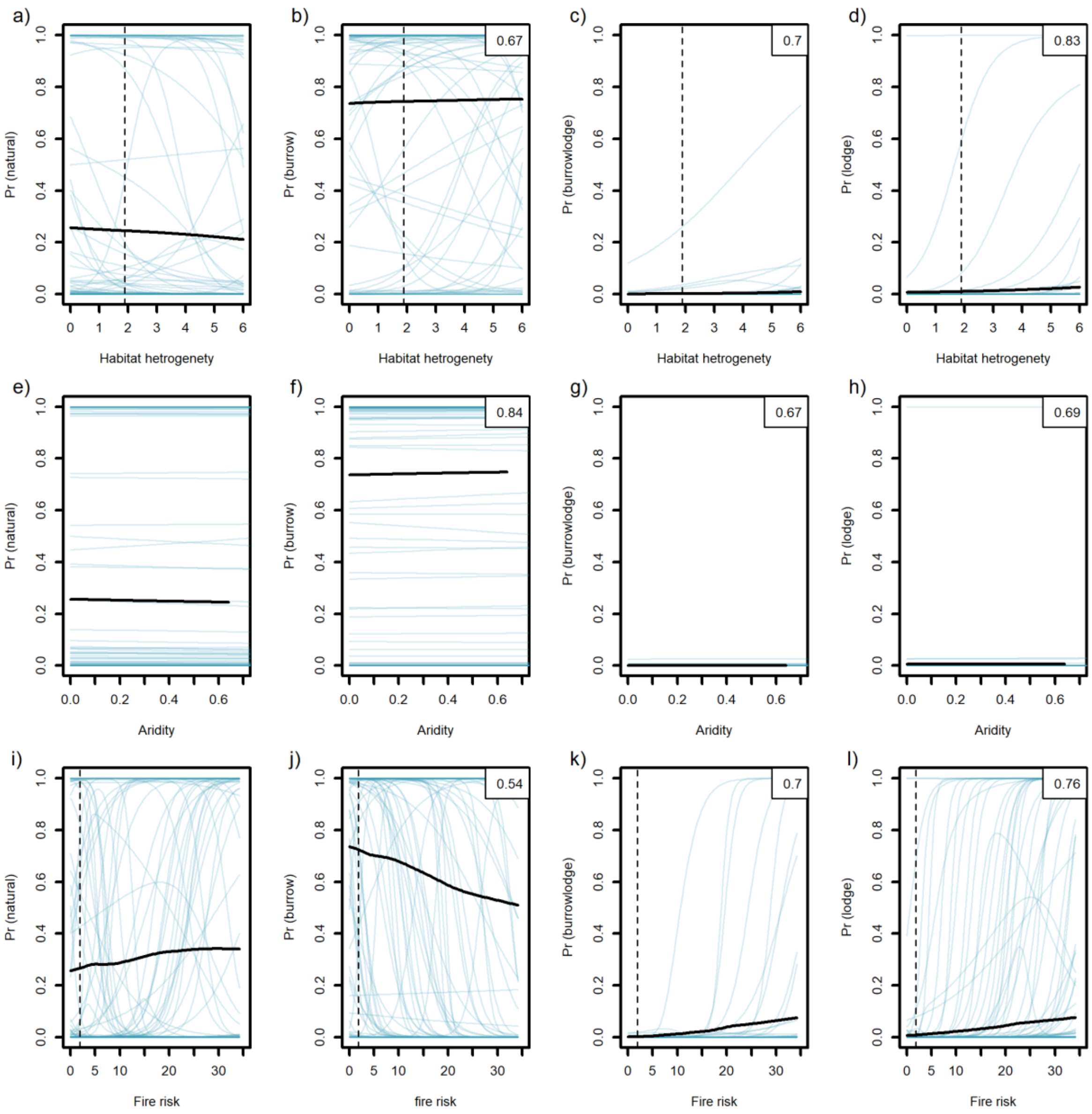


Figure II.E. Illustrating evolutionary transitions in sheltering habit as a function of the predictors. Columns show (from left to right) the probability of natural shelter, burrows, burrow + lodge, lodge, while rows show (from top to bottom) predicted changes in those probabilities as a function of number of habitat heterogeneity (a–c), aridity (d–f) and fire risk (g–i). The numbers in the legends are the posterior probabilities (PP), i.e. the proportion of the posterior distribution that supports a given association; these were not available for natural shelter, as this was the reference category. Within each row, all other predictors were held at their baseline value (dotted black line). Solid black lines are the predicted means, thin coloured lines are 100 random samples drawn from the posterior to illustrate uncertainty.

Table II.A Ecological and life history variables of Myozmorpha rodents with different sheltering habits (lodge/burrow/natural).

	mean	median	SD
Fire risk (lodge)	0.210	0.103	0.324
Fire risk (burrow)	0.725	0.132	2.231
Fire risk (natural)	0.720	0.108	1.345
Aridness (lodge)	0.566	0.803	0.416
Aridness (burrow)	0.426	0.319	0.406
Aridness (natural)	0.158	0.004	0.260
Body length (lodge)	188.9	202.3	45.490
Body length (burrow)	136.6	120.5	59.530
Body length (natural)	148.5	127.0	70.844
Body mass (lodge)	274.4	249.3	264.369
Body mass (burrow)	147.4	55.0	308.571
Body mass (natural)	178.6	58.5	353.050
Body length/mass (lodge)	1.2	0.8	1.069
Body length/mass (burrow)	2.4	2.2	1.594
Body length/mass (natural)	2.2	2.3	1.392
Habitat heterogeneity (lodge)	3	3	1.065
Habitat heterogeneity (burrow)	2	2	1.263
Habitat heterogeneity (natural)	2	2	1.242

Chapter 2

Higher proactivity in later-borns: effects of birth date on personality in a small mammal

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III.1. Abstract

In short-lived animals, individuals born earlier in the breeding season frequently reproduce within the season of birth. Consequently, it has been proposed that those born early benefit from a more proactive behavioral type to compete for reproductive opportunities whereas later-borns adopt a more reactive personality to conserve energy to survive through the non-breeding season and reproduce in the following year. However, being proactive could also benefit later-borns in acquiring decreasing resources in the late breeding season. We investigated personality differences depending on the date of birth in relation to resource variation in a free-living population of the bush Karoo rat (*Otomys unisulcatus*). This species constructs stick lodges, a critical resource protecting the rats from the harsh semi-desert environments, but the availability of vacant lodges decreases with increasing population density during the breeding season. We predicted an increased occurrence of proactive phenotypes during the later breeding season, contrasting with the commonly assumed decrease in proactive phenotypes in late season due to lack of reproductive opportunity. We behaviorally phenotyped $n = 99$ individuals through repeated behavioral tests and found consistent individual differences along a proactive-reactive gradient. Most importantly, later-borns showed greater activity, boldness and exploration tendencies, indicating a more proactive personality. In addition, among early-born females, individuals which reproduced showed no differences in personality compared to those which did not reproduce. Our results indicate that seasonal differences in personality types in the bush Karoo rat may be driven by resource constraints in the late season rather than by differences in reproduction opportunities.

Keywords: behavioral phenotype, consistent individual differences, *Otomys*, pace-of-life syndrome

III.2. Introduction

For animals living in seasonal environments, reproduction typically coincides with periods of high resource abundance (Whittier and Crews 1987). The timing of birth during such highly concentrated reproductive periods can lead to different life history trade-offs and thus to alternative phenotypic developmental trajectories (Roff 1993; Varpe 2017). In many short-lived species, such as rodents, individuals born early during the breeding season can reach sexual maturity and reproduce within the same season (Tkadlec and Zejda 1995; Montiglio et al. 2014). In contrast, individuals born later experience a shorter resource-rich period and are less likely to reproduce within the season of their birth. Thus, they need to survive through the non-productive period to reproduce in the following year (Lambin and Yoccoz 2001). Consequently, the timing of birth within the season may shape distinct behavioral traits in early and late born offspring to adaptively cope with their different survival and reproduction challenges.

Over the past decade, behavioral studies have gained a deeper understanding of consistent individual differences (animal personality), how these are maintained and their association with life history (Réale et al. 2007; Biro and Stamps 2008). The pace-of-life syndrome proposes that the trade-off between current versus future reproduction leads to differences in behavioral traits (Réale et al. 2010; Dammhahn et al. 2018): in seasonal breeding rodents, individuals born early which have an opportunity to reproduce within the season of birth, should benefit from an active and risk-taking personality that could be advantageous when acquiring resources needed for reproduction. In contrast, being less bold and less risk-taking may be more adaptive for later-borns because such a personality type will contribute to saving energy, increasing the probability of surviving through the non-breeding season until they can reproduce in the following year (Gracceva et al. 2014). Such an association between personality and the timing of birth has been reported, for example, in eastern chipmunks (*Tamias striatus*), in which birth cohorts with early reproductive opportunities were faster explorers than those reproducing at a later age (Montiglio et al. 2014). Similarly, in European shags (*Phalacrocorax aristotelis*), chicks hatched early in the breeding season had higher social ranks and showed higher levels of aggression compared to those hatched later (Velando 2000). However, another study suggests a differential association between personality and timing of birth: in short-lived common voles (*Microtus arvalis*); individuals captured in spring (mostly late-born cohorts from the previous year) were bolder than those captured at other times of the year (Eccard and Herde 2013). This contradiction among different studies suggests the necessity to investigate the effect of seasonal environmental factors, which may contribute to explain the emergence of differences in behavioral types between different seasonal birth cohorts.

Apart from reproductive trade-offs that underly the pace-of-life continuum, ecological conditions can also be important drivers of personality (Dammhahn et al. 2018; Jablonszky et al. 2018; Montiglio et al. 2018). Individuals with proactive phenotypes are usually more successful in competing for resources (Sih et al. 2004; Smith and Blumstein 2008). During the late breeding season, resource availability typically declines, while population density increases at the same time. Being proactive can be beneficial for individuals born late in the season in competition for limited resources. Therefore, two alternative hypotheses exist: (1) early-borns are more proactive to acquire enough resources for reproduction *versus* (2) late-borns are more proactive to acquire enough resources for survival. Therefore, to understand the association between personality and the birth timing, further investigations, preferably under natural conditions are necessary.

The seasonal breeding bush Karoo rat (*Otomys unisulcatus*), a short-lived small mammal living in arid environments of South Africa, is an appropriate model to study the association between birth timing and personality. This species shows a distinct ecological feature that can result in intense resource competition during the breeding season. Bush Karoo rats construct “stick lodges” from dry plant material as refugia (Vermeulen 1988; Pillay 2001), providing a favorable micro-climate that protects the rat from the harsh ambient environment (Vermeulen 1988; Brown and Willan 1991; Du Plessis et al. 1992). A stick lodge is costly to build and is commonly used by only one adult individual in this solitary species (Makuya et al. 2024), although it can be reused by others after the builder disappears. Thus, vacant stick lodges represent a limited survival resource, and the availability decreases in the late breeding season when subadult individuals start to occupy stick lodges of their own. As more lodges become occupied, individuals born later face increasing difficulties in finding unoccupied lodges or will even need to build new ones. In this situation, having a proactive personality becomes adaptive as it could lead to finding and competing for unoccupied lodges, or in competing for building materials for constructing new lodges (Vermeulen 1988).

Our aim was to investigate the effect of the date of birth on personality in adult bush Karoo rats. First, we studied whether free-living bush Karoo rats show consistent personality traits in activity, boldness and exploration behavior. Next, considering the potential effects of increasing population density on the availability of stick lodges, we predicted that such personality traits would be associated with birth timing, as later-borns would adopt a more proactive (active, bold and/or explorative) behavioral type. Finally, we studied whether there was a seasonal change in behavior, specifically whether the proactive response decreased in the food restricted dry season when compared to the food rich moist season. We conducted a field study over two years (2022 - 2023) and repeatedly quantified six behavioral parameters related to three different behavioral personality traits, activity, boldness and exploration (sensu Réale et al. 2007), which was compared between individuals born earlier and later during the breeding season.

III.3. Materials and Methods

III.3.1. Study site and study population

Our study population occurred in the arid Succulent Karoo, a biodiversity hotspot in South Africa, characterized by variable climate and low precipitation. Bush Karoo rat breeding activity coincides with season (Wolhuter et al. 2022). Reproduction is concentrated in the moist period from July to November, followed by the hot and dry non-breeding period from December to June. Bush Karoo rats have a relatively short life span (1 - 2 years). The earliest age at sexual maturity is between 5 - 6 weeks, and the reproductive period spans over 4 - 5 months per year (Vermeulen 1988; Wolhuter et al. 2022). Offspring born early in the breeding season can reach sexual maturity within the season of their birth (Wolhuter et al. 2022). The competition for reproductive resources mostly concerns individuals born early in the season, while the availability of stick lodges is relevant for the survival of all individuals and may be especially limiting for those born late in the season.

The study was conducted in the Goegap Nature Reserve, Northern Cape Province, South Africa. The field site in the semi-arid Succulent Karoo (Cowling et al. 1999) is characterized by an annual rainfall of 160 mm/year on average, and by temperatures varying from −1.5 to 24 °C during winter and from 4 to 42 °C during summer (weather station at the field site). Most of the rainfall occurs in winter, creating abundant vegetation that supports the onset of reproductive activity in our study population (Wolhuter et al. 2021). The field site for the study is approximately 4.5 ha.

III.3.2. Stick lodge surveys

Stick lodge surveys were conducted twice a year, at the beginning of the breeding season in July and after the breeding season in January. We classified the stick lodges, which built within shrubs, into three size categories: (i) small: lodges with a height below 20 cm; (ii) medium: lodges with a height from 21-50 cm; and (iii) large: lodges that almost covered the entire shrub with a height above 50 cm (Schradin 2005). For every lodge, we recorded whether it was old (several years old) or whether it was newly built within the past few months, based our field records.

For each season, we calculated the total number of stick lodges on the field site as the total of old lodges surveyed in January (e.g. lodge survey in January 2023 for the breeding season that started in July 2022). Because we wanted to have a measure of available old lodges, we recorded these separately from lodges that were built within the prevailing season (the new lodges). More fine-scaled data on changes in the numbers of available stick lodges during 2022 and 2023 were not available for this study.

III.3.3. Trapping and individual tagging

In the field site, trapping was carried out at all occupied stick lodges throughout the year as part of a long-term data collection. The field site was split into 6 trapping areas, with trapping being carried out at two areas simultaneously by two people for three days, before switching to two other areas. Additional trapping was done at lodges with previously unmarked juveniles and focal individuals for behavioral tests. Trapping was done 5 days a week, and occurred before sunrise. The traps were set at lodge entrances and checked every 30 min. All traps were closed within two hours after sunrise to avoid overheating. We used Sherman traps and locally produced metal (Sherman-like) live traps (26 × 9 × 9 cm), which had small holes in the sides to allow circulation of air.

At first capture, bush Karoo rats were individually marked with aluminum band ear tags in both ears (0.25 g per tag) with a unique individual number (National Band and Tag Co., Newport, KY, USA). During re-trapping, we always checked for infections at the ear tags, which would have resulted in the removal of the tag on the affected ear; such cases never occurred during the study period. Birth date was estimated from the animals' body mass, based on the linear association between age and body mass in the bush Karoo rat as published in Pillay (2001). Trapping data used for our study spanned from 1st January 2022 to 14th December 2023. When a female born within the season showed signs of pregnancy/lactation (palpable embryos at late pregnancy stage; lactation as evident by the developmental stage of the mammary glands), or when a female had dependent young (as evident by juveniles trapped at the same stick lodge prior to the next breeding season), this female was considered as having reproduced during the season of birth ('precocious reproduction').

III.3.4. Assessment of changes in population density

Based on trapping data, we recorded the population density of adult (older than 5 weeks) bush Karoo rats (*n*/ha) at the beginning of the breeding season in July and again after the breeding season in January for both seasons. Therefore, for each month, we counted the total number of trapped adult bush Karoo rats and divided this number by the size of the field site. We were able to mark and monitor the population through observations because the field site is an open terrain (dispersed shrubs with sandy areas in between), the bush Karoo rat is diurnal, and occupied stick lodges showed clear signs of occupancy. At lodges with signs of occupancy where we did not trap an individual within 3 days, we continued with additional trapping. We also conducted behavioral observations (described in Makuya et al. 2024), enabling us to identify occupied lodges and unmarked juveniles.

III.3.5. Experimental procedure

Trapping of focal individuals was conducted using the same method as described above. Individuals were transported to a field laboratory situated next to the field site (less than 10 min walking distance) for behavioral testing. Except when checking ear tags and performing behavioral tests, the rats remained in their traps during the whole time. After the test procedure, individuals were released next to their stick lodge, i.e., at the site where they had been trapped.

Focal individuals underwent up to four repetitions of behavioral tests. Because the field site changed from the moist to dry season with a decrease in food abundance over time, we measured behavioral repeatability at short term (two-week interval) and long term (16-week interval, in the moist and dry seasons) to account for the seasonal variation of food abundance. The test schedule was determined by age; the first and second tests were conducted at early adult stage (age class “young adults”), with the first age at approximately 6 weeks when they reach sexual maturity (Pillay 2001). The second test was scheduled two weeks later. The third and fourth tests were conducted at fully adult stage (age class “older adults”), with the third test scheduled when individuals were approximately 20 weeks old, and the fourth test two weeks later.

As was evident from our trapping data, females usually disperse for shorter distances and therefore were more likely be continually caught using our trapping protocol. Thus, in the first year, the selection of focal individuals was limited to females and included four behavioral test replicates. In the second year, both males and females were selected as focal individuals. However, due to time constraints, the rats underwent only the first and second behavioral tests in the second year. Due to unpredictable field conditions, trapping of focal individuals was not always successful, which led to delays for repeated behavioral tests in some cases. The average age for "young" adults (at the 1st and 2nd test) was 54 days, and the average age for "older" adults (at the 3rd and 4th test) was 151 days. Because our study involved individually-marked focal animals, the experimenter(s) were not naive to individual identities during testing.

Population density of small mammals in our field site typically decreases dramatically during the dry season to the onset of the next breeding season, when it is only approximately a quarter of the density at the end of the breeding season (Nater et al. 2018). As expected, many individuals disappeared from the field site throughout the study, mainly due to predation. We could not predict which individuals would disappear, so we tested as many individuals as possible at the onset of the breeding season.

During the first year (2022), we tested a total of 56 individuals, out of which 37 individuals were successfully trapped and underwent the last two (3rd and 4th) tests as older adults: 19 of them underwent all four tests (i.e. two times during older adult stage and two times during young adult stage), eight individuals were tested three times (i.e. two times during older adult stage and one time during young adult stage), and 10 individuals were only tested two times (i.e. two times during older adult stage). This was not the case for 19 individuals that had disappeared prior to the last testing during older adult stage. During the second year (2023), we tested a total of 43 individuals, out of which 29 underwent all two tests; note that during the second year, we only carried out two tests during the younger adult stage (see details above). The remaining 14 individuals could only be trapped and tested for the 1st test. Overall, out of the total of 99 individuals tested in 2022 and 2023, 66 individuals did not disappear prior to the end of the testing.

As a consequence of the disappearance of some animals in combination with the differences in (re-)trapping success, the individuals had different experiences when undergoing the different tests. All 99 individuals of our sample were tested at least one time, n = 78 individuals underwent at least a 2nd test, n = 30 individuals underwent at least a 3rd test and only n = 19 individuals underwent all four tests.

III.3.6. Behavioral tests

One to a maximum of four individuals were trapped for behavioral tests per day. A white chamber (100 cm long, 85 cm wide and 65 cm high) made of melamine panels was used as a test arena (Figure III.1). Before introducing a new individual into the arena, the arena was always thoroughly cleaned using 95% alcohol and air dried. All tests were video-recorded and later analyzed using the software BORIS (Friad and Gamba 2016) and Single Mouse Tracker (Icy software, De Chaumont 2012). Focal individuals underwent three successive behavioral tests directly after the morning trapping. To minimize observer bias, blinded methods were used when all behavioral data were recorded and/or analyzed.

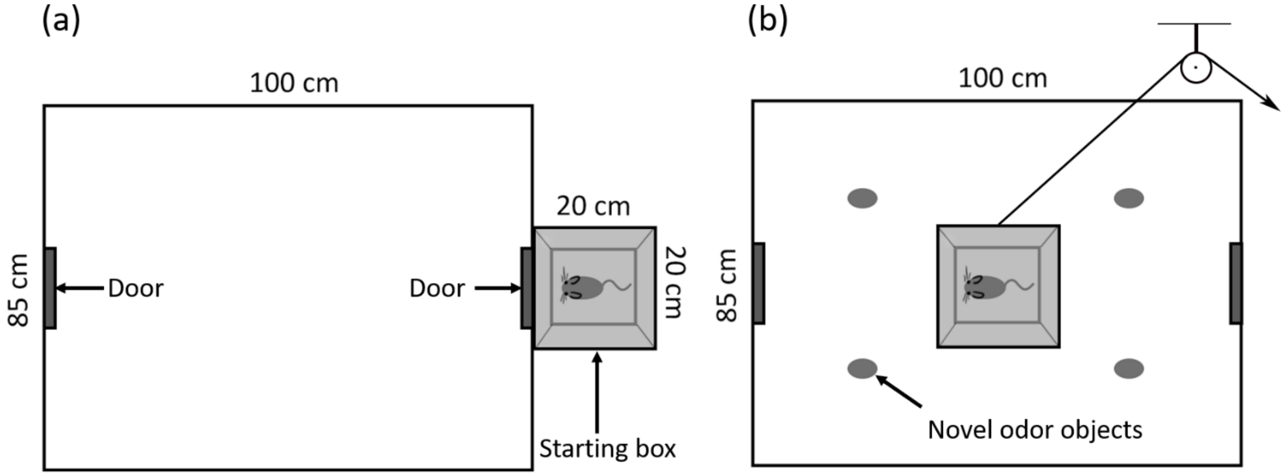

Figure III.1. Experimental setting used for (a) starting box/open field tests and (b) novel odor tests, either orange skin, tomato sauce, peanut butter or strawberry jam (for the 4 replicates) were used to provide novel odors carried in the identical sieve balls. Note that the starting box inside the arena in (b) was lifted by a pulley system once the experiment started

Starting box– This part of the apparatus (the starting box) consisted of a 10 cm^3 black acrylic and opaque square box with one side that could be opened (door) and a lid at the other side. The open side was directly attached to the test arena and separated by a closed door (Figure III.1a). After individuals were placed into the starting box via the lid, they were allowed to calm down for 3 min in the closed box. Then the door was opened and we recorded whether the animal entered the test arena in the following 10 min. If the animal did not enter the arena within this time, it was gently nudged in using a plastic ruler (2 × 30 cm) by reaching into the box through the lid.

Once the individual had entered the arena, the door was closed to prevent its return into the starting box.

Open field test - Once the rat had entered the arena, the open field test began (Figure III.1a). During the following 5 min, the individual could freely explore the arena. We recorded three behavioral parameters: (1) the distance travelled, defined as the total distance of locomotion measured in cm; (2) the % time the individual was active in the arena, defined as the total time minus the time being immobile (i.e. no obvious movements for more than 10 seconds); and (3) the % time the animal spent exploring the walls and corners of the arena, defined as sniffing or putting the front paws against the walls.

Novel odor test - During our preliminary tests, bush Karoo rats did not show notable interactions with plastic toys presented as visual novel objects. However, interactions were observed when objects were applied with novel odors (e.g., orange peel). We therefore did not apply classical novel object tests (Denninger et al. 2018) but instead measured the animals' exploration behavior towards objects carrying novel odors in a standardized setting.

After the open field test was completed, the animal remained in the arena and was confined again by the experimenter using the same black acrylic square box. The box was attached to a fixed pulley system so it could be lifted to release the individual with minimum disturbance. The focal individual was first placed in the center of the arena while covered by the box. Then, four identical hollow metal, egg-shaped sieve balls (4.5 × 3.9 cm, steel) providing the same novel odors were placed inside the arena, 10 cm away on the extended diagonal of the black box (see Figure III.1b). The source of odor used in the 1st test was orange peel, tomato sauce was in the 2nd test (two weeks later), peanut butter was used in the 3rd test and strawberry jam in the 4th test. After setting up the arena, the rat was allowed to calm down for 5 min inside the box, then the box was lifted and the individual was given 5 min to explore the four metal balls. We recorded two behavioral parameters: (1) the time the animal spent exploring the objects, defined as the total (summed-up) duration the individual sniffed or touched one of the four tea balls; and (2) the number of objects explored, defined as the total number of tea balls, which were sniffed or touched by the individual during the test (range from 0 − 4).

III.3.7. Quantification of seasonal food abundance

Because the repeated behavioral tests were conducted in two seasons with variable food availability, we quantified seasonal changes in the abundance of food plants and considered the potential effects on individual behavioral performance during testing. Food plant abundance was measured monthly using the Braun-Blanquet method as part of the long-term data collection on the field site, assessed by the average number of food plants from eight 2 m × 2 m plots randomly located in the field site (Werger 1974; Schradin and Pillay 2006). The resulting index was used in the statistical analysis (see details below) as an estimate of the food plant availability at the time of the different test sessions.

III.3.8. Statistical analysis and sample sizes

In total, 99 individuals ($n_{\text{males}} = 15$, $n_{\text{females}} = 84$) were tested in 226 behavioral tests. We considered potential effect of multiple test replicates per individuals, as such repeated testing may lead to habituation effects (Salomons et al. 2010). The sample sizes available during the different test replicates (hereafter referred to as "test sequence"), see more details above, in the last paragraph of section "Experimental procedure".

Statistical analyses were carried out in R, version 4.3.0 (R Core Team 2023). In the first step, we checked for repeatabilities of the six behavioral variables quantified in the starting box test, open field test and in the novel odor test, across the four different test sessions, as well as for associations between these behavioral variables. All six response variables (behavioral variables, given in Table III.1) were scaled for analysis. This analysis (with $n = 99$ individuals) was done using a single, multivariate generalized linear mixed-effects model GLMM (i.e., with six response variables) based on the R package *MCMCglmm* (Hadfield 2010). The predictors were year and sex (2 levels each) and test sequence (number of tests the individual has done before, 4 levels), with random effects for individual ID. We applied a weakly informative prior, allowing the data to primarily inform the posterior distributions. One chain was run with 100,000 iterations. The first 5,000 iterations were discarded as burn-in, and every 100th iteration was retained (thinning interval = 100), resulting in 950 samples per chain. The response variables followed appropriate distributions: a categorical distribution for the latency to enter the arena, poisson distribution for the number of objects explored (count variable from 0 to 4), and Gaussian distribution (after some transformations, see details below Table III.1) for the remaining four continuous behavioral variables. As the early disappearance of some animals prior to the completion of the four test sessions in the year 2022 or of the two test sessions in 2023 may have potentially created a calculation bias, we repeated the analysis by a multivariate GLMM with a subsample of $n = 66$ animals (out of the original $n = 99$ individuals) which were still present (i.e. trapped and tested) during the last test sessions of both years of study. See more details above, in the section "Experimental procedure". However, this more conservative analysis revealed highly similar findings, as presented in Tables III.C, III.D in Suppl. Materials.

Repeatabilities across the (up to) four repeated tests per behavioral parameter (see Table III.1) and pair-wise correlation coefficients between the different behaviors (see Table III.3) were calculated based on the within-individual and among-individual variance matrices provided by this model. Associations between the different behavioral variables were considered statistically significant ($P < 0.05$) when the 95% Bayesian credible intervals of the correlation coefficients (R) did not overlap zero (Houslay and Wilson 2017). However, in case of repeatabilities over time, as per definition only non-negative values can be obtained and thus the 95% credible intervals cannot overlap zero, P-values could not be calculated based on the above-mentioned method (Houslay and Wilson 2017). Consequently, our inference on repeatabilities was only based on interpretation of the 95% credible intervals. We calculated the overall (long-term) repeatability, based on all (up to) four behavioral tests of our 99 focal individuals over all age classes (young adult at first and second tests, older adult at third and fourth tests; $n = 226$ measurements for each behavioral variable), as well as short-term repeatability, based on the first two behavioral tests for 99 young adults with a total of $n = 145$ measurements for each behavioral variable.

In the second step, we tested the effects of the date of birth (covariate, 1st July as baseline; see the rather consistent distribution of birth dates along the season in Figure III.2) on the six different behavioral variables (see Table III.3). Therefore, using the R package *lme4* (Bates et al. 2015), we applied separate models - a generalized linear mixed-effects model (GLMM) for binomial data with a logit link for the probability to enter the test arena (see Table III.3a), and linear mixed-effects models (LMM) for all remaining (continuous) behavioral variables (see Table III.3b-f). To obtain a normal distribution of model residuals (verified by visually checking normal probability plots) and homogeneity of variances (by plotting residuals versus fitted values) for LMMs, we square-root transformed the distance travelled and the % time the animals spent exploring the walls and corners of the arena, and log [x+1] transformed the time the animal spent exploring the object in the novel odor test. Individual identity was always included as a random (intercept) factor. All models included the age class at testing (“young adult” at the 1st and 2nd tests or “older adult” at the 3rd and 4th tests; 2 levels), the sex of the focal animals and the year of testing (all factors with 2 levels), the test sequence (factor with 4 levels) and the food plant abundance at testing (covariate). Because we were interested in whether possible differences between earlier- and later-born individuals were only apparent in young adults or in older adult individuals, we also tested the 2-way interaction between date of birth and age class. When non-significant, this interaction was removed from the models and these were recalculated (Engqvist 2005). *P*-values were calculated by type-3 Wald chi-square tests (Bolker et al. 2009).

We also tested whether the behavioral responses of early-born females (i.e., females born until/including the 5th week of the breeding season, when the last reproducing female was born) in the different tests were associated with their actual reproductive activity during their season of birth. Using the R package *lme4* (Bates et al. 2015), we applied GLMMs for binomial data with a logit link using the same transformations for some of the behavioral variables (now used as predictors in our model) as described above. Each model included one behavioral variable, and all included year of testing (2 levels) as fixed variance. Individual identity was always included as a random (intercept) factor. Also, *P*-values were calculated by type-3 Wald chi-square tests.

III.4. Results

III.4.1. Seasonal differences in population density and stick lodge availability

In both years of the study, the adult population density showed dramatic variation between the breeding/non-breeding seasons. Population density increased during the breeding season from July to January by 120.7% on average. Specifically, during the first year of study (Jul 2022 – Jan 2023), the adult density increased by 81.4% from 12.6 to 23.4 individuals/ha, and during the second year (Jul 2023 – Jan 2024), it increased by 160% from 6.5 to 16.9 individuals/ha. However, the population also dramatically decreased during the non-breeding season by 72.0% between January to July 2023.

In the breeding season starting in July 2022, 172 old lodges (i.e. existing ones) were available and 26 new lodges were built. The availability of old lodges decreased during the breeding season, from 3.1 to 1.6 lodges/adults from July 2022 to January 2023. In the breeding season starting in July 2023, 194 old lodges were available and 9 new lodges were built. The availability of old lodges decreased from 6.9 to 1.8 lodges/adults from July 2023 to January 2024. When only considering the large lodges with a height above 50 cm, which can be assumed to be the most valuable resource, this seasonal difference was more pronounced. The availability of such large lodges decreased from 0.8 per adult individual to 0.4 in 2022/2023, and from 1.7 to 0.4 in 2023/2024.

III.4.2. Pattern of seasonal reproduction

We quantified the temporal distribution of reproductive events during the breeding season using the estimated dates of birth of the juveniles trapped, based on a sample of *n* = 226 juveniles (129 born in 2022 and 97 born in 2023, Figure III.2). The annual start of the reproductive season was determined by the occurrence of at least three juveniles born on different dates within a week (i.e., apparently from different litters), revealing a highly similar onset of the reproductive season between the two years of study (2022: 19th July; 2023: 14th July). In 2022, the mean date of birth was on 29th August, and during the reproductive season in 2023, it was on 8th September.

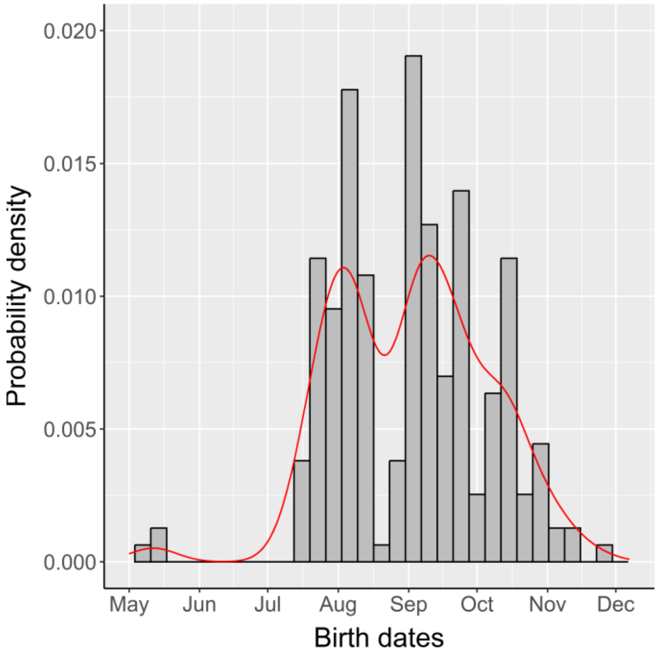

Figure III.2. Distribution of reproductive activity (assessed by the frequency of birth events) during the breeding season in the bush Karoo rat, given as density probability (red line). Data from *n* = 226 individuals captured during the years 2022 and 2023, including the 99 focal individuals which underwent behavioral tests

III.4.3. Consistent individual differences in behaviour

We analyzed the consistency of six behavioral variables recorded in up to four repeated starting box tests, open field tests and novel odor tests. Overall, we found notable long-term consistencies across time (i.e., repeatability) and thus across different age classes (young to older adults), with respect to three of the four behavioral variables recorded in the starting box and open field tests. These variables were the probability to enter the arena within 10 min, the distance travelled, and the % time the individual spent exploring the walls and corners of the arena (Table III.1a). In contrast, the % time the rats were active in the open field arena as well as both behavioral variables measured during the novel odor tests showed very low repeatabilities with large credible interval closely approaching zero (Table III.1a).

Regarding short-term consistency, when only considering the first two tests during which individuals could be considered as young adults, we found repeatabilities similar to long-term consistency in the starting box and open field test, but again no noticeable repeatability in the novel odor test (Table III.1b).

Table III. 1 Repeatability (*R*, including its 95% credible interval *CI*) of behavior parameters measured in repeated starting box (SB), open field (OF) and novel odor (NO) tests of 99 individuals. Analysis by a multivariate GLMM including individual identity as a random factor, year, sex and test sequence (4 levels) as fixed variance. (a) Long-term repeatability was based on all (up to) four behavioral tests of all age classes (*n* = 226 measurements for each behavioral variable), (b) Short-term repeatability was based on (up to) two behavioral tests during young adult stage (*n* = 145 measurements for each behavioral variable)

	(a) Long-term repeatability		**(b) Short-term repeatability**	
	R	***CI*$_{95\%}$**	***R***	***CI*$_{95\%}$**
SB - Probability to enter arena	0.699	[0.483, 0.872]	0.477	[0.050, 0.860]
OF - Distance travelled [1]	0.364	[0.204, 0.521]	0.384	[0.141, 0.610]
OF - % Time active	0.167	[0.025, 0.308]	0.219	[< 0.001, 0.417]
OF - % Time exploring walls and corners of arena[1]	0.253	[0.093, 0.427]	0.317	[0.039, 0.536]
NO - Time exploring object [2]	0.119	[< 0.001, 0.325]	0.038	[< 0.001, 0.158]
NO - Number of objects explored	0.127	[< 0.001, 0.364]	0.051	[< 0.001, 0.244]

[1] square-root transformation of dependent variable

[2] log [x+1] transformation of dependent variable

We also found significant associations among the parameters recorded in the starting box test and open field test. Specifically, the probability to enter the arena, the distance travelled, the % time the animals showed activity and the % time the animals spent exploring the walls and corners of the open field arena were positively and significantly correlated at the between-individual level (Table III.2).

Table III.2 Associations between the different behavioral parameters, based on measurements taken from 99 individuals of different age classes. Analysis by a multivariate GLMM including individual identity as a random factor, and year, sex and test sequence (4 levels) as fixed variance. Correlation coefficients (among individual-level) are given, values given in bold indicate that the 95% credible interval s do not overlap zero, otherwise they are given in brackets. Note that results stem from the same model as used for the calculation of Table III.1a, more details, including the credible intervals, are given in Table III.A in Suppl. Materials

	PEA	**DT**	**%TA**	**%TEA**	**TEO**	**NOE**
PEA		**0.763**	**0.840**	**0.780**	(0.549)	(0.454)
DT			**0.786**	**0.620**	(0.484)	(0.429)
%TA				**0.848**	(0.605)	(0.470)
%TEA					(0.494)	(0.372)
TEO						(0.614)
NOE						

PEA: Probability to enter arena; DT: Distance travelled (square-root transformed); %TA: % Time active; %TEA: % Time exploring walls and corners of arena (square-root transformed); TEO: Time exploring object (log [x+1] transformed); NOE: Number of objects explored

III.4.4. Effects of birth date on personality traits

All behavioral parameters recorded in the starting box and open field tests were significantly associated with the individual date of birth (Table III.3). The probability to enter the arena (Table III.3a, Figure III.3a), the distance travelled (Table III.3b, Figure III.3b), the % time active (Table III.3c, Figure III.3c) and the % time exploring the walls and corners of the arena (Table III.3d, Figure III.3d) were all significantly higher in individuals born later in the season. The interaction between the date of birth and age class at testing was never statistically significant, indicating that the significant effects of date of birth on behavior (Table III.3a-d) were independent of age class. In contrast, the two parameters recorded during the novel odor test were not significantly associated with date of birth (Table III.3e, f). We found a significant and positive effect of the current food plant abundance only for the total time spent exploring the objects carrying the novel odors (Table III.3e). Specifically, the higher the food availability around the time of testing, the longer the individuals explored the novel odor.

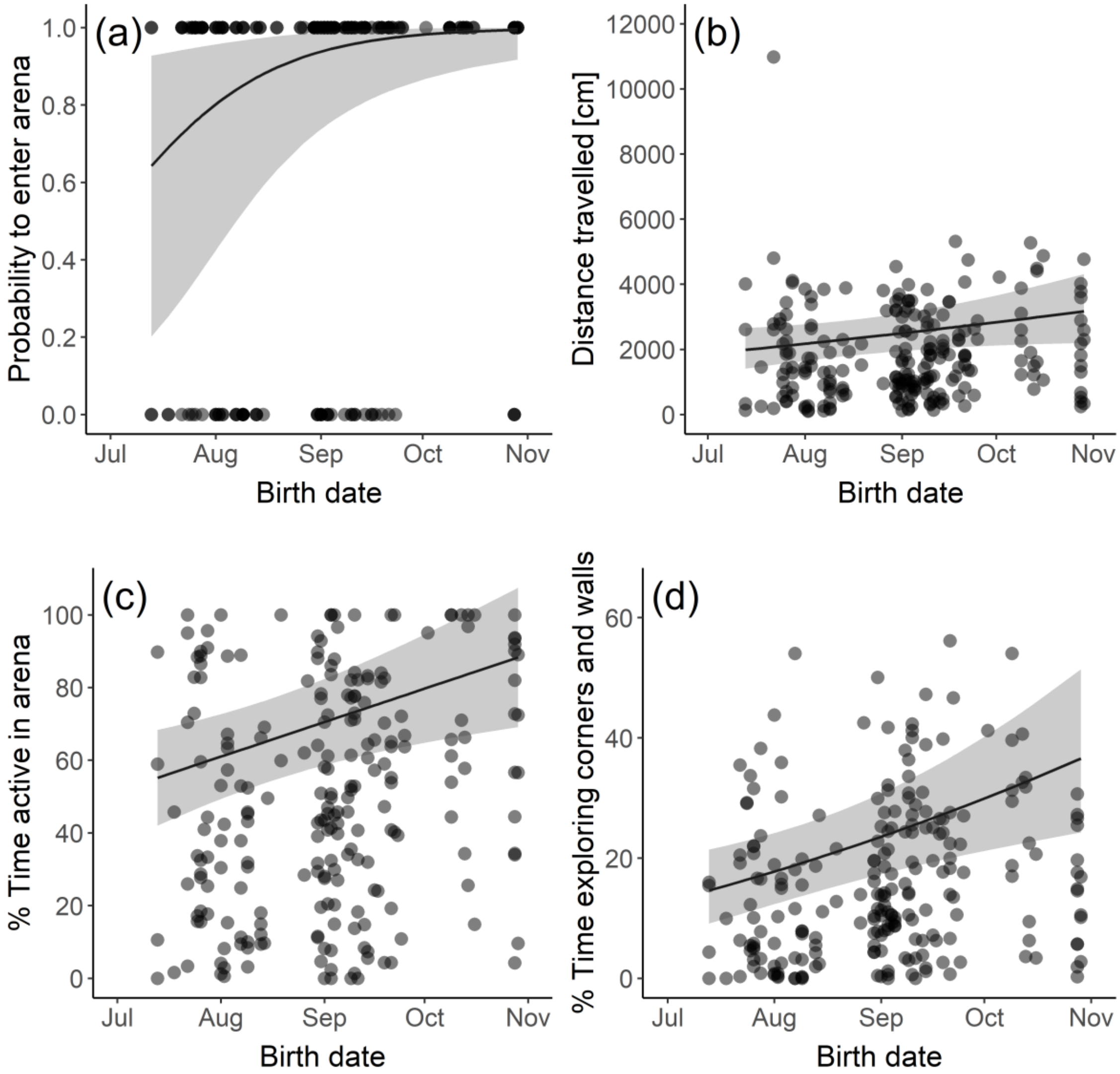

Figure III.3. Effects of birth date within the breeding season on different behavioral traits in the bush Karoo rat. All effects presented here are statistically significant. Regression lines (including 95% confidence intervals given as grey shadings) are based on parameter estimates as given in Table III.3

In two parameters measured in the open field, we found significant sex differences; males travelled a longer distance in the arena (Table III.3b) and spent a higher % time being active (Table III.3c). We also found highly significant effects of the test sequence (number of tests the individuals had experienced, range from 0 - 3) regarding the distance travelled, the % time active, and the % time of exploring walls and corners in the open field arena (Table III.3b-d). Post hoc comparisons revealed that for these three parameters, the values were significantly higher during the first test compared to all subsequent test sessions (post-hoc statistics in Figure III.A in Suppl. Material).

III.4.5. Personality-specific reproduction of early-born females

Out of 84 females tested, 9 (10.7%) had already reproduced in the breeding season of their birth. All reproducing females were born early in the breeding season, during in the first 3 weeks of the season in 2022 and during the first 5 weeks of the season in 2023.

There were no significant associations between any of the six behavioral variables in early-born females (birth dates during the first 5 weeks of the breeding season, *n* = 27), and the probability of reproduction during the same season (GLMM for binomial data, all $P > 0.50$; see details in Table III.B in Suppl. Materials).

Table III.3 Effects of different predictor variables on behavioral traits (a-g) of 99 individuals, repeatedly measured up to 4 times in starting box (SB), open field (OF) and novel odor (NO) tests. Analysis by a multifactorial GLMM including individual identity as a random factor. The 2-way interaction between age class at testing and the date of birth during the reproductive season was tested in all models but was never statistically significant ($P > 0.05$). Significant effects are given in bold

Dependent variable	Predictors	χ^2	*df*	$\beta \pm$ SE	*P*
(a) SB - Probability to enter arena	Date of birth within seaso	6.065	1	0.043 ± 0.017	**0.014**
	Age class at testing [old]	0.002	1	–0.041 ± 1.003	0.967
	Sex [m]	3.493	1	2.446 ± 1.309	0.062
	Food plant abundance at testing	0.630	1	0.383 ± 0.483	0.427
	Test sequence [2nd]	2.623	3	–0.806 ± 0.525	0.454
	[3rd]			–0.529 ± 0.993	
	[4th]			–0.092 ± 1.116	

	Year [2nd]	3.258	1	–1.554 ± 0.861	0.071
(b) OF - Distance travelled [1]	Date of birth within season	4.000	1	3.017 ± 1.508	**0.045**
	Age class at testing [old]	0.885	1	–3.189 ± 3.389	0.347
	Sex [m]	5.541	1	9.151 ± 3.888	**0.019**
	Food plant abundance at testing	0.822	1	1.459 ± 1.610	0.365
	Test sequence [2nd]	91.163	3	–15.774 ± 1.706	**< 0.001**
	[3rd]			–16.216 ± 3.461	
	[4th]			–21.940 ± 3.934	
	Year [2nd]	0.063	1	0.728 ± 2.898	0.802
(c) OF: % Time active	Date of birth within season	8.608	1	0.306 ± 0.105	**0.003**
	Age class at testing [old]	1.110	1	–7.531 ± 7.149	0.292
	Sex [m]	3.266	1	13.183 ± 7.295	0.071
	Food plant abundance at testing	0.931	1	3.414 ± 3.539	0.335
	Test sequence [2nd]	51.848	3	–25.279 ± 3.932	**< 0.001**
	[3rd]			–22.149 ± 7.226	
	[4th]			–40.905 ± 8.195	
	Year [2nd]	1.345	1	–6.245 ± 5.386	0.246
(d) OF: % Time exploring walls and corners of arena [1]	Date of birth within season	10.610	1	0.021 ± 0.006	**0.001**
	Age class at testing [old]	4.524	1	–0.875 ± 0.412	**0.033**
	Sex [m]	0.479	1	0.308 ± 0.445	0.489
	Food plant abundance at testing	1.968	1	0.280 ± 0.199	0.161
	Test sequence [2nd]	41.058	3	–1.197 ± 0.215	**< 0.001**
	[3rd]			–1.359 ± 0.418	
	[4th]			–2.274 ± 0.475	
	Year [2nd]	0.695	1	0.276 ± 0.331	0.405
(e) NO: Time exploring object [2]	Date of birth within season	2.497	1	0.204 ± 0.129	0.114
	Age class at testing [old]	3.007	1	–0.518 ± 0.299	0.083
	Sex [m]	0.025	1	0.052 ± 0.328	0.873
	Food plant abundance at testing	6.700	1	0.373 ± 0.144	**0.010**
	Test sequence [2nd]	6.810	3	–0.319 ± 0.155	0.078
	[3rd]			0.013 ± 0.304	
	[4th]			0.284 ± 0.345	
	Year [2nd]	4.806	1	–0.535 ± 0.244	**0.028**
(f) NO: Number of objects explored	Date of birth within season	1.264	1	0.091 ± 0.081	0.261
	Age class at testing [old]	3.199	1	–0.351 ± 0.196	0.074
	Sex [m]	0.445	1	0.141 ± 0.211	0.505
	Food plant abundance at testing	3.252	1	0.170 ± 0.094	0.071
	Test sequence [2nd]	1.894	3	–0.146 ± 0.111	0.595
	[3rd]			–0.135 ± 0.195	

[4th]			–0.062 ± 0.217	
Year [2nd]	2.164	1	–0.232 ± 0.158	0.141

[1] square-root transformation of dependent variable

[2] log [x+1] transformation of dependent variable

III.5. Discussion

We studied whether the date of birth during the breeding season affects personality in a seasonally breeding rodent, the bush Karoo rat. We hypothesized that individuals born later in the season should adopt a more proactive personality because such a behavioral type would be advantageous for finding/building their own stick lodges. This was confirmed by our findings: later-born individuals were bolder and more active and explorative in behavioral tests, suggesting a more proactive personality in these rats than in those born earlier. We did not find support that proactivity has evolved to support reproduction in early-born females because females that reproduced within the season of their birth did not show higher proactivity compared to females that did not reproduce within the same season. Finally, while food abundance decreased from the moist breeding season to dry non-breeding season, this did not affect the proactive responses.

Individuals displayed higher levels of some behaviors during the first test compared to all subsequent tests (Suppl. Material, Figure III.A), even in three behavioral parameters which were notably repeatable over time. Such decreases in the expression of behaviors related to activity and exploration is frequently explained by the animals' habituation to the test arena, i.e. learning about its structural elements, thus leading to a loss of motivation to explore (Bolivar et al. 2000; Salomons et al. 2010). Accordingly, a study in laboratory mice showed that the introduction of novel, tactile cues during repeated open-field testing could prevent such decreases in behaviors indicative of exploration (Chen et al. 2023). In contrast, in our setting, the open field arena constituted a novel environment only during the first trial, triggering comparatively higher levels of exploration-related behaviors. Nevertheless, as shown in our study, such an initial change in population-level test responses over the first two test sessions does not call into question the existence of consistent individual rank differences in personality. Similar findings have been reported in other studies conducting behavioral phenotyping in small mammals, frequently showing notably higher or lower responses (dependent on the kind of test) during the first test repeat compared to subsequent ones (Võikar et al. 2004; Matsunaga and Watanabe 2010; Lewejohann et al. 2011).

Despite such changes over time in the absolute levels of some of the behaviors considered, we found consistent individual differences in measurements of activity, boldness and exploration as well as significant associations between these different variables, confirming findings obtained in other small mammals under field conditions (e.g., Lantová et al. 2011; Eccard and Herde 2013). Individuals in our study that were more active were also bolder and more explorative, suggesting a behavioral syndrome which we describe as "proactivity" (Koolhaas et al. 1999). Similar associations have been reported in other small mammals under field conditions; for example, more exploratory European rabbits (*Oryctolagus cuniculus*) were bolder during early age, and were less sociable and tended to be more aggressive as subadults (Rödel et al. 2015). Furthermore, bent-wing bats (*Miniopterus fuliginosus*) showed positive associations between traits reflecting boldness, activity and exploration, described by the authors as 'proactiveness' (Kuo et al. 2024).

The main hypothesis of our study, that later-borns are more proactive, was based on the assumption that such individuals face more intense competition for stick lodges, a critical and limiting resource for survival in their harsh ambient environment. As it is typical for a short-lived seasonal breeder, population density of bush Karoo rat peaks during the late breeding season, and such a high population density has the potential to negatively affect resource availability (White 2008). Accordingly, in our study, we found a sharp rise in population density during the course of the breeding season and an associated and notable decrease in stick lodge availability. Although there was always more than one lodge available per adult, lodges differed in their quality, such that the availability of large high-quality lodges decreased to below one lodge per adult by the end of the breeding season. The availability of smaller lodges was higher but they were usually less steady and in poor condition, thus needing a higher investment in building and repairing. The emergence of new lodges during both seasons suggests that the existing lodges were not able to meet the demand of the increasing population. Thus, stick lodges clearly represented a limited resource at the end but not at the start of the breeding season.

Individuals born at high population density during the late breeding season can be expected to be at a disadvantage at locating and occupying vacant stick lodges. Due to their young age and relatively small body size, they can be expected to be less competitive than older and larger individuals born earlier. As a result, they would need to invest in either finding unoccupied lodges or building their own ones, and both would require travelling and exploring a broader range of their habitat. In support, a link between increased space use and a more proactive personality has been found in North American red squirrels (*Tamiasciurus hudsonicus*) in which individuals with higher activity levels in standardized tests were re-trapped over a larger range of the study site (Boon et al. 2008). Under field conditions, the trait combination of being more exploratory and more active, as found in our study (see also Perals et al. 2017), could contribute to an increased efficiency in searching for stick lodges or of building materials. Thus, being more proactive could be beneficial in later-born individuals in response to the increasing difficulty of acquiring stick lodges.

The life history of bush Karoo rats allows individuals born early to have the chance for precocious reproduction within the same season. In our study, precocious reproduction occurred in 10.7% (n = 9) of the females, which is lower than in some other seasonally breeding rodents or lagomorphs (greater Guinea pig *Cavia magna*: 18.8%, Kraus et al. 2005; European rabbits in a Mediterranean habitat: 18.6%, Soriguer 1981). In our study, females reproducing during their season of birth were born relatively early, all before the middle of the breeding season. However, when only considering early born females, we did not find support for a higher proactivity associated with precocious reproduction. In addition, females born early, i.e. the ones that had an opportunity to reproduce, were generally less proactive than those born later during the season (see Figure III.3).

We suggest that the emergence of a lower proactivity in earlier-born bush Karoo rats has possibly evolved due to ecological constraints. Our study population experiences a short breeding season and individuals have to survive a long dry season thereafter. Such a harsh environment could limit the benefits of precocious reproduction. Reproducing at young age can even have negative fitness consequences on both the first litters and the mothers (Lambin and Yoccoz 2001; Rödel et al. 2023), and furthermore a more proactive personality has negative consequences on survival (Smith and Blumstein 2008; Cole and Quinn 2011; Luna et al. 2020), for example through increased predation risk (Rödel et al. 2015; Denoël et al. 2019). Even though earlier-born females may benefit from being proactive in competition for reproductive resources, the survival impact might decrease the general fitness of both the young females and their litters to below the threshold for surviving the extremely harsh non-productive period. As a result, the benefit of being proactive may depend on the time of birth during the breeding season: for earlier-born individuals, being a proactive breeder may not be adaptive due to the harsh ecological environments, while for later-borns, the scarcity of life-critical resources (stick lodges) makes the risk of being proactive worthwhile in exchange of better chances in acquiring stick lodges.

In conclusion, our study presents an example of personality differences in association with a key life history trait, the timing of birth within the season. Bush Karoo rats born later in the season showed higher proactivity and we suggest that such an association has evolved in response to the availability of survival resources, particularly the reduced availability of vacant stick lodges. Being more active, bolder, and more exploratory could be adaptive under such conditions because it could help later-borns explore more habitat to find unoccupied lodges or building materials. Our study highlights the importance of investigating not only reproduction opportunity, but also potential survival challenges to better understand the diverse mechanisms underlying the integration between life history and behavioral traits.

Declarations

Ethics approval

The study was conducted according to accepted international standards regarding the guidelines for the use of animals in behavioral research (Vitale et al. 2018), and the legal requirements (section 20 permit) of South Africa, where the study was carried out. Ethical clearance (2022/05/02B) was provided by the Animal Research and Ethics Committee of the University of the Witwatersrand, Johannesburg, South Africa. No injuries or mortalities occurred in any study animals; all individuals were successfully released at the exact sites from where they were trapped.

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Competing interests

The authors declare no conflicts of interest.

Author contributions

JQ, HGR and CS conceived the study. Data collection was performed by JQ and LM, data analysis was performed by JQ and HGR. The first draft of the manuscript was written by JQ and HGR, all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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III.6. Supplementary Material

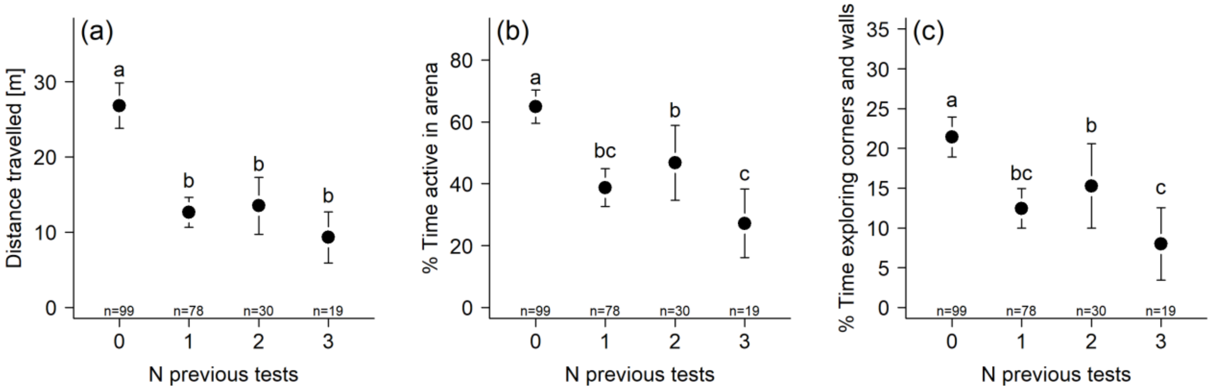

Figure III.A. Pair-wise comparisons between the numbers of previous tests done on the three behavioral parameters for which a significant effect of this factor has been shown in Table 3. Zero (on x-axis) indicates that the animals underwent this test for the first time (test sequence = 1). Mean values with 95% confidence intervals are given. Pairwise comparisons (post hoc to significant effects of the factor “Test sequence”; see Table 3) were done LMMs using a sequential Bonferroni correction (Holm 1979). See details on transformations with of the different response variables in Table 3. Significant differences between groups are indicated by different letters inside the Figures.

Table III.A Correlation coefficients and 95% credible intervals (CI) between the different behavioral parameters recorded in repeated starting box, open field and novel odor tests, based on measurements taken from 99 bush Karoo rats of different age classes (same model as given in Table 1a). Analysis by a multivariate GLMM including individual identity as a random factor, and year, sex and the number of the test session (4 levels) as fixed variance. Lines given in bold indicate that the 95% credible interval s do not overlap zero, and thus these associations can be considered as statistically significant.

Association	mean *R*	95% CI [lower, upper]
PEA - DT	**0.763**	**[0.573, 0.930]**
PEA - %TA	**0.840**	**[0.644, 0.982]**
PEA - %TEA	**0.780**	**[0.530, 0.974]**
PEA - TEO	0.549	[−0.534, 0.988]
PEA - NOE	0.454	[−0.833, 0.970]
DT - %TA	**0.786**	**[0.579, 0.955]**
DT - %TEA	**0.620**	**[0.325, 0.864]**
DT - TEO	0.484	[−0.372, 0.963]
DT - NOE	0.429	[−0.755, 0.973]
%TA - %TEA	**0.848**	**[0.637, 0.979]**
%TA - TEO	0.605	[−0.507, 0.994]
%TA - NOE	0.470	[−0.857, 0.992]
%TEA - TEO	0.494	[−0.534, 0.984]
%TEA - NOE	0.372	[−0.838, 0.979]
TEO - NOE	0.614	[−0.611, 0.992]

PEA: Probability to enter arena; DT: Distance travelled (square-root transformed); %TA: % Time active; %TEA: % Time exploring walls and corners of arena (square-root transformed); TEO: Time exploring object (log [x+1] transformed); NOE: Number of objects explored

Table III.B Effects of different behavioral variables on the probability of precocious reproduction in females born early in the breeding season (with a birth date during the first 5 weeks, *n* = 27). Analysis by multifactorial GLMMs for binomial data including individual identity as a random factor and year as fixed variance. Note that the effects of the different behavioral variables were tested in separate models, since several of these were strongly collinear (see Table III.3). None of the effects were statistically significant.

Predictors	χ^2	*df*	$\beta \pm$ SE	*P*
Probability to enter arena	0.061	1	0.896 ± 3.617	0.804
Year [2^{nd}]	0.225	1	2.044 ± 4.308	0.635
Distance travelled [1]	0.002	1	−0.004 ± 0.107	0.967
Year [2^{nd}]	0.180	1	1.771 ± 4.176	0.672
Time active	0.002	1	0.001 ± 0.053	0.989
Year [2^{nd}]	0.181	1	1.732 ± 4.076	0.671
Time exploring walls and corners of arena [1]	0.009	1	0.090 ± 0.927	0.923
Year [2^{nd}]	0.172	1	1.693 ± 4.088	0.679
Time exploring object [2]	0.024	1	0.211 ± 1.376	0.878
Year [2^{nd}]	0.202	1	1.894 ± 4.216	0.653
Number of objects explored	0.045	1	0.270 ± 1.280	0.833
Year [2^{nd}]	0.216	1	2.080 ± 4.475	0.642

[1] square-root transformation of dependent variable

[2] log [x+1] transformation of dependent variable

Table III.C Repeatability (*R*, including its 95% credible interval *CI*) of behavior parameters measured in repeated starting box (SB), open field (OF) and novel odor (NO) tests **of a subset of 66 individuals**, which were all still present in the population during the last testing session of the year of study (four test sessions in 2022, and two test sessions in 2023) and were all at least tested for two times (resulting in a total of $n = 178$ measurements for each behavioral variable). Analysis by a multivariate GLMM over all available (up to four) test sessions, including individual identity as a random factor, year, sex and test sequence (4 levels) as fixed variance

	R	***CI*$_{95\%}$**
SB - Probability to enter arena	0.503	[0.244, 0.775]
OF - Distance travelled [1]	0.301	[0.097, 0.509]
OF - % Time active	0.123	[< 0.001, 0.274]
OF - % Time exploring walls and corners of arena[1]	0.216	[0.042, 0.406]
NO - Time exploring object [2]	0.078	[< 0.001, 0.260]
NO - Number of objects explored	0.077	[< 0.001, 0.274]

[1] square-root transformation of dependent variable

[2] log [x+1] transformation of dependent variable

Table III.D Associations between the different behavioral parameters, based on measurements taken **from of a subset of 66 individuals**, which were all still present in the population during the last testing session of the year of study (four test sessions in 2022, and two test sessions in 2023) and were all at least tested for two times (resulting in a total of *n* = 178 measurements for each behavioral variable). Analysis by a multivariate GLMM over all available (up to four) test sessions, including individual identity as a random factor, and year, sex and test sequence (4 levels) as fixed variance. Note that results stem from the same model as used for the calculation of Table II.C. Correlation coefficients (among individual-level) are given, values given in bold indicate that the 95% credible interval s do not overlap zero, otherwise they are given in brackets

	PEA	**DT**	**%TA**	**%TEA**	**TEO**	**NOE**
PEA		**0.717**	**0.688**	**0.702**	(0.342)	(0.457)
DT			**0.729**	**0.596**	(0.318)	(0.477)
%TA				**0.758**	(0.418)	(0.478)
%TEA					(0.289)	(0.392)
TEO						(0.510)
NOE						

PEA: Probability to enter arena; DT: Distance travelled (square-root transformed); %TA: % Time active; %TEA: % Time exploring walls and corners of arena (square-root transformed); TEO: Time exploring object (log [x+1] transformed); NOE: Number of objects explored

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CHAPTER 3

Associations between metabolic rate and personality in a seasonally breeding small mammal are driven by date of birth

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IV.1. Abstract

Consistent individual variation in behavior (personality) can have an influence on energy demands. However, studies focusing on the link between animal personality and resting metabolic rate (RMR) often found weak or no associations. We investigated whether personality is associated with RMR and short-term metabolic rate responses to an acoustic stressor in free-living bush Karoo rats (*Otomys unisulcatus*), and therefore we measured personality and metabolic rate in 78 adult female rats. Individuals showed a proactive behavioral syndrome (positive associations between the repeatable traits: activity, boldness and exploration), repeatable RMR and a general increase in metabolic rate in response to the acute acoustic stressor. Significantly higher RMR was associated with proactive personality traits. However, a more detailed path analysis revealed that this apparent association was in fact driven by the animals' date of birth within the breeding season: individuals born later in the season were more proactive, having higher RMR and a lower metabolic response to acoustic stress, but there was no significant direct association between personality and any metabolic rate variable. This finding can explain why previous studies report contradictory results regarding the personality-RMR relationship: their association is indirect, driven by shared underlying factors such as birth timing or possibly other ecological/life history traits that are context-specific.

Keywords

behavior, behavioral performance, life history, metabolic rate, phenotypic correlation, stress response

IV.2. Introduction

From fundamental biological processes to complex behaviors, energy fuels every function of living organisms (Brown et al., 2004). Consistent individual differences in behavior, or animal personality, are prevalent characteristics observed in animals (Bell et al., 2009; Réale et al., 2007). Because different personality types can lead to varying levels of energy demanding activity and stress response, personality has been predicted to be also related to individual energy budget and metabolism (Careau et al., 2008).

The rate at which an animal oxidizes substrates to produce energy is its metabolic rate (MR). The basal metabolic rate represents the minimum energy expenditure necessary to sustain basal biological function (McNab, 1997), a major component of daily energy costs (Daan et al., 1990; Nagy et al., 1999; Speakman and Selman, 2003) and it is often used as a valid proxy for assessing the energetic consequences of behavioral traits. As a more easily measurable parameter, resting metabolic rate (RMR) is frequently used as an approximate substitute for basal metabolic rate. Bolder, more active and more exploratory individuals have been suggested to have higher resting metabolic rate than shy, inactive individuals (Mathot and Dingemanse, 2015). This is because such energy-costly behaviors promote energy acquisition, as for example by spending more time exploring and foraging facilitates greater access to food and other resources, providing net energy gain to sustain a generally higher level of metabolism. Studies in several taxa investigated the link between individual differences in RMR and personality traits, including fish (Killen et al., 2012; White et al., 2016), birds (Bouwhuis et al., 2014), and mammals (Careau et al., 2015; Jäger et al., 2017). In a synthesis of these studies, Mathot and Dingemanse (2015) reported that around half of these studies provided positive correlations, but the remaining ones found no or negative correlations. This raises the question why species differ in their association between personality and RMR, and how the association between these traits is mediated.

Other aspects of energy metabolism, such as the metabolic response to acute stress, may be also related to personality (Jäger et al., 2017). Physiological stress functions to quickly provide energy to overcome critical situations (stressors), typically via behavior (Schradin et al., 2023). Personality traits could affect the display of such behavioral responses, including activity and boldness. In many animals, acute stress, such as induced by the appearance of a predator, can trigger a freeze-or-flee response, i.e., individuals either reduce activity ("freeze") or try to escape ("flee"; Eilam et al., 1999), while at the same time triggering the sympathetic stress response to immediately activate energy supplies (Härle et al., 2006). More proactive and less proactive animals have been reported to show differential stress responses at the short-term and at the longer term (Santicchia et al., 2020). Whilst the immediate, sympathetic stress response has been shown to be more pronounced in more proactive individuals, less proactive individuals typically show a stronger activation of the HPA (hypothalamic-pituitary-adrenal) stress axis (Koolhaas et al., 1999; Duparcq et al., 2019). These differences, in turn, might also affect the dynamics of metabolic responses in animals with different personality types. It is surprising that the relationship between the metabolic consequences of the stress response and personality has so far hardly been studied.

Both, metabolic rate and behavioral traits are influenced by multiple factors. For example, previous studies demonstrated that early-life environments can have long-lasting effects on personality traits. In laboratory rats (*Rattus norvegicus*), heavier offspring were bolder and more exploratory, and also litter size influenced behavioral responses and anxiety (Rödel and Meyer, 2011). In zebra finches (*Taeniopygia castanotis*), nutritional restriction early in life affected physiological traits, with individuals experiencing such restrictions as nestlings exhibiting higher basal metabolic rates in adulthood (Careau et al., 2014). Thus, individual variation in behavior and RMR may be concomitantly driven by external factors, leading to apparent correlative but not causal associations of metabolic-behavioral traits.

In short-lived, seasonal breeding rodents, the date of birth within the breeding season has been repeatedly shown to strongly influence individual’s early-life experiences, and this influence can persist to adulthood and even lead to distinct life history trajectories (Roff, 1993; Rödel et al., 2009; Varpe, 2017). Early- and late-born cohorts typically face distinct environmental conditions depending on their time of birth: resources and reproduction opportunities are usually rich in the early breeding season, but continually decrease over time. This could lead to differing reproduction-survival trade-offs between early/late born individuals, expressed as within-population differences in life history, behavioral and physiological aspects (Eccard and Herde, 2013; Montiglio et al., 2014). Thus, we hypothesize, that the date of birth within the breeding season could be an important factor influencing the possible correlations between behavior and energy metabolism.

We quantified personality traits and metabolic rates at resting/stressful situations in a small rodent, the bush Karoo rat (*Otomys unisulcatus*). Our study was done in the Succulent Karoo, South Africa, a seasonal environment with superabundant food in moist spring, followed by very hot and dry summers with very low food availability. Previous studies have confirmed the existence of personality in this species (Agnani et al. 2020). Importantly, the results from a larger dataset of the study species found that individuals born later in the breeding season adopted a comparatively more proactive (bolder, more active and explorative) personality than earlier-borns (Qiu et al., in press), making bush Karoo rats a suitable study species for our question in how far personality, metabolism and timing of birth are related to each other.

We studied whether personality traits are associated with RMR and metabolic response to acute stress in bush Karoo rats, considering environmental and life history factors, especially the individual birth date within the breeding season. A previous study on the same population did not find a significant correlation between RMR and the two personality traits, docility and exploration (Agnani et al., 2020). Therefore, we considered a larger array of personality traits (activity, boldness, exploration) and measurements of metabolic rates under different conditions. Specifically, we hypothesized that (*i*) RMR is associated with personality traits, with bolder, more active and/or exploratory individuals having higher RMR, that (*ii*) individuals with a more proactive personality show a lower metabolic rate in response to an acute stressor (i.e., experiencing reduced MR increase after exposure to this stressor), and (*iii*) that the date of birth is positively correlated with personality and with energy metabolism, with later-born individuals being more proactive, having higher RMR, and showing a lower MR stress response. Finally, (*iiii*) by the aid of a path analysis to disentangle potential causal processes, we hypothesize that the association between personality and metabolic rate (MR) is not direct but is instead driven by their shared relationship with date of birth.

IV.3. Materials and Methods

IV.3.1. Study species and study site

The bush Karoo rat is a diurnal, small (weighing 61–156g) solitary rodent (Wolhuter et al., 2022). The studied population is the same in Chapter 2, new-born individuals used in this study was born between the moist period form mid-July to late November (Qiu et al., in press). Our study population inhabits the semi-arid habitats of South Africa, specifically in the Succulent Karoo region of the Goegap Nature Reserve, Northern Cape, South Africa. The semi-arid Succulent Karoo is a biodiversity hotspot (Cowling et al. 1999), characterized by an annual rainfall of 160mm/year on average, and by temperatures varying from −1.5 to 24°C during winter and from 4 to 42°C during summer (data from a weather station at the field site). Most of the rainfall occurs in winter, leading abundant ground vegetation that supports the onset of reproduction in bush Karoo rats (Wolhuter et al. 2021). More information about the study site and study species can be found in "III.3.1. Study site and study population" from Chapter 2.

IV.3.2. Study area and trapping

We collected data at a study site of approximately 4.5ha from August 2022 to December 2023. Bush Karoo rats construct and take refuge in "stick lodges", which they construct from dry plant materials and can be up to 0.5m high (Vermeulen 1988; Brown and Willan 1991; Du Plessis et al. 1992), making them easy to locate in the field. Trapping and marking were carried out at all occupied stick lodges throughout the year as part of our long-term data collection; therefore, focal individuals for this study could be identified by their aluminum band ear tags carrying a unique individual number (National Band and Tag Co., Newport, KY, USA). We used Sherman traps and locally produced metal traps (26×9×9 cm) of Sherman trap style. Traps were set at lodge entrances before sunrise and checked every 30min. All traps were closed within two hours after sunrise (i.e., trapping was stopped) to avoid the animals overheating.

The field site was divided into six areas for daily trapping, which was always carried out at only two of these areas at the same time by research assistants and colleagues for three days, before moving on to the next two areas. Daily trapping was done to mark and track the study population. Additional trapping for focal individuals for this study was done by JQ and research assistants. Captured focal individuals were transported whilst inside the trap to a field laboratory, which was less than a 10min walking distance from the field site. More information about trapping procedure can be found in "III.3.3. Trapping and individual tagging" from Chapter 2.

IV.3.3. Focal animals and sample size

Females used in Chapter 2 was selected as focal individual in this study. Captured focal individuals were transported whilst inside the trap to a field laboratory, which was less than a 10min walking distance from the field site. We studied only females, the more philopatric sex. We measured behavioral responses (in standardized tests) and metabolic rate in the same morning of trapping in up to four rats at a time (see details below). Thereafter, individuals were released back at their lodge within 3-6h after capture. Except from checking their identity, performing behavioral tests and metabolic rate measurements, the rats remained in the trap until they were released. This was done because they were accustomed to the traps and showed no obvious signs of distress when inside, compared to keeping them in unfamiliar transparent cages.

All rats were scheduled for four repeated (behavioral and metabolic) tests at two age classes. The first behavioral and metabolic rate tests were scheduled at an age of approximately six weeks, the age when bush Karoo rats reach sexual maturity (Pillay 2001). A second test session scheduled approximately two weeks later. For more information of the test schedule, see "III.3.5. Experimental procedure" from Chapter 2. In the first year of study, individuals (20 out of 52 focal individuals) that survived long enough were re-tested at an older age at approximately 20 twenty weeks old (3rd test), and again two weeks later (4th test). Due to logistical constraints in the second year of study, focal individuals only underwent up to two tests at an age of approximately six weeks and again two weeks after (27 focal individuals). Trapping of focal individuals was not always successful, so that tests and measurements were sometimes delayed or not carried out due to temporary or permanent disappearance of the individuals. The average age at the 1st and 2nd test was 54 days (age class: young adult, range: 34–100 days), and the average age at the 3rd and 4th test was 151 days (age class: older adult, range: 140−154 days). Birth date was estimated from the animals' body mass, based on the linear association between age and body mass in the bush Karoo rat as published in Pillay (2001).

IV.3.4. Personality tests

Boldness, activity and exploration were measured using staring box and open field tests. The test arena was a white chamber (100cm long, 85cm wide and 65cm high) made of white coated plywood panels, with two liftable doors symmetrically located on the two short sides of the rectangular arena (more details in "III.3.6. Behavioral tests"). For testing, rats were individually introduced into the starting box, which was a 10cm^3 black acrylic and opaque squared box connected to the arena. The starting box was separated from the test arena by a closed door.

Starting box test (SB) – After the focal individual rested for 3min in the starting box (habituation time), the door to the test arena was lifted and we recorded the probability to enter arena, defined as whether the animal entered the test arena in the following 10 min.

Open field test (OF) – The open field test began once the rat had entered the arena. Thereafter, the door was closed to prevent it from returning into the starting box. The behavior of the focal individual in the open field was video recorded for 5min. We quantified two behavioral variables: (1) the distance traveled, defined as the total distance of locomotion in the arena measured in cm, and (2) the % time exploration, defined as the time the animal spent sniffing or putting its front paws against the walls or into the corners.

IV.3.5. Respirometry

After the behavioral tests, individuals were transferred back to their original traps to rest for 2-3 hours. Respirometry measurements were obtained after the behavioral test of the last individual of the day, at least 4 hours after sunrise, which corresponds to the non-active period of bush Karoo rats.

Metabolic rate was measured by oxygen consumption using a flow-through system with excurrent flow. The system included a RH-300 water vapor analyzer (Sable Systems International, SSI, Las Vegas, Nevada), a FoxBox respirometer (Sable Systems International, SSI, Las Vegas, Nevada), one metabolic chamber and two channels (one for the test chamber and one for baseline). The baseline channel was directly connected to ambient air while the test channel was connected to a 1-liter metabolic chamber containing the focal individual. A three-way valve was used to control the airflow, directing it either into the test channels holding the focal individual or into the baseline channels for baseline recordings.

Ambient air was drawn from outdoors at a flow rate of around 700ml/min, first through a spiral copper tube to have full thermal exchange to stabilize the air flow temperature at 30℃ (Pelt 5, SSI). Water vapor, carbon dioxide and oxygen concentration were measured in both chambers using the RH-300 water vapor analyzer and the O_2 sensor of the FOXBOX respirometer (SSI, Las Vegas, Nevada), respectively. For calibration, see descriptions in the user manual. Data were recorded and analyzed using the ExpeData software package (SSI, Las Vegas, Nevada). During the metabolic rate experiments, we observed the behavior of the animals live on a computer monitor, situated outside the test area. Therefore, all activities of the focal individual during the metabolic rate measurement were recorded and transferred via a webcam (C170, Logitech).

Individual O_2 consumption ($mL^{-1}\ h^{-1}$) was calibrated for H_2O and CO_2 and calculated using the equations for the pull system (Lighton, 2018). Body mass-scaled RMR was calculated as individual O_2 consumption divided by individual body mass measured before entering the chamber.

Small rodents are sensitive to threat signals (Mobbs and Kim, 2015), such as to auditory cues (Mongeau et al., 2003). Based on this sensory capacity, we measured individual metabolic responses to an acoustic stressor. A key finder (Thousandshores Deutschland GmbH, model HL-KF02A, manufacturer model KF02A, 5mm×2mm ×0.5mm) controlled by a remote was placed in advance inside the respirometry chamber, separated from the focal individual by a honeycomb metal plate. Pressing the remote control produced a 10s alarm, consisting of a sequence of high-frequency short beeps of around 90dB. This alarm sound was assumed to induce acute stress in the animals. This was confirmed by our preliminary experiments and direct observation, verifying that bush Karoo rats showed either a startle response and/or freezing behavior to the playback of this acute acoustic stressor. Furthermore, we had verified in preliminary experiments that the playback of this sound led to an increase in metabolic rate above the resting state.

The metabolic rate recordings started with a 5min baseline measurement, where after the airflow was switched to the test channel for at least 20min to record metabolic rate at resting state. As the O_2 concentration stabilized when the focal individual remained at rest (immobile, as seen on the computer monitor), the key finder was triggered by a remote control, producing an acute auditory stimulus (alarm) for 10s. The focal individual experienced the alarm sound twice, with a 10min interval. Resting metabolic rate was retained as the lowest 5s mean O_2 consumption over 10min before the first alarm. The metabolic response to this acute stressor was measured using two variables: (1) max. relative MR stress response, calculated as the maximum O_2 consumption within 1min after the alarm sound, divided by the O_2 consumption at resting state; and (2) integral MR stress response, calculated as the mean integral of O_2 consumption during 1min after the acoustic stimulus divided by the O_2 consumption at resting state in 1min. For both variables, the mean of the two repetitions was used for statistical analysis.

After the metabolic rate measurements, the focal individuals were given succulent plants and bait (a mixture of bran flakes, salt and sunflower oil) as compensation for missed foraging opportunities, before being released back to the stick lodge from where they had been captured.

IV.3.6. Statistical analyses

For each individual, we included data only from test sessions during which we managed to collect both MR measurements and behavior data. 78 females were tested 155 times during the 1st, 2nd, 3rd and 4th tests, among which 58 females were tested 83 times during the 1st and 2nd test (34−100 days old, mean of 55 days), 37 females were tested 71 times during the 3rd and 4th test (138−213 days old, mean of 150 days). Statistical analyses were carried out using R software, version 4.4.1 (R Core Team, 2024).

Repeatability – Repeatability (consistency over time) of behavioral and metabolic variables was analyzed using linear-mixed-model (LMM)-based intra-class correlations, including individual identity as a random intercept factor, using the R package *rptR* (Stoffel et al. 2017). Repeatability was measured as short-term repeatability (1st and 2nd test session) when the individuals were still young adults and as long-term repeatability (1st to 4th test session) including both age classes. *P*-values were calculated using Monte-Carlo permutation tests (10,000 permutations of the model) implemented in the package *rptR*.

All behavioral and metabolic variables (given in Tables IV.1, 2) were scaled and some of them were transformed for analysis (see below) in the same way as the path analysis. Our previous study using the same data set found significant differences over time regarding the behavioral measurements. That is, individuals showed a generally higher level of behavior in the first test session than in the subsequent ones, possibly due to habituation effects (Qiu et al., in press). Such strong population-level differences over time (over consecutive test sessions) with respect to the animals' behavioral responses, as well as their metabolic rates, can potentially mask the detection of individual-based repeatabilities. Thus, we included the number of tests the individual has experienced before (0/1/2/3) as a fixed factor to control for the possible influence of such differences among test sessions.

Association between behavioral traits and metabolic rate – In the first step, we tested for direct associations between the three behavioral variables (predictors: probability to enter arena; distance traveled; % time exploration) and metabolic rate variables (three different response variables, used in separate models: RMR; max. MR stress response; integral MR stress response). To establish whether there was a direct relationship, we explicitly did not include any further predictor variables, such as the individual date of birth, in these models. This was done by LMMs (linear mixed-effects models) using the R package *nlme* (Pinheiro et al. 2023). Due to collinearities between the three behavioral variables, they were considered separately in different models, i.e. 9 models were calculated in total (see Table IV.3). All models included individual identity as a random intercept factor.

P-values were calculated using Monte Carlo permutation tests (10,000 permutations) in the *pgirmess* package (Giraudoux 2022). Even though permutation tests do not rely on a normal distribution of model residuals (Good 2005), we verified whether variances were homogenous for all models by plotting fitted values versus the residuals (Faraway 2005), since unequal variances in permutation testing can inflate type I error rates (Huang et al. 2006). Thus, we homogenized model variances by applied transformations to two of the MR variables: the response variable, max. MR stress response, was square-root transformed after adding a value of 4.53 to obtain positive values, and the integral MR stress response variable was log-transformed after positivizing all values by adding 23.73. These transformations of these two MR variables were also used later in the LMM-based path analysis, as described below.

Path analysis – In the second step, we examined the chain of relationships among date of birth, behavioral traits and metabolic variables, considering further possible predictors using path analysis (Shipley, 2009). The date of birth affects behavioral traits in the bush Karoo rat (Qiu et al., in press), and we aimed to test whether the date of birth would directly and/or indirectly (via its effects on behavioral traits) affect the different MR variables. In other words, we aimed to explore whether the date of birth possibly affected the variation of both, individual behavioral traits as well as metabolic variables.

Path analyses were carried out with the R package *piecewiseSEM* (Lefcheck, 2016), based on combinations of LMMs and a GLMM (generalized linear mixed-effects model) for binomial data with a logit link. The latter was used for modelling effects on the binary behavioral response variable ‘probability to enter the test arena’ (see details on the structure of the complete path model in Table IV.A in Suppl. Materials). LMM and GLMM were calculated using the R functions *lmer* and *glmer* (package *lme4*; Bates et al., 2015, linked to the package *piecewiseSEM;* Lefcheck, 2016), including individual identity and the number of tests the individual has experienced before (0/1/2/3) as a random intercept factor. We calculated separate path models for the different response variables: RMR, max. MR stress response, and integral MR stress response. Initially, we constructed directed acyclic graphs to examined the causal relationships of each of the metabolic variables with the three personality traits (probability to enter arena, distance traveled and time exploration), the individual date of birth within the season, the year of testing (2022/2023), age class at testing (young adult/older adult), ambient temperature (°C) and food abundance (number of food plant per 4sqm square, Werger, 1974; Schradin and Pillay, 2006). Because path analyses use only covariates, the 2-level factors, age class and year, were transformed into numerical variables and included the values −1 and +1 (Lefcheck, 2016). The expected collinearities between the different behavioral variables (see Qiu et al., in press) were implemented into the path models as correlated errors (Lefcheck, 2016).

All variables were scaled for analysis to obtain standardized slopes (β), where the absolute value of the standardized slope (beta weight) can be interpreted as the relative effect size of an association (Lefcheck 2016). For each response variable in the path diagram, we also report (multiple) marginal R^2 (see Fig. 1), which represented the proportional explained variance excluding the contribution of random factors (Nakagawa and Schielzeth, 2013). For all LMMs, we checked for the normal distribution of model residuals (verified by visually checking normal probability plots) and homogeneity of variances (by plotting residuals versus fitted values; Faraway, 2005). To adjust the residuals to a normal distribution, we square-root transformed the % time the animals spent exploring, square-root [x+4.53] transformed the max. MR stress response and log [x+23.73] transformed the integral MR stress response. We verified the goodness of fit of the global path models using chi-squared tests (Lefcheck, 2016).

IV.4. Results

IV.4.1. Consistent individual differences in behavior

We found significant repeatabilities over time for all three behavioral variables at the short-term as well as at the long-term (Table IV.1). Inter-individual differences in these behaviors remained consistent both during the repeated measurements within around two weeks of time in young adults (1st and 2nd test; Table IV.1a), as well as at the long-term over different age classes, i.e. in young and older adult stage (all four test sessions; Table IV.1b).

Table IV.1. Repeatability estimation (R, including its 95% confidence interval $CI_{95\%}$) of behavioral variables measured in repeated starting box (SB) and open field (OF) tests.

	(a) Short -term repeatability			**(b) Long-term repeatability**		
	R	***CI***	***p***	***R***	***CI***	***p***
Probability to enter arena (SB)^1	0.993	[0.987, 0.999]	**0.002**	0.552	[0.117, 0.979]	< **0.001**
Distance traveled (OF)^2	0.495	[0.167, 0.734]	**0.003**	0.353	[0.141, 0.542]	< **0.001**
% Time exploration (OF)^2	0.584	[0.294, 0.779]	< **0.001**	0.387	[0.178, 0.569]	< **0.001**

Analysis of data from 78 female bush Karoo rats by GLMM-based intra-class correlations (^{1}binomial distribution, ^{2}Gaussian distribution), including individual identity as a random intercept factor and number of tests the individual has experienced before as fixed variance. (a) Short-term repeatability was based on (up to) two behavioral tests during young adult stage (58 individuals, $n = 85$ measurements for each behavioral variable). (b) Long-term repeatability was based on all (up to) four behavioral tests of all age classes (78 individuals, $n = 156$ measurements for each behavioral variable). P-values were calculated by permutation tests (10,000 Monte-Carlo permutations); significant effects ($p < 0.05$) are highlighted in bold.

IV.4.2. Consistent individual difference in measures of MR

We also found significant repeatabilities over time for RMR, both at the short-term and long-term (Table IV.2). The repeatability of the max. MR stress response was significant (R = 0.367, p = 0.041, Table IV.2a) at the short term (within two test sessions during two weeks as young adults). No significant repeatabilities or tendencies of such were found for the integral MR stress response.

Table IV.2. Repeatability estimation (R, including its 95% confidence interval $CI_{95\%}$) of three metabolic variables.

	(a) Short-term repeatability			(b) Long-term repeatability		
	R	***CI*₉₅%**	***p***	***R***	***CI*₉₅%**	***p***
RMR	0.417	[0.064, 0.683]	**0.017**	0.391	[0.182, 0.551]	**< 0.001**
Max. MR stress response	0.367	[0.028, 0.648]	**0.041**	0.064	[< 0.001, 0.260]	0.257
Integral MR stress response	< 0.001	[< 0.001, 0.373]	> 0.999	0.012	[< 0.001, 0.230]	0.478

Analysis of data from 78 female bush Karoo rats by LMM-based intra-class correlations (for Gaussian distribution), including individual identity as a random intercept factor and the number of previous tests as fixed variance. (a) Calculations on short-term repeatabilities were based on data from (up to) two behavioral tests during young adult stage (58 individuals, $n = 85$ measurements for each behavioral variable). (b) Long-term repeatabilities were based on data from all (up to) four behavioral tests of all age classes, i.e. from young adult stage to older adult stage (78 individuals, $n = 156$ measurements for each behavioral variable). *P*-values were calculated by permutation tests (10,000 Monte-Carlo permutations); significant effects ($p < 0.05$) are highlighted in bold.

IV.4.3. Association between personality traits and variables of MR

RMR was significantly and positively associated with the two behavioral variables measured in the open field test. That is, individuals with higher RMR traveled longer distances and showed more exploration behavior in the open field (Table IV.3a).

For most individuals, we found rather clear, short-term increases in metabolic rates after the playback of the acoustic stressor, as evident by the mostly positive values of the maximal MR stress response and integral MR stress response (Figure IV.2b, c). However, we did not find any significant associations of these two metabolic variables with any of the three behavioral variables using LMM (Table IV.3b, c).

Table IV.3. Associations between behavioral traits and metabolic rate variables measured in repeated starting box (SB) and open field (OF) tests.

	(a) RMR		**(b) Max. MR stress response**		**(c) Integral MR stress response**	
	β±SE	***P***	***β±SE***	***P***	***β±SE***	***P***
Probability to enter arena (SB)	0.037±0.184	0.846	0.185±0.185	0.330	0.099±0.185	0.596
Distance traveled (OF)	**0.191±0.075**	**0.014**	−0.031±0.081	0.706	−0.058±0.081	0.475
% Time exploration (OF)	**0.174±0.078**	**0.028**	−0.069±0.081	0.399	−0.065±0.081	0.420

Analysis of data from 78 female bush Karoo rats by LMM with one metabolic rate parameter as dependent variable per model. Due to collinearities between the three behavioral variables (see Fig. 1), three separate models were calculated for each personality trait as predictors (covariates), all including individual identity as a random intercept factor. Standardized estimates (*β*) with standard errors are given. *P*-values were calculated by permutation tests (10,000 Monte-Carlo permutations); significant effects ($P<0.05$) are highlighted in bold.

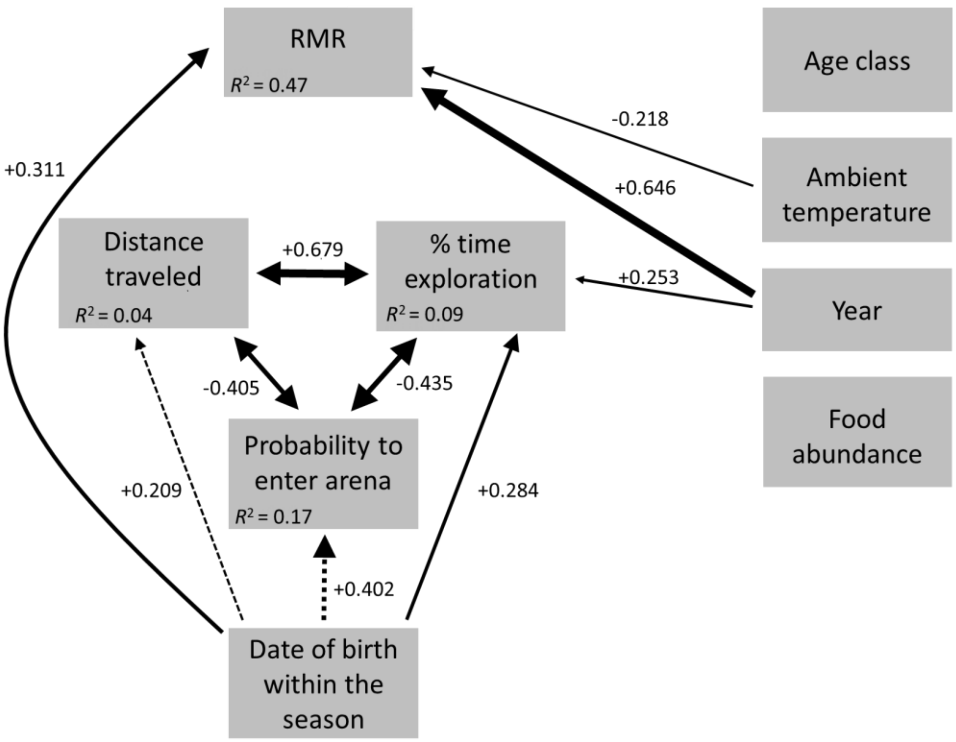
IV.4.4. Factors affecting the association between personality and MR

Our path analysis confirmed significant associations between all three behavioral traits, thus forming a behavioral syndrome. Individuals, which traveled a higher distance in the open field also spent more time exploring the arena, and such individuals were more likely to enter the open arena. (Figure IV.1). All of these three behavioral traits were associated to the individual date of birth. As already shown in our recent study (Qiu et al., in press), later born individuals were significantly more exploratory (β=0.284, Figure IV.1)) and showed a tendency of traveling greater distance in the open field (β=0.209, P=0.063), and also tended to enter the open arena with a higher probability within the 10 min of testing (β=0.402, P=0.062; Figure IV.1; details in Suppl. Materials, Table IV.A).

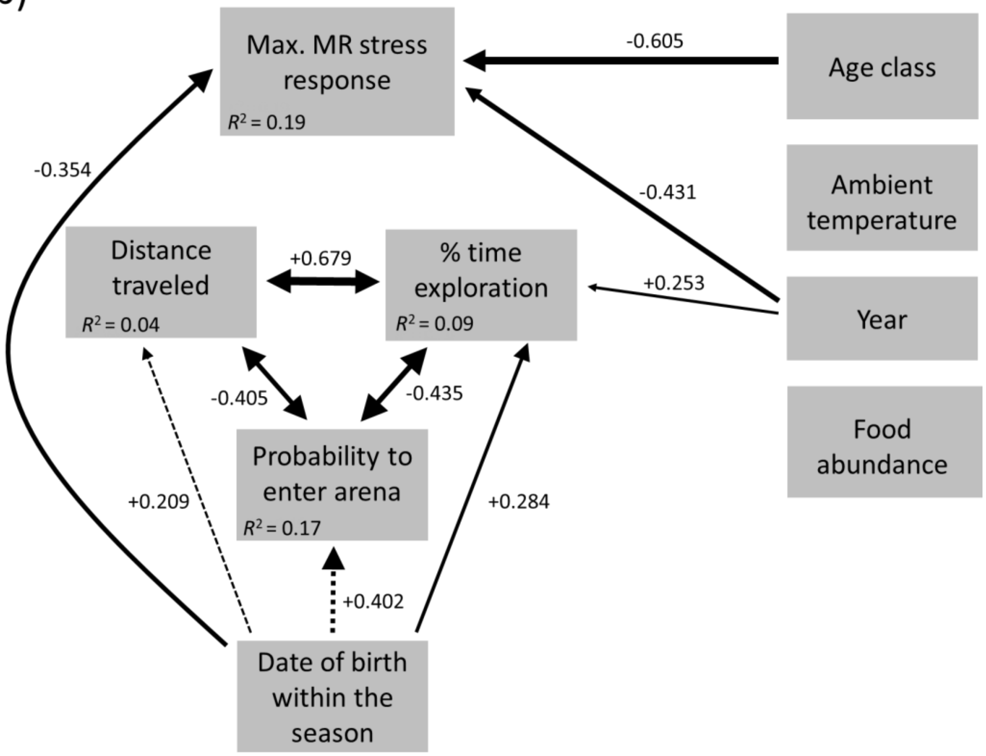
We found direct and significant effects of the date of birth within the breeding season on all metabolic rate variables. Later-borns had a significantly higher RMR (β=0.311, Figures. IV.1a, 2a), a lower max. MR stress response (β=–0.354; Figures. IV.1b, 2b), and a lower integral MR stress response (β=–0.352, Figures. IV.1c, 2c). However, there were no significant and direct associations between any of the behavioral variables and the animals' RMR (Figure IV.1a), their max. MR stress response (Figure IV.1b), or their integral MR stress response (Figure IV.1c).

We also found some significant effects of other confounding factors on the three metabolic rate variables. RMR decreased with increasing ambient temperature (β=–0.218, Figure IV.1a; see Figure IV.A in Suppl. Materials). There was also a significant year effect; the % time exploration (β = 0.253) and RMR (β = 0.646) measured during the second year was significantly higher than during the first year (Figure IV.1a), and the Max. MR stress response measured during second year was significantly lower than during the first year (β = –0.431, Figure IV.1c). Furthermore, Max. MR stress response decreased significantly at older age (β=–0.605, Figure IV.1b; see Figure IV.B in Suppl. Materials). Food abundance had no significant effects on any of the behavioral or metabolic variables tested (Figure IV.1a-c).

(a)



(b)


Max. MR stress response
$R^2 = 0.19$
-0.605
Age class
-0.354
-0.431
Ambient temperature
Distance traveled
$R^2 = 0.04$
+0.679
% time exploration
$R^2 = 0.09$
+0.253
Year
-0.405
-0.435
Food abundance
Probability to enter arena
$R^2 = 0.17$
+0.209
+0.284
+0.402
Date of birth within the season

(c)

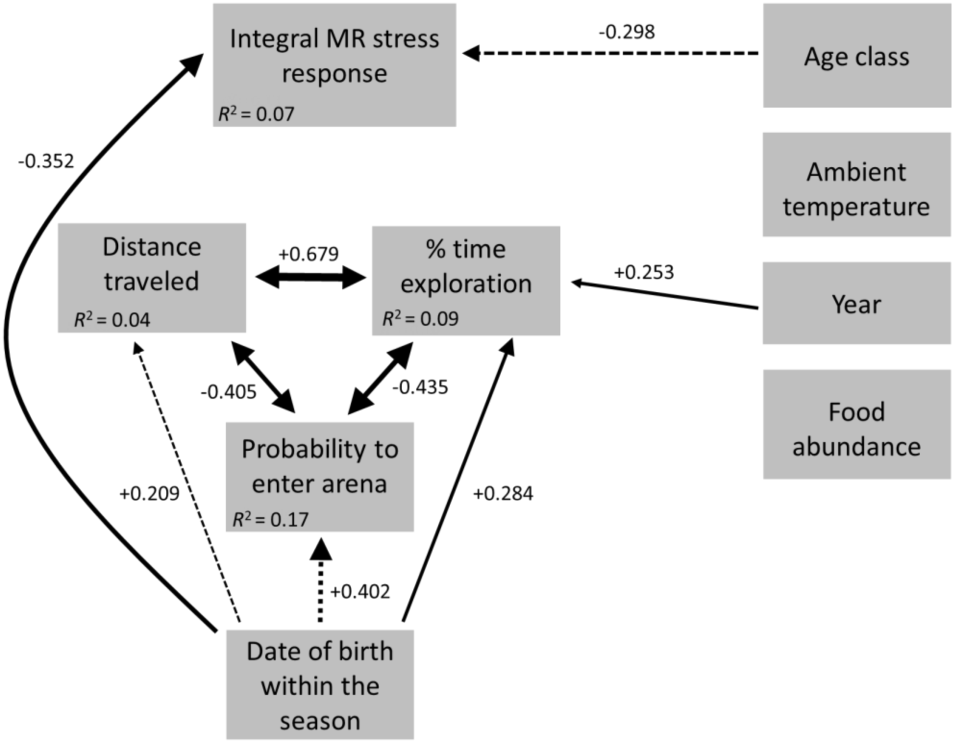

Integral MR stress response
$R^2 = 0.07$
-0.298
Age class
-0.352
Ambient temperature
Distance traveled
$R^2 = 0.04$
+0.679
% time exploration
$R^2 = 0.09$
+0.253
Year
-0.405
-0.435
Food abundance
Probability to enter arena
$R^2 = 0.17$
+0.209
+0.284
+0.402
Date of birth within the season

Figure IV.1. Path models for the effect of date of birth, personality traits and other variables on metabolic rate variables in the bush Karoo rat. Response variables in the different path models were (*a*) resting metabolic rate RMR (ml O_2 per h and g body mass), (*b*) the maximal MR stress response (%, within 1 min) and (*c*) the integral MR stress response (%, within 1 min); all models including year (2022, 2023), individual age class (young or old), ambient temperature and food abundance as fixed variables, see table S1 for details. Standardized estimates are given next to the arrows connecting the different variables; arrow thickness reflects the absolute value of the standardized estimates. Solid arrows represent significant associations ($p < 0.05$) and dashed arrows indicate statistical tendencies ($p < 0.10$); non-significant associations ($p > 0.10$) are not depicted. The two-sided arrows between the different behavioral variables indicate collinearities among them, which were implemented into the path models as correlated errors. Marginal R^2 (given in the gray boxes) summarize the effects of all predictor variables towards a variable.

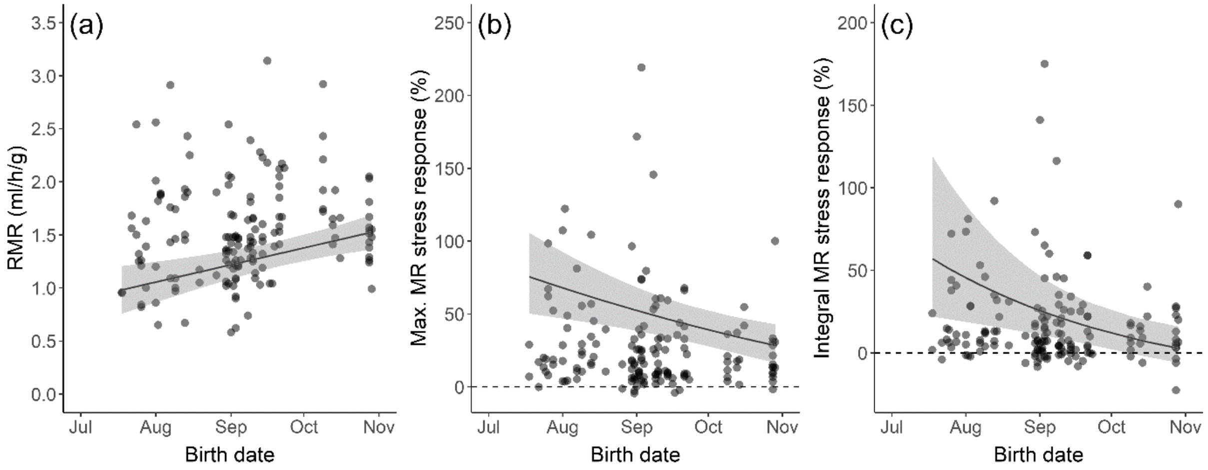


Figure IV.2. Effects of birth date within the breeding season on metabolic rate variables in the bush Karoo rat. All effects presented here are statistically significant, see statistics in Fig. 1a-c. Regression lines (including 95% confidence intervals given as gray shadings) are based on parameter estimates obtained by a path analysis based on combined LMM and GLMM, regression line of (b, c) are based on back transformed parameter estimate (see more details in Suppl. Materials, Table IV.A).

IV.5. Discussion

Variation in resting metabolic rate between-individuals has often been assumed to be related to personality (Mathot and Dingemanse, 2015). However, results from previous studies were inconsistent when testing this hypothesis, indicating that other additional factors might be important mediators in this relationship (Mathot and Dingemanse, 2015). Here, we studied whether the date of birth within the breeding season could concurrently influence between-individual differences in metabolic rate as well as personality differences in bush Karoo rats. In our first analysis, without considering any potentially confounding ecological factors, we indeed found RMR and personality were significantly correlated. However, when applying a path analysis with other factors taken into account, we found the date of birth as the underlaying factor influencing both personality and RMR, but there was no direct link between RMR and personality.

Animal personality can affect the total energy budget available for behaviors and other biological activities. That is, personality-driven consistent variation in behavior might contribute to the between-individual differences in basal metabolic rate (BMR), because more energy-demanding personality types are expected have an increase energy expenditure, which might also affect their necessary energy intake. Three energy management models have been proposed to explain the energy allocation for behavior and BMR, hypothesizing that energy available for behavior and BMR could either (1) constrain each other (negative correlation), (2) be independent, or (3) be positively associated (increased behavioral performance when BMR is higher). Our first results align with the performance model, which hypothesizes that individuals with higher metabolic rates are predicted to display more energy-demanding behaviors, probably because they need to increase their net energy gain to maintain the elevated total expenditure (Mathot and Dingemanse, 2015).

However, our more detailed analysis (path analysis) suggests that there is in fact no direct link between RMR and personality. That is, a significant correlation between RMR and energy-demanding personality traits was only apparent when further factors were not taken into account. Not considering such external factors could result in a bias, because these may simultaneously influence both metabolic rate and personality traits. For example, a previous study on great tits (*Parus major*) has reported such an effect, as in this study the association between BMR and risk-taking behavior was mediated by predator disturbances, where the great tits exhibited alternative BMR-behavior associations under low or high predation pressure (Mathot et al., 2015). In our study, when we accounted for external influences in our path analysis, the direct link between RMR and personality disappeared, although individuals born later in the season were more active and explorative (indicative of an energy-demanding personality) and had higher RMR compared to those born earlier. This suggests that the date of birth simultaneously, yet independently, influences both, personality and RMR.

We also hypothesized that the metabolic rate response to acute stress would be associated with energy-demanding personality traits. Accordingly, we found a general pattern of temporary fluctuation in MR after the acoustic stressor was triggered, similar to the “peak-decay” pattern observed in various features involved in stress response (Taborsky et al., 2021). Later-born individuals showed a lower level of MR increase after acute stress (relative to their own RMR levels) compared to earlier-borns, indicating higher resistance to acute stressors. We hypothesis that due to increased population density and resource constraints, individuals born later in the season need to put more effort into foraging and searching for shelters than earlier-borns. This will increase the possibility of exposure to various environmental stressors and could lead to stronger habituation effects in later-borns, expressed as reduction in their stress responses. Energetically, this could be adaptive by allowing them to save energy when coping with non-risky but frequently encountered stressors. Importantly, as we could show by our path analysis, the MR stress response has no direct link with personality type, but similar to RMR, low MR stress response and proactive personality traits are both independently correlated to date of birth.

For short-lived species experiencing seasonally changing environments, individuals born early or late in the breeding season may encounter markedly different ecological conditions, producing distinct life history trajectories. The date of birth can represent various aspects of the ecological and social environment during an individual's early life, influencing both physiological and behavioral development (Roff, 1993; Varpe, 2017). For instance, European shag (*Phalacrocorax aristotelis*) chicks that hatched earlier in the breeding season adopted higher social ranks and exhibited greater levels of aggression compared to those hatched later (Velando, 2000). Furthermore, using data from the UK Biobank, Didikoglu et al. (2020) found that the season of birth influenced humans as well, with individuals born in summer having higher basal metabolic rates than those born in early winter. In bush Karoo rats, individuals born early in the breeding season benefit from a "silver spoon" effect: they experiencing a longer resource-rich period prior to the onset of the dry season, and a lower population density causing lower competition for vacant stick lodges. While those born later face an environment with more intense resource competition, particularly due to the scarce availability of stick lodges. To ensure survival, they may adopt a more active and exploratory personality while maintaining a higher RMR to gain greater ability to mobilize energy, which could enable them to search for resources or compete for shelters more effectively (Qiu et al., in press).

Apart from the date of birth, we also identified other factors influencing MR variables. Similar to the general findings in other studies in rodents (Whitaker et al., 1990; Zhang and Wang, 2006), bush Karoo rats exhibited higher RMR at lower ambient temperatures. MR stress response was lower in older than in younger adults, which could be due to a reduced stress response as apparent in some mammalian species by decreased stress hormone (corticosteroid) levels with increasing age (Lendvai et al., 2015; Oh et al., 2018). Furthermore, in our study, it may be simply due to an increasing habituation to repeated testing at older age. The significant year effect observed in our analysis could also be the result of differences in the age distribution in our samples obtained during the two years of study. In the second year, individuals were tested only as young adults, which could have increased the overall mean response compared to the first year, when individuals were tested as both young and older adults.

In conclusion, our study reveals that the date of birth within the breeding season plays a crucial role in shaping both personality and metabolic traits in seasonally breeding bush Karoo rats. Individuals born later in the breeding season exhibited higher resting metabolic rates, lower metabolic responses to acute stress, were more active and showed more exploration. However, no direct association between metabolic rate and personality occurred. These results indicate that the date of birth is a shared cause for both physiological and behavioral variation in this seasonal breeding small mammal. The findings from our path analyses could contribute to explain why previous studies reported contradictory results regarding the personality-RMR relationship: their association could be indirect, driven by shared underlying factors such as birth timing or possibly by other ecological/life history traits. Our findings underscore the importance of taking in consideration such external parameters, especially life history factors, as potential drivers when studying the relationship between energy metabolism and animal personality.

Acknowledgements

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IV.6. Supplementary Material

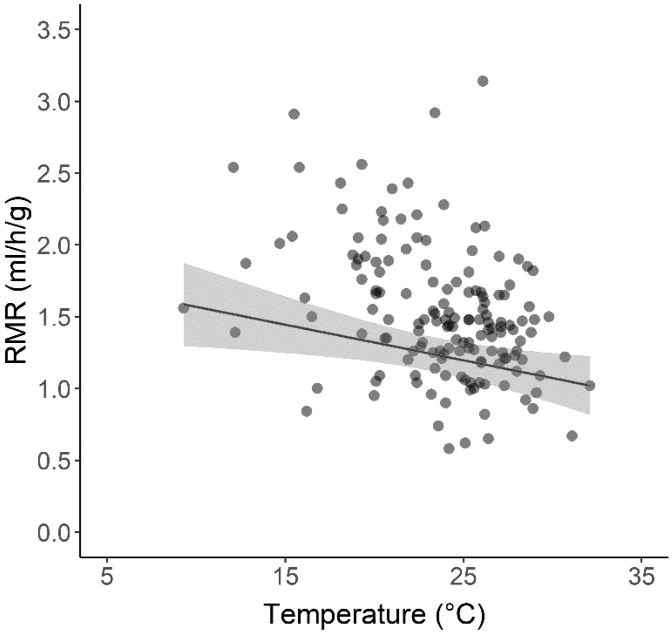

Figure IV.A. Effects of temperature on resting metabolic rate (RMR) in the bush Karoo rat. The effect presented here is statistically significant, see statistics in Figure IV.1a. Regression lines (including 95% confidence intervals given as shadings) are based on parameter estimates in the path analysis (Table IV.A).

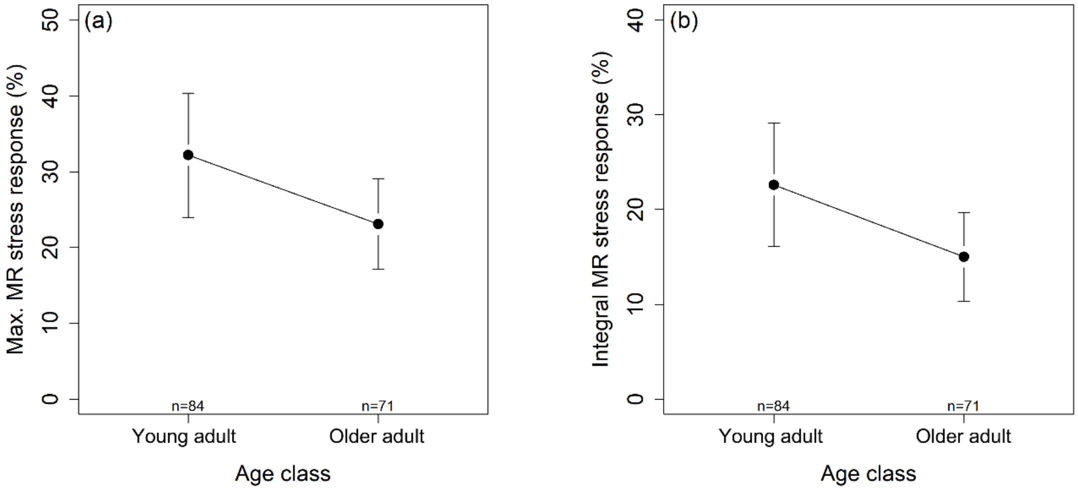

Figure IV.B. Metabolic responses to acute stress in different age classes in the bush Karoo rat. Mean values with 95% confidence intervals are given. Young adult stage: 34-86 days old, on average 56 days±48SE; older adult stage: 138-213 days old, on average 149 days±48SE. All effects presented here are statistically significant; see Figure IV.1b, c for details.

Table IV.A Summary of path analyses of 78 female bush Karoo rats for the effects of various fixed variables on (a) resting metabolic rate RMR, (b) max. MR stress response (%, within 1 min), and (c) the integral MR stress response (%, within 1 min). Details on the structures of the paths are given in Figure IV.1a-c. Analyses with GLMM (for binomial data) and LMM including individual identity as a random intercept factor. Note that all the lines in the table labelled as (a-b-c) apply in the same way to the different path diagrams given in Fig. 1a, b and c. Standardized estimates (*β*) including their standard error are given. Significant effects are given in bold, statistical tendencies are highlighted with $^+$.

Dependent variables	Predictors	*β*±SE	*P*
(a) RMR	Distance traveled	0.095±0.092	0.301
	% Time exploration[1]	−0.033±0.944	0.730
	Probability to enter arena	0.025±0.163	0.730
	Age class	0.194±0.104	0.067$^+$
	Food plants abundance	0.045±0.141	0.750
	Temperature	−0.208 ±0.083	**0.014**
	Birth date	0.317±0.086	**<0.001**
	Year	0.651±0.100	**<0.001**
(b) Max. MR stress response[1]	Distance traveled	−0.064±0.000	0.586
	% Time exploration[1]	0.006±0.156	0.617
	Probability to enter arena	0.100±0.491	0.266
	Age class	−0.610±0.324	**<0.001**
	Food plants abundance	−0.087±0.591	0.620
	Temperature	0.122±0.062	0.239
	Birth date	−0.362±0.010	**0.002**
	Year	−0.439±0.300	**<0.001**
(c) Integral MR stress response[2]	Distance traveled	−0.064±0.000	0.307
	% Time exploration[1]	0.001±0.002	0.400
	Probability to enter arena	−0.001±0.001	0.754
	Age class	−0.283±0.076	**0.001**
	Food plants abundance	−0.201±0.150	0.184
	Temperature	0.004±0.015	0.788
	Birth date	−0.008±0.002	**<0.001**
	Year	−0.171±0.015	**0.021**
(a-b-c) Distance traveled	Age class	−0.002±0.128	0.989
	Food plants abundance	0.074±0.158	0.639

	Temperature	0.023±0.093	0.807
	Birth date	0.211±0.111	0.061$^+$
	Year	0.005±0.118	0.966
(a-b-c) % Time exploration[1]	Age class	0.204±0.132	0.124
	Food plants abundance	−0.104±0.164	0.526
	Temperature	−0.065±0.097	0.504
	Birth date	0.287±0.118	**0.016**
	Year	0.254±0.124	**0.028**
(a-b-c) Probability to enter arena	Age class	−0.097±0.455	0.612
	Food plants abundance	−0.191±0.640	0.478
	Temperature	−0.137±0.405	0.421
	Birth date	0.394±0.512	0.067$^+$
	Year	−0.117±0.503	0.550

[1] square-root transformed for analysis

[2] log transformed for analysis

General Discussion

V.1. Main findings

In my thesis, I first investigated the ecological and natural history characteristics of lodge-building in rodents in a comparative study. Then, I focused on one of the lodge-building species, the bush Karoo rat (*Otomys unisulcatus)*, to investigate the link between life history, behavior and physiology in a seasonally changing environment.

In Chapter 1, I identified three main forms of sheltering habits in Myomorpha rodents: natural shelter, burrows, and lodges, and investigated how natural history and ecological factors, especially aridity and fire risk, influence the distribution of lodge-building species. I found six independent evolutionary origins for the occurrence of lodge-building rodents, the majority of them construct dry stick lodges in arid habitats with low fire risk.

In Chapter 2, I investigated how personality of bush Karoo rats differs based on the time of their birth within the breeding season. Individuals born earlier in the season experienced a less competitive environment with abundant resource and lower population density, and most importantly, have the opportunity to breed within the season in which they were born. Those born later are not only unable to breed within the season, but also faces decreased resource availability under higher population density. Under the reproduction directed pace-of-life framework, earlier-borns are expected to adopt a “fast” pace of life with bold, active and explorative personalities to compete for reproduction resources. This chapter provided evidence for the existence of a proactive behavioral syndrome in bush Karoo rats, which was associated with individual’s date of birth. In contrast to the prediction that earlier-borns would be more “proactive”, I found later-born individuals exhibited higher levels of proactive behavioral traits. This is possibly related to challenging ecological and social conditions experienced by individuals born in the later breeding season, in particular the greater competition for the limited availability of stick lodges.

In Chapter 3, I investigated the relationship between metabolic rate and personality, considering the individual’s date of birth as common factor. I found that later-born individuals exhibit higher resting metabolic rates and lower metabolic rate responses to acute stress, but no direct association between energy costly personality types (high proactiveness) and any metabolic rate variables. This finding indicates that personality and energy metabolism are not directly associated but are linked via their association with date of birth, which could be the shared driver for the relationship between life history, behavior, and metabolism in bush Karoo rats.

V.2. Influence of date of birth: reproduction opportunity and survival resources

For short-lived mammals, new-born individuals can differ in their experience of environmental conditions, resource availability and reproductive opportunities depending on their date of birth (Eccard and Herde, 2013a; Montiglio et al., 2014), leading to different survival-reproduction strategies (Stearns, 1998), and ultimately result in diverse of life history strategies, behaviors, and physiological development.

V.2.1. Reproduction-directed pace-of-life

Reproduction-prioritized life history (r-selection) is common in small mammal with short lifespans, their behavioral and physiological characteristic could covaries with this life history strategy and contributing to a "fast" pace-of-life continuum, which increase resource acquisition for reproduction at the cost of survival (Réale et al., 2010; Wolf et al., 2007). Differences in reproduction opportunity by date of birth within the season exists in bush Karoo rats, but the influences seem to be limited. The breeding season in bush Karoo rats is restricted for 3-4 months in spring, and most individuals have to survive the long dry season (summer and autumn) before they can reproduce in the next year. In other seasonal breeding rodents, newborn individuals have a longer time window to reach the sexual maturity and prepare for reproduction within the breeding season in which they were born, that often lasts for 6 months during spring and summer (Eccard and Herde, 2013b; Merritt et al., 2001). Consequently, more individuals can participate in the reproduction activity and benefit from adopting a “fast” pace-of-life, exhibiting a more proactive personality (more active, explorative and bolder) and a high RMR, which facilitate precocious reproduction prior to the onset of the non-breeding season. However, in my study population, this reproduction-driven “fast” pace-of-life seems to be absent, only few early-borns (11.9 % of all focal females in behavioral tests) managed to reproduce in the season of their birth, despite more that were able to reach the age of sexual maturity.

V.2.2. Influence of ecological constraints on pace-of-life

Apart from the driving force of reproduction, an increasing number of studies have highlighted the importance of considering ecological constraints in the pace-of-life relationship within species or population. Montiglio et al (2018) incorporated the role of natural history and ecological constraints into the pace-of-life framework and discussed how constraints such as high predation pressures or limiting resources can shape the relationships between life history, behavior and physiology. For example, the role of behavioral traits in resource gathering can be adjusted by the scarcity and distribution of the resources, animals that forage on patchy food sources are more likely to benefit from actively exploring the environment than those that forage for food that is abundant and more evenly distributed (MacArthur and Pianka, 1966).

In this thesis, I proposed that differences in resource competition based on the date of birth within the season shaped the relationships between life history, behavior, and physiology in bush Karoo rats, because the differences in reproductive opportunities were absent or small. Although earlier-born individuals experience relatively mild ecological conditions during their own development, reproducing at an early age can have fitness cost on the young mother and their offspring, (Lambin and Yoccoz, 2001), it is not worthwhile if the fitness cost makes the female and their offspring cannot survive through the following harsh dry season. The low incidence of reproducing whining the same season of birth suggest the reproductive value for early-born bush Karoo rats was probably diminished, reducing the influence of reproduction in shaping “fast” pace-of-life among early-borns. In fact, I found behavior and physiology were associated with the date of birth, but in a direction opposite to theoretical predictions. Later-born individuals displayed characteristic of a 'fast' pace-of-life, with bolder, more active, and more explorative personalities and higher RMR.

Later-born individuals have no opportunity to initiate immediate reproduction after reaching adulthood, as the breeding season was ceased due to low food availability, but they encounter more severe survival challenges. On the one hand, they are born into an already populated environment with reduced resource availability. On the other hand, they are at a disadvantage in competing with older and more mature conspecifics (individuals born in the previous year and those born earlier- in the same year). Under such conditions, the classic pace-of-life theory predicts that they would benefit form a “wait-and-see” approach, which would result in them avoiding conflict (being shy and less aggressive) and predation risk (decreased activity and exploration) to optimize their survival until conditions environment become favorable again for reproduction. This would predicted that they show a more reactive personality and lower RMR to conserve energy (Careau et al., 2008; Rimbach et al., 2017), However, a reactive personality syndrome can be maladaptive in situations with high competition for limited resources. When necessary resources cannot be available for every individual, such that having a “slow” and energy conservative strategy could reduce chances of securing enough resources to support their own survival. As a result, survival pressure can also shape behavioral and physiological characteristic that help individuals acquire resources in highly competitive environments (Briffa et al., 2015; Cole and Quinn, 2011; Pettersen et al., 2020).

V.3. Divergence by date of birth: the role of resource competition

Maintaining a proactive personality and high RMR can be advantageous for competing for resources, but poses higher predation risk (Dubois and Binning, 2022) and such a strategy could be energetically expensive to maintain (Careau and Garland, 2012). The influence of food quality is supported by several field studies, for example, mass-independent BMR increases with habitat productivity in degus (*Octodon degus*; Bozinovic et al., 2009). Previous studies in African striped mice (*Rhabdomys pumilio*; Rimbach et al., 2018), a sympatric species of bush Karoo rats in our field site, found a decrease in RMR with lower food abundance. However, this was not the case in the bush Karoo rat. In Chapter 2 and 3, I tested the effect of food plant abundance on personality traits and RMR. Although the food plant abundance decreased considerably over the course of the breeding season, it had no significant effect on any metabolic rate parameters nor on personality. Thus, differences in food availability does not explain why later-born individuals have higher RMR. Another resource with significant importance to bush Karoo rats are the stick lodges, which offer crucial protection against the extreme and unpredictable semi-desert environmental conditions. Due to increasing population density, the availability of vacant stick lodges becomes increasingly scarce toward the end of the breeding season, leading to intensified lodge competition that mostly concerns later-borns.

V.3.1. Stick lodges

Shelter construction is an important adaptation in small rodents against the harshness of the external environment (Eadie, 1953; Young et al., 2017). Whether building underground or aboveground, such structures can provide critical protection for their survival and reproduction. Bush Karoo rats construct stick lodges, which are a typical example of this shelter-dependent lifestyle (Vermeulen, 1988). Lodge-building is a relatively rare form of shelter construction in rodents, but like burrows, lodges can offer protection from predators and buffer against fluctuations in the ambient environment (Du Plessis et al., 1989; Du Plessis et al., 1992). A previous study found that bush Karoo rat lodges create microenvironments with more suitable temperature and humidity ranges than the ambient environment (Du Plessis et al., 1989).

Building a new stick lodge is an expensive investment (Vermeulen, 1988). However, once built, a well-constructed lodge can be long-lasting, providing shelter for generations after the original builder has disappeared (Schradin, 2005). There are several ways for a new-born bush Karoo rat to occupy their own stick lodge: constructing a new lodge, finding an unoccupied lodge, or even inheriting the birth lodge from their mother (unpublished data). In Chapter 2, I demonstrated the decrease in stick lodge availability during the breeding season, suggesting an intensified lodge competition for later-born individuals.

V.3.2. Ecological constraints for the later-borns: food and stick lodge availability

Bush Karoo rats are strictly herbivorous (Stuart, 2013) and rely on the protection of stick lodges to survive (Du Plessis et al., 1992). A decrease in food abundance and a reduction in stick lodge availability are two ecological constraints that occur in the late breeding season. Stick lodges are patchy distributed in the field site and can be monopolized by individuals. Lodges are difficult to construct but can be used for generations, making them low in renewability. In addition, one lodge is usually occupied by only one individual, which actively defends it by expelling others (Makuya et al., 2024). Although direct physical conflict is rarely observed in bush Karoo rats (Makuya et al. 2024), we have observed in the field that individuals actively chasing away outsiders (conspecific or other rodent species) from their stick lodge. Competition for lodges is likely a form of contest competition (Jensen, 1987; Holdridge et al., 2016), with individuals rejecting others from sharing this sheltering resource of high value. (Holdridge et al., 2016; Jensen, 1987).

During the late breeding season, all individuals are equally affected by the reduced food availability, but have unequal access to stick lodges: those more competitive stand advantages in finding and occupying an empty lodge. The behavioral and physiological characteristic found in later-borns likely represents an increased competition ability in access to empty lodges and actively defending it. When the number of lodges is insufficient to meet the sheltering needs of newborn individuals, individuals that failed in the competition for vacant lodges can still benefit from these characteristics when searching for building materials to construct new ones.

My results show no notable association between food abundance and behavioral traits or metabolic measures in the bush Karoo rat; suggesting the scarcity of stick lodges is likely the primary driver that promotes a proactive personality syndrome in later-borns. Later-born individuals are already at a disadvantage when directly competing for lodges already occupied by older and larger individuals, as a result, they need to explore unknown areas to find unoccupied lodges or building materials to construct new ones (Spiegel et al., 2017). The increased necessity for exploration and the ability to defend lodges may favor the emergence of proactive behavioral traits in later-born individuals.

A proactive personality brings higher competitive ability but is energetically costly (Careau et al., 2008). One would expect individuals to reduce energy budgets in other aspects, such as resting metabolic rate, to maintain an equilibrated energy balance under lower food abundance conditions (Rimbach et al., 2018). However, energy-demanding behavioral traits, such as exploration, can also result in net energy gain by increasing foraging efficiency to support the energy cost and maintain a higher RMR (Careau et al., 2008). The findings that later-born individuals showed higher RMR suggest the decreased food abundance is not an ecological constraint limiting their energy metabolism. Even though food availability decreases during the late breeding season, these individuals are still able to maintain an energy-costly personality (more proactive) and higher RMR, possibly by gaining enough net energy through active foraging. A higher RMR indicates that more energy is available for basal biological activities, which improves physical function and competitive abilities and also possibly enhanced thermoregulation (Sobrero et al., 2011), enabling them to better cope with external temperature changes when lack of stick lodges or only occupy lodges of low quality. Although maintaining a proactive personality and spending more time foraging to support the high energy budget comes with the survival cost of increased predation risk, it may be worthwhile if it improves their chances of securing the occupancy of stick lodges.

For early-borns, the ease of finding stick lodges, or even inheriting their birth lodges from their mother, reduces the benefit of actively traveling and exploring the habitat in search of lodges. Even during the late breeding season, those born earlier are naturally at an advantage in defending their stick lodges against the dispersing later-borns due to their larger body size. Furthermore, due to low reproductive activity, earlier-born individuals may benefit from exhibiting a "slow" and energy-conservative strategy to increase survival, characterized by relatively reactive behavioral traits (shyer, less active and explorative) and maintaining a lower RMR than later-borns, because the resource competition are less pronounced. When survival is not limited by certain critical resources, been shy and stay inside the lodge instead of actively traveling the field site can be adaptive as it helps conserve energy and reduces exposure to potential risks.

My field studies on the bush Karoo rats also offer insight into the broader ecological and evolutionary processes that influence the pace-of-life strategies in small mammals. The patterns observed in bush Karoo rats may reflect similar processes occurring in other species facing variable resource landscapes, emphasizing the role of resource competition in exploring the relationship of life-history, behaviors and physiology.

V.4. Relationship between personality, metabolic rate and life history

Associations between behavior and metabolism are well-known (Careau et al., 2008). There has been accumulated interest in exploring the relationship between animal personality and the variation in metabolic rate, particularly in explaining the inter-individual variation in resting metabolic rate by animal personality (Careau et al., 2008). RMR is measured in resting animals to exclude the influence of behavior, but this could result in a bias in personality, as proactive individuals are more likely to be excluded because they are “restless” during the measurements (Careau et al., 2008; Jäger et al., 2017). In addition, being “restless” (or simply more active) requires more energy, potentially affecting the energy available for RMR. Apart from the potential influence on RMR, proactive behaviors (boldness, activity and explorations) are directly associated with increased levels of physical activity. Thus, their energetic influences on non-resting activities, such as metabolic rate fluctuation in response to stressful situation, should also be considered, but few studies have investigated the influence of personality on energy metabolism during a non-resting state.

Three energy management models have been proposed to explain the relationship between behavior and basal metabolic rate (BMR): energy available for BMR either has no association, a positive or a negative association with energy available for behavior (Careau et al., 2008; Mathot and Dingemanse, 2015). The pace-of-life integration into the energy performance model, hypothesizing that energy available for RMR is positively associated with energy available for behavior. In Chapter 3, I demonstrated that later-born individuals show more energy costly behavior (activity and exploration) and higher level of RMR, supporting the hypothesis that higher RMR is associated with higher expression of energy-costly behaviors that brings net energy gain.

My thesis supports the positive integration between behavior and RMR but suggests an alternative association with life history strategy. Similar to energy demanding “proactive” personality, higher RMR in bush Karoo rat were found in later-borns but not in earlier-borns. We constructed path models to explore the association at different levels, attempting to disentangle the significance of the path with birth date as the underlaying factor that potentially affect personality and RMR, and comparing it with the path that directly associates personality traits with RMR. External factors that may have influenced these associations were controlled for in the analysis, such as food abundance, ambient temperature and individual age at testing. However, none of the external factors explained the high RMR in later-born bush Karoo rats. As observed in many other studies (Clarke et al., 2010; van Ooijen et al., 2001), individual RMR (measured at thermoneutrality) was higher when ambient temperatures were lower. Combined with shorter photoperiod, this supports that individuals born early in the breeding season that experience lower ambient temperature and shorter day length should have increased metabolic rate (Lynch, 1973; Song and Wang, 2006). However, the significant effect of ambient temperature cannot explain the divergence in bush Karoo rats, because bush Karoo rats born later when it was warmer (late spring vs. early spring) had higher RMR. There was no significant effect of age on body mass-scaled RMR, thus suggesting no underlying influence of age when individual was measured.

By integrating all variables in the path model, the results showed that both personality and RMR were significantly correlated with birth date, but personality and RMR had no direct association with one another. This suggests that variation in RMR does not necessarily directly influence personality type. This finding helps explain why previous studies report contradictory results regarding the personality-RMR relationship (Mathot and Dingemanse, 2015): their association is indirect, driven by shared underlying factors such as birth timing or other ecological/life history traits that are context-specific to studied populations/species.

I used the same path model structure to investigate how metabolism in a non-resting state is associated with personality traits and the date of birth. The results indicate that later-born individuals have a lower energetic response to an acute acoustic stressor. Although they have higher RMR, the levels increased less following the acoustic stressor than in earlier-born individuals. One possible explanation for this could be habituation to stressful situations (Grissom and Bhatnagar, 2009; Jean Kant et al., 1985; Valsamis and Schmid, 2011). Maybe due to overpopulated environment and increased resource competition during early life stage, they were more frequently exposed to stressful stimuli (e.g., socio-negative conspecific encounters, unpredictable environmental disturbance when actively exploring unknown environments), which led to a form of habituation to environmental stressors. In contrast, earlier-born individuals, who face less competition for resources, tend to adopt a more conservative behavioral strategy characterized by remaining within familiar environments (“stay at home”). They are generally shyer, less active, and less explorative in unfamiliar field sites, making them less accustomed to potentially stressful environmental stimuli. Consequently, these individuals may exhibit stronger stress responses due to their limited habituation to general environmental stressors. The measurement of the two variables for metabolic stress response shows consistent results, providing a new perspective on metabolic measurement during non-resting states and offers evidence of the metabolic response to acute stress, highlighting how it shares common drivers with personality and RMR.

V.5. Limitations of the thesis

To obtain a more comprehensive assessment of animal personality and its relationship with life history traits and metabolic rates, there is room for improvement in at least two aspects not addressed in my thesis: confounding factors in field studies and the experimental design of behavioral tests.

A typical constraint of field studies is limited information about what individuals have experienced in the field, such as feeding status, physical condition and previous reproduction, all of which can have potential effects on an individual's behavioral performances and energy metabolism. When trapping individuals for behavioral tests and metabolic rate measurements, ideally, all focal individuals should be trapped and tested repeatedly at the same age. But, in reality, trapping can be delayed or failed for several reasons. First, due to the high mortality rate in the study population, less than a quarter of the new-born individuals remained in the field by the time of the final test in the first year (Chapter 2). The dramatic decrease in sample size over time was inevitable, and I compensated for this by studying as many new-borns as possible.

Secondly, individuals typically disperse from their birth lodges during juvenile or young adult stage, so it was harder to trap some of them during this period when they actively travel and switch lodges. As a result, these individuals had delayed testing or were absent from the tests during some periods of their lives. This could influence the repeatability of personality traits, because previous experiences and test intervals influence individual performances (Groves and Thompson, 1970; O'Neill et al., 2018; van Oers et al., 2005). Similar influence could also occur in metabolic stress response measurement as only a marginal significance was found for short term repeatability. Finally, males were more difficult to track than females, and they were included as focal individuals only in the second year, leading to a sample size bias towards females. This potentially affected accuracy in estimating influence of sex on behavioral traits, and contributed to the significant year differences in the model.

Exploration was tested in two different aspects: exploration in a novel environment (open field test) and to novel objects (novel odor test). I did not find significant repeatability for the exploration to novel objects, and therefore variables measured in this test were not used in further investigations. There are several possible reasons why this experiment failed to capture the exploration traits. First, to avoid habituation to the novel objects, the odor presented for each test was different. However, the missing tests of some individuals resulted in a different sequence of experiencing these novel odors. Some individuals experienced their first novel odor test with orange peel and second with tomato sauce, while individuals which missed the first test experienced their first order with tomato sauce. The general preferences or avoidance for certain odors make novel odor tests more sensitive to missing tests than other behavioral tests. To avoid this problem, one can always use the same novel odor at different test sequences. But this then leads to a habituation problem in that the smell is no longer "novel" and individuals may not explore the odor at all.

V.6 Future perspectives

V.6.1. Ecological value and conservation of lodge-builders

In the first chapter, I focused on the influence of ecological and natural history factors on the distribution and evolution of lodge-building rodents, but I did not assess the ecological value of lodge builders on their local environment. "Animal architect" species like bush Karoo rats are known for their ability to manipulate the environment to make it more suitable for their own living, which often leads to changes in habitat conditions for other species (Hansell, 2005; Hunter, 2009). A well-known example are the lodge-building beavers (*Castor* spp.), often referred to as "ecosystem engineers" due to their ability to altering the paths of streams and rivers to create a pond, where they build their lodges (Baker and Hill, 2003). Their building activities have a great impact on the landscape, creating "beaver wetlands" that change local ecological communities, with benefits for a variety of wetland species (Law et al., 2016; Smith and Mather, 2013). The ecological value of other lodge-builders is less studied. Although the influence may not be as visible as the beaver dams, empty stick lodges built by bush Karoo rats could serve as an "oasis" in the harsh environment, offering protection against predators and providing a suitable thermal environment not only for themselves but also for other small animals in general. Previous work in our field site has reported that stick lodges build by bush Karoo rats offer shelter for stripe mice (Schradin, 2005). As a further example; it has been reported that stick lodges (or “middens”, built of sticks plus other plant materials) of packrats (*Neotoma* spp.) provided an important microhabitat for arthropods (Thies et al., 1996; Whitford and Steinberger, 2010). Overtime, the decomposition of building materials (dry plants) and the accumulation of droppings left by lodge owners might influence nutrient availability in soil (Gleixner, 2013; Liang et al., 2017), affecting the surrounding plant communities.

The long-lasting stick lodges has its weaknesses. My thesis revealed that most lodge-building species inhabit arid environments, building lodges of dry sticks and twigs. The flammable building materials make their lodges vulnerable to wildfire. Stick lodges can be a potential fire starter or acted as an accelerant in the fire event. To date, studies of fire occurrence in the distribution of lodge-building species are limited (Kerley and Erasmus, 1992). This sensitivity to wildfire should be considered in the evaluation of threats in conservation work and fire control. For example, prescribed fires (Nowell et al., 2018) in North American forests should be evaluated for the negative impact on lodge-building packrats (Howard et al., 1959; Simons, 1991). In some situations, burning down stick lodges and constructing materials (dry plants matters) with controlled fire could even be used as a means of controlling overpopulated lodge-building rodents.

V.6.2. How resource constraints influence behaviors and energy metabolism

In bush Karoo rats, the availability of stick lodges likely represents an important ecological constraint that drives individual behavioral and physiological differences. Lodge dependency is a unique characteristic in bush Karoo rats. In other populations or species, the type of resources that could act as ecological constraints depend on the species/population characteristic and the specific environmental challenges they face. Any resource that is critical for surviving in their prevailing environment could drive the development of competitive personality types. The need for reproductive resources is another common driver of personality variation, but its effects may only become evident when reproduction is not restricted by prevailing ecological conditions (Montiglio et al., 2018).

I propose that future studies should consider the date of birth within the season as an important co-factor influencing between-individual differences in behaviors and metabolic rate. Similar to the driving force of reproduction for the “fast” pace-of-life, resource competition can promote a suit of “proactive” behavioral traits and high RMR that increase an individual’s ability to access enough resources to ensure survival. Understanding these dynamics can provide valuable insights into the behavioral and energetic strategies the animals adopt to cope with environmental challenges and resource limitations.

V.6.3. Functional link between animal personality and energy metabolism: future direction

Three Energy management models provide a hypothetical framework for linking metabolic rate and personality (Careau et al., 2008; Mathot and Dingemanse, 2015). Significant associations between behavioral traits and RMR have been supported in the literature (performance model: Cutts et al., 1998; allocation model: Vaanholt et al., 2007), but inconsistent findings make the direction of these associations and the underlying mechanisms unclear. In Chapter 3, I demonstrated a positive energetic correlation in later-born individuals, where energy-demanding behavioral traits are associated with a high RMR. Similar to how behavioral syndromes can be environment-dependent, the energetic link between behaviors and RMR can also be modulated, or even cancelled out, by ecological conditions. The positive association in bush Karoo rats is likely due to intense resource competition occurring in later-borns, one would expect that in other seasonal breeding populations/species where earlier-born individuals more actively engaged in reproduction, differences in reproductive opportunities may drive a similar behavior-RMR relationship in earlier-born individuals.

As relationship between metabolic rate and personality is driven by date of birth in bush Karoo rats, similarly, other ecological factors such as food availability, predation pressure, and social interactions can potentially be the key in modulating this relationship in other species. High resource availability may alleviate energetic constraints, thereby weakening the covarying energetic link between metabolic rates and behavioral traits. Conversely, populations under food limitation may favor performance or allocation strategy, either reducing energy expenditure by reducing RMR and behavior cost (exhibiting reactive personality) or distributing more energy for actively foraging while maintaining lower RMR. Predation pressure can influence this relationship, favoring shy and non-active behavior to reduce detectability by predators but have little influence on individual metabolic rate. I propose that future studies should consider the link between behavior and energy metabolism as an expression of underlying factors, particularly focusing on ecological constraints that impact individual fitness. A better understanding of these ecological drivers would provide further insight into how natural selection shapes the relationship between energy expenditure, behavior, and fitness.

V.7. Concluding remarks

My thesis aimed to investigate the relationship between personality, life history, and physiology in the lodge-building bush Karoo rat. By testing this relationship under the pace-of-life framework, I found evidence for "proactive" behavior syndromes in the study species. Individuals born later in the breeding season were behaviorally more proactive, had higher RMR and lower metabolic response to acute stressor. The divergence of personality and physiology depending on date of birth is likely driven by ecological constrains during the late breeding season: although later-borns do not compete for reproduction, the increasing competition for survival resources, such as stick lodges likely drive behavioral and physiological traits that promote access to these limited resources.

This thesis presented for the first time (1) a phylogenetic comprehensive analysis of the evolution of lodge-building behavior in Myomopha rodents in relation to ecology and natural history, especially the influence of aridity and fire risk; (2) personality in bush Karoo rats is associated with life history: individuals born later in the breeding season are bolder, more active and explorative; and (3) date of birth as life history factor that explains the indirect association between personality and resting metabolic rate.

The first part of my thesis (Chapter 1) improved our understanding of the sheltering strategies used by mouse-like rodents. By analyzing data from 515 Myomorpha rodents, I was able to construct a phylogenetic tree and identify independent evolutionary origins for lodge-building behavior. Additionally, the study revealed natural history patterns and preferred environmental characteristics of lodge-building species. Although relatively rare, lodge-building species can have significant ecological value by offering crucial shelters for other small animals from predators and harsh climatic conditions. This study provided a reference for the conservation work for these lodge-building species, particularly in wildfire management because of the fire vulnerability of their lodges.

The second part of my thesis considered the relationship between personality and life history traits under the pace-of-life framework. By conducting repeated behavioral tests in 99 new born bush Karoo rats, I provided evidence for the repeatable behavioral traits and the existence of “proactive” behavioral syndromes. I found that an individual’s personality is linked to their date of birth within the breeding season, a life history factor that represents cohort differences between earlier-/later-born individuals in resource availability and reproductive opportunities. This study on bush Karoo rats provides an example where, when reproductive opportunities are limited, resource competition—in this case the intense competition for stick lodges—may possibly promote the emergence of proactive personality traits in later-born individuals.

Based on this understanding, Chapter 3 went one step further by including energy metabolism into this framework. By combining the behavioral data with metabolic rate data from 78 new born bush Karoo rats, I found that active and explorative personality traits are indirectly associated with resting metabolic rate via a shared factor, the date of birth within the breeding season, later born individuals had higher activity, exploration and RMR level. This re-enforced the finding of Chapter 2 and highlighted date of birth as a key underlying factor in the personality-RMR relationship, suggesting the inconsistencies in previous study results may reflect differences in the key factor (e.g., ecological or life-history traits) specific to the study population or species, rather than a direct link between RMR and personality.

In addition, this study provided support for individual differences in metabolic stress response: later born individuals had lower metabolic fluctuations under the influence of acute stress, which could reflect an energy-saving strategy or a habituation to acute environmental stressor in the later-borns. This study involved the investigation of the influence of date of birth on behavior and energy metabolism in a wild population, which is likely driven by intensity of resource competition depending on date of birth within the breeding season.

Overall, my thesis provides insights into the adaptive limitation of lodge-building rodents in high fire-prone habitat, and highlights the importance of ecological constraints, such as competition for scared resources, in shaping the relationship between life history, personality and physiological traits. This is the first study to show that competition for survival resources during the late breeding season, rather than competition for reproduction resources during early season, may ultimately lead to the emergence of different personalities and to differences in energy metabolism.

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Appendices

Appendix A:

Qiu J, Olivier CA, Jaeggi AV, Schradin C (2022) The evolution of marsupial social organization. *Proceedings of the Royal Society B.* 289:20221589

Appendix B:

Qiu, J. & Schradin, C. (2024). Lodge-building in rodents: relationships with ecological and natural history factors. *Journal of Zoology*. https://doi.org/10.1111/jzo.13207

Appendix A:

PROCEEDINGS B

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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

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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

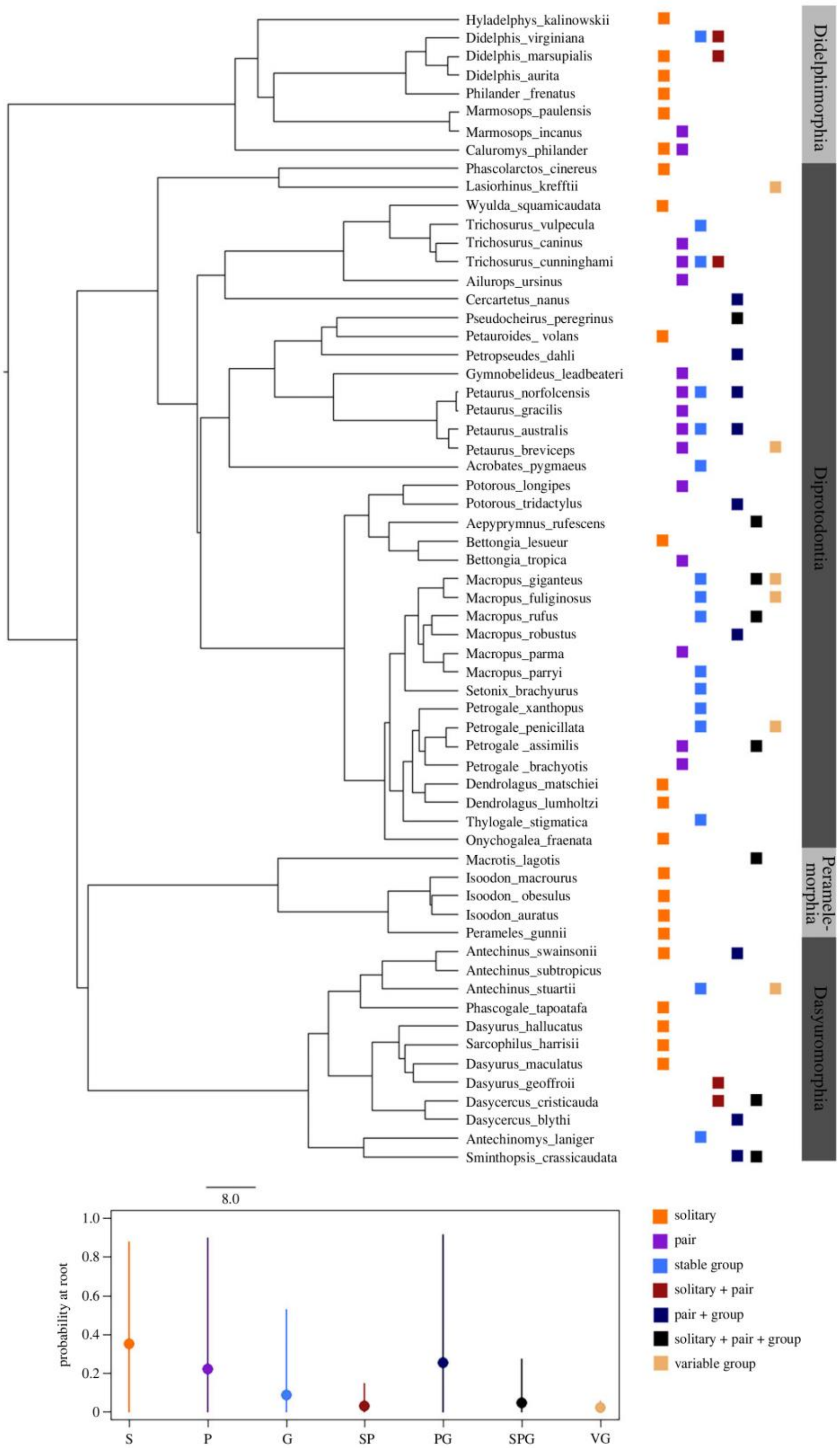

Figure 1. Phylogeny of 62 marsupial species with available data and the probability of each kind of social organization at the root of the phylogeny (i.e. the last common ancestor of all marsupials). The different forms of social organization recorded for each species at the population level are shown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

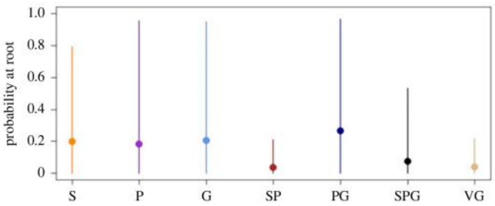

Figure 2. The probability of different kinds of social organization for the last common ancestor of Australian marsupials. S: solitary, P: pair, G: stable group, SP: solitary + pair, PG: pair + group, VG: variable group. (Online version in colour.)

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 B:

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ORIGINAL RESEARCH

Lodge-building in rodents: relationships with ecological and natural history factors

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Myomorpha; lodge-building; shelter; phylogenetic; arid environments; wildfire; habitat heterogeneity; aridity.

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Abstract

Mouse-like rodents often take cover in natural shelters or burrow underground where they build simple nests. A few species build extensive shelters above ground, called lodges, mounds or houses. Here, we present the first phylogenetically controlled comparative study on the ecological factors of habitat heterogeneity, environmental aridity and fire risk related to nesting habits in mouse-like rodents (Myomorpha, 326 genera). Twenty species from seven genera were found to build lodges, and they mainly occur in arid environments with low fire risk. Most lodge-building species (14 out of 20) belong to the pack rats (genus *Neotoma*), which in phylogeny only represent one event of evolution of lodge building and therefore limit the statistical power of the phylogenetically controlled analysis. The Bayesian phylogenetic mixed-effects models show a phylogenetic signal of 0.43 for 515 Myomorpha species. Under this moderate to strong phylogenetic relatedness, we did not find specific factors being associated to the evolution of sheltering habit in Myomorpha. We suggest studying the importance of aridity combined with low fire risk for lodge building on the species level, for example, by studying the limits of species distribution ranges depending on these factors.

Introduction

Many animals construct external structures as an adaption against the harshness of the local environment. Such structures extend beyond the individuals' body and are thus one example of extended phenotypes (Dawkins, 2016; Woods et al., 2021). Eusocial insects such as termites, ants and bees build nests that offer protection for hundreds to millions of individuals (Hölldobler & Wilson, 2009; Korb, 2003; Lüscher, 1961); many fish and bird species construct nests during the breeding season to incubate and raise their offspring (Barber, 2013). Among mammals, apes build leaf nests for sleeping (Prasetyo et al., 2009), bears prepare dens for hibernation (Diedrich, 2011) and rodents are famous for constructing burrow systems (Hayes et al., 2007; Kinlaw, 1999). The protective nature of external structures could be especially important for small animals as they often face high predation risk (Deeming, 2023; Erlinge et al., 1983; Leahy et al., 2016; Lima et al., 2001) and are prone to thermal stress (Blanckenhorn, 2000; Klockmann et al., 2017).

As the largest order in mammals, rodents show a high diversity in ecological niches occupied and in shelter usage. Some use natural shelters such as tree holes and rock crevices, in which they build simple nests, or create their own architecture, most commonly underground burrows (Frank & Layne, 1992; Hayes et al., 2007; Zhang et al., 2003), or/and relatively rare above ground shelters (Whitford & Steinberger, 2010). Burrows offer protection for their nest, and for some species below ground foraging opportunities (Kinlaw, 1999; Zhang et al., 2003). Fewer species build shelters above ground, which are called houses (Birkenholz, 1963), middens (Campos et al., 2019) or lodges (Vermeulen & Nel, 1988; Wolhuter et al., 2022). Lodge building in rodents is rare and could represent an adaptation to specific environments.

Lodges are structures built above ground, usually made of plant material, offering protection for the nest which lays inside (Jackso et al., 2002). Beavers (*Castor spp.*) are famous for building extensive lodges inside ponds they create with beaver dams (Baker & Hill, 2003). North American pack rats (*Neotoma spp.*) use urine, plant and animal materials to build middens above ground, which are extremely sturdy and can last for thousands of years after being abandoned (Betancourt et al., 2021). Bush Karoo rats (*Otomys unisulcatus*) from South Africa and greater stick-nest rats (*Leporillus conditor*) from

Australia build extensive stick lodges which offer protection against the arid and hot climate (Copley, 1999; Moseby & Bice, 2004; Robinson, 1975; Vermeulen & Nel, 1988). For small rodents, lodges are energetically expensive to build but can offer protection for generations (Onley et al., 2022; Vermeulen & Nel, 1988).

Specific climate conditions can make the investment of lodge-building adaptive. For example, the temperature inside the lodges of bush Karoo rats from semi-deserts in South Africa varies less than ambient environment: The temperature inside is higher than outside in cold winter nights (ambient: 6.1–9.9°C; lodge: 10.5–12.1°C), and in general lower in hot summer days (ambient: 17.7–35.5°C; lodge: 19.7–21.5°C); water vapour pressure inside lodges is always higher and less variable than ambient environments in winter (ambient: mean = 5.8 mm Hg, CV = 19.7%; lodge: mean = 7.4 mm Hg, CV = 14.3%) and also in summer (ambient: mean = 10.9 mm Hg, CV = 19.2%; lodge: mean = 14.1 mm Hg, CV = 15.8%; Du Plessis et al., 1992). If lodges generally offer a favourable micro-climate, they may be especially adaptive in environments with extreme temperatures and aridity. Lodges built in arid and hot habitats may offer protection against the harsh ambient conditions, but the high temperatures and low rainfall can create low fuel moisture in such habitats. The dry plant material used to build these lodges is highly flammable and vulnerable to wildfires (Jackson et al., 2004; Kerley & Erasmus, 1992). In the event of a wildfire, the lodges that are meant to offer protection against the harsh environmental conditions might present a deadly trap. Thus, lodge building is likely an adaptation for arid environments with low fire risk.

Ecological factors and natural history shape evolution, but how they influence and interplay with the evolution of lodge-building behaviour is less clear. Ecological factors that can influence the evolution of lodge building include fire risk, aridity and habitat heterogeneity. As sheltering habit may evolve as an adaptation to specific habitats, species that occur in multiple types of habitats may develop either a consistent sheltering habit that is universally adaptive to all the habitats they live in or the ability to show multiple sheltering habits depending on the local environment. Regarding natural history factors, the protective nature of lodges could be especially important for animals with small body sizes, as they are more sensitive to thermal stress (Blanckenhorn, 2000; Klockmann et al., 2017), or alternatively, a larger body size may bring advantages in carrying building materials and in defending their precious lodges against competitors. Considering the overlap of food sources and building materials, plant-based diet can be expected to facilitate lodge building and maintenance, animals feeding on green plant materials may be more efficient in collecting sticks, and the food remains can contribute as building materials (Betancourt et al., 2021). Lodges may offer protection against the heat during the day for nocturnal species, or offer protection against predators for diurnal species (Betancourt et al., 2021). In sum, the natural history factors of body size, diet and activity pattern might influence the evolution of lodge building. Despite these potential influences, how this distinct trait in sheltering habit may differentiate these lodge-building species from their relatives in ecological and natural history remains unknown.

We conducted a comparative study focusing on sheltering habits for mouse-like rodents (suborder Myomorpha) to determine what ecological and natural history factors were associated to lodge building. The extreme arid environment, where the lodge building may be adaptive, is often associated with high climate fire risk, which puts the flammable lodges at risk. Specifically, we predicted that (1) lodge building is more common in arid environments as an adaption to highly variable or extreme ambient temperature/humidity and (2) lodge building is more common in areas with low fire risk.

Materials and methods

Database on shelter use

We searched for information on shelter use of the 1655 species of Myomorpha (classified by IUCN, 2022) in the 'Handbook of the Mammals of the World. Vol. 7. Rodents II' (Wilson et al., 2017). Our search yielded sheltering information for 532 species (seven families, 201 genera). However, the type of sheltering was not clear for 11 species (e.g. the book only stated that the species use shelters without stating the type of shelter, or whether the species constructed shelters or used shelters that had been constructed by other species). For these species, we searched for additional information from online sources (i.e. publications and photos of shelters), which resulted in sheltering information for seven more species (included in the 532 species, see Appendix S1). Shelter type was categorized as natural shelter (nests inside dense vegetation, rock crevices, tree holes or shelters build by other species), burrows and lodges (shelters above ground constructed by sticks and other materials). Because some species can use more than one types of shelter, we classified shelter use into seven categories: lodge, burrow, natural, lodge + burrow, lodge + natural, burrow + natural, and lodge + burrow + natural.

Natural history variables

As important natural history variables that may affect preferred sheltering types and the ability of shelter construction (see introduction), we recorded body mass and body length, diet and activity patterns from the 'Handbook of the Mammals of the World. Vol. 7. Rodents II' (Wilson et al., 2017). Habitat type was obtained from the species description in the IUCN Red List of Threatened Species. Habitat heterogeneity was then calculated as the total number of habitats occupied per species (Olivier et al., 2022; Qiu et al., 2022). Table 1 summarizes the categories of these variables.

Aridity

Aridity was estimated based on the Koppen-Geiger climate classification map (Beck et al., 2018), which presents global climate classification maps from 1980 to 2016. Based on threshold values and seasonality of monthly air temperature

Table 1 Variables considered in this study on myomorph shelter use

	Variables	Category/Quantification
Shelter	Shelter type	Natural shelter, burrow and lodge
Body size	Body length	Average head–body length (mm)
	Body mass	Average body mass of both sexes (g)
Diet	Diet	Insectivorous, Omnivorous and Herbivorous
Behaviour	Activity pattern	Diurnal, nocturnal, both and others (crepuscular, polyphasic and activity pattern unclear)
Habitat	Habitat type	Forest, savanna, shrubland, grassland, wetlands, rocky areas, cave and subterranean habitats, desert and artificial
	Habitat heterogeneity	The number of habitats types occupied per species
	Fire risk	Total burnt area during 20 years (2001–2020) within the species distribution range/species distribution range
	Aridity	Percentage of arid habitat within the species' distribution range (category B according to Koppen-Geiger climate classification)

and precipitation, the Koppen-Geiger system classifies global climate into five main classes: tropical, arid, temperate, cold and polar (Beck et al., 2018). To focus on aridity, we coded the arid areas as one and non-arid areas as zero. By comparing this map with species distribution polygons, we could determine how much of the species distribution area falls into the arid climate classification. The levels of aridity for each species was then calculated by the percentage of arid area in each species distribution polygon, ranging from 0 (no distribution in arid climate) to 1 (totally distributed in arid climate).

Species distribution information was obtained from the IUCN Red List of Threatened Species, based on definitions of presence, areas coded as 'extant', 'probably extant' and 'possibly extant' were considered as the distribution area of the species. From the 516 species included in the phylogenetic model, the distribution of 12 species contained areas where the species were introduced (category 'Extant & Introduced' in the IUCN). Only three species had considerable introduced area (Polynesian rat, *Rattus exulans*; house rat, *Rattus rattus*; and Oriental house rat, *Rattus tanezumi*). We included these areas in this study because (1) the species would not be able to become resident in introduced area if they are not pre-adapted to the local environments and (2) origin and introduced area were sometimes difficult to distinguish, and natural dispersal may be involved, especially for globally spread species such as the house mouse (*Mus musculus*), for which the IUCN Red List of Threatened Species gives no information about their native origin.

Fire risk

We were interested to know if species building lodges do not occur in areas that frequently burnt (high fire risk). Thus, we calculated fire risk by the proportion of historically burnt area in this study. The data were produced by a data mining process using MODIS burnt area product Collection 6 (MCD64A1, https://lpdaac.usgs.gov/products/mcd64a1v006/). The entire product is available under the umbrella of the Global Wildfire Information System (GWIS, Boschetti et al., 2022), which provides numerous data services to report and forecast the global activity of wildfire. With this global burnt area map, we used all data available from 2001 to 2020, the fire information was presented by "tile", the smallest special unit that sum up the fire event and burnt area within a standardized square, 0.25*0.25°). Burnt area was acquired daily with accuracy of 1 ha, and overlapping in space on different days were counted separately (see Artés et al., 2019 for more details).

By comparing the species distribution ranges with this fire dataset, we were able to obtain the cumulated burnt area from 2001 to 2020 (km^2, cumulated data of 20 years) in each species distribution range. Specifically, for each species, the tiles from the fire map that had its centroid intersect located within the species distribution polygon were selected to add up to the burnt area, multiple fires events from the same tile of the 20 years were included. This value was then divided by species distribution range (km^2) to get a comparable fire risk between species (see Appendix S2 for detailed calculation).

Statistical analysis

Phylogenetic comparative analyses were conducted in R v.3.6.1, using the R packages brms (Bürkner, 2017, 2018), RStan (Stan Development Team., 2020) and Rethinking (McElreath, 2020). The modelling and R code were adapted from Jaeggi et al. (2020) and Qiu et al. (2022). Habitat heterogeneity, aridity and fire risk were included in the Bayesian phylogenetic mixed-effects model to estimate whether they have an influence on the evolution of shelter use. Aridity was weakly correlated with fire risk (Pearson's $r = -0.02$), we therefore included them as independent variables in the model. We conducted an alternative model to test for the potential interaction between aridity and fire risk, which did not give any significant differences; therefore, we excluded the interaction from the main model. The phylogenetic relationships and their uncertainty were represented by a sample of 100 phylogenetic trees, downloaded from the phylogeny subsets of online database VertLife (http://vertlife.org/phylosubsets/), which produce distributions of trees with subsets of taxa (Jetz et al., 2012). Phylogenetic signal (λ) was calculated as the proportion of random factors variance captured by the phylogenetic random effects, representing the tendency of related species to resemble each other more than species drawn at random from the same tree. The model employs a categorical error distribution, fitted with two Markov Chain Monte Carlo (MCMC) chains, undergoing a total of 2000 iterations each, with the first 1000 iterations in each chain designated as burn-in to allow for parameter convergence. The shelter categories were combined to simplify the model and increase statistical power: For, the main analysis, we used three categories: natural shelter (natural), burrows (burrow and burrows + natural) and lodge (lodge, lodge + burrow and lodge + natural). As some lodge-building species also dig burrows, we ran an additional phylogenetic analysis with four categories: natural shelter (natural), burrows (burrow and burrows + natural), lodge (lodge and lodge + natural) and burrow + lodge.

Results

Shelter usage

Out of the 532 species of Myomorpha with available data, 145 species use natural shelters, 320 species dig burrows and 14 species construct lodges, with the remaining 53 species having more than one form of shelter use: 47 species use natural shelters and dig burrows, one species construct lodges and use natural shelters and five species construct lodges and dig burrows. No species use three types of shelters at the same time, reducing the shelter usage categories to six for statistical analysis (Fig. 1). In total, we found 20 species that build lodges. Of these, three species (Round-tailed muskrat, *Neofiber alleni*; Common muskrat, *Ondatra zibethicus*; Water mouse, *Xeromys myoides*) are semi-aquatic and construct lodges upon or nearby water, the other 17 species are terrestrial and construct dry lodges on the ground (for species details, see Appendix S1). Fourteen of 20 lodge-building species belongs to the pack rat (*Neotoma*), a lodge-building genus. One exception in this genus is *N. mexicana*, which generally does not build lodges and was thus recorded as non-lodge building in our data source. However, it is important to note that they can use lodges build by other species and were reported to be capable of building lodges inside naturals shelters such as rock cracks (Cornely & Baker, 1986).

Description of natural history and ecological factors

The majority species were herbivorous, and this was more pronounced in lodge-building species (Appendix S3: Fig. S1; lodge 89%, burrow 54%, natural 56%). Most species were nocturnal independent of shelter use (Appendix S3: Fig. S2). The most common habitat was forest (270 species), followed by shrubland (240 species), grassland (216 species) and artificial (191 species). Mean habitat heterogeneity was two and did not differ between the species with different sheltering habit (Appendix S3: Fig. S3). Lodge-building species had a lower body length/mass ratio than others (Appendix S3: Table S1; lodge: 1.2 ± 1.07; burrow: 2.4 ± 1.5; and natural: 2.2 ± 1.39).

The mean aridity of lodge-building species was higher than species that dig burrows or live in natural shelters (lodge: 0.566 ± 0.416; burrow: 0.426 ± 0.406; and natural: 0.158 ± 0.260; Fig. 2, Appendix S3: Table S1). Fire risk was lowest where lodge-builders occur (lodge: 0.210 ± 0.324, burrow: 0.725 ± 2.231; and natural: 0.720 ± 1.345; Fig. 2, Appendix S3: Table S1).

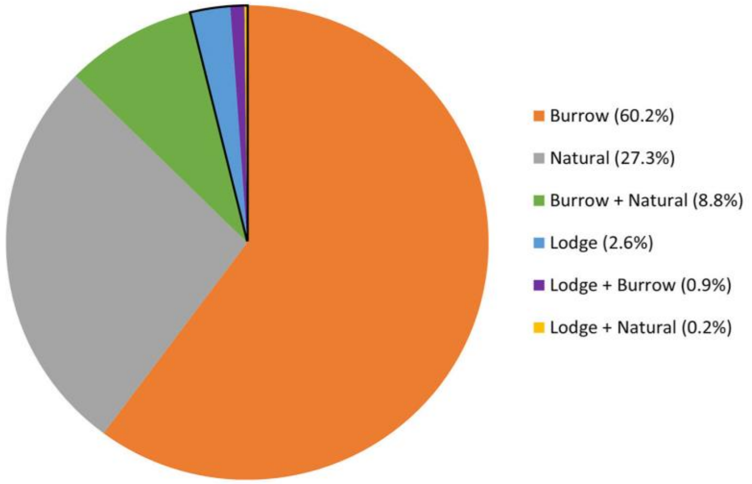

Figure 1 Five hundred and thirty-two Myomorpha species with available information on shelter use. Burrow: only construct burrows; Natural: only use natural shelters; Burrow + Natural: construct burrows and use natural shelters; Lodge: only construct lodges; Lodge + Burrow: construct lodges and burrows; Lodge + Natural: construct lodges and use natural shelters. The 20 species that build lodges are framed by black line.

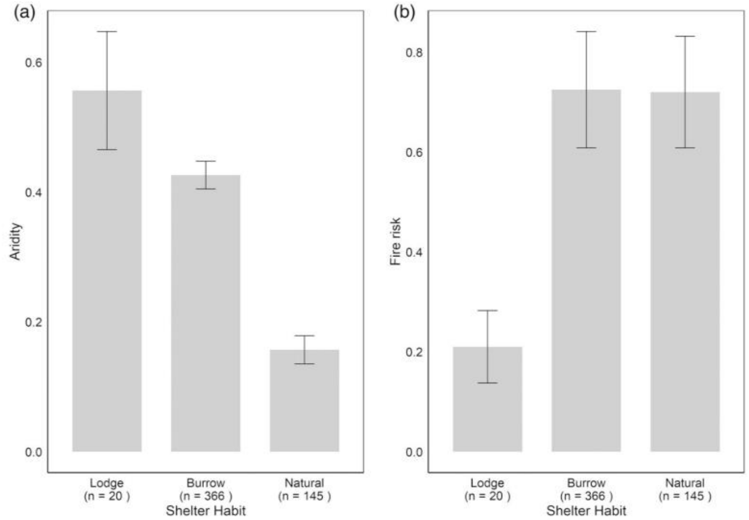

Figure 2 The association of sheltering habit with (a) aridity, ranging from 0 (no distribution in arid habitat) to 1(totally distributed in arid habitat) and (b) fire risk, i.e. total area burnt during 20 years within the species distribution range (km^2)/species distribution range (km^2), both as mean ± SE. Data available for 531 Myomorpha species.

Phylogenetic comparative analyses

The phylogenetic signal ($\lambda = 0.43$) was moderate to high for the 515 Myomorpha species in the model. Phylogenetic distribution showed six independent evolutionary origins of lodge-building behaviour (Fig. 3). In the phylogenetically controlled analysis, the associations of lodge building with ecological factors (habitat heterogeneity, aridity and fire risk) were non-significant (Fig. 4). The additional model with four categories gave similar results (Appendix S3: Fig. S4).

Discussion

We studied whether lodge-building rodents occur especially in harsh arid areas with low fire risk, which would benefit them with a mild micro-climate within the lodge without the risk that their lodge becomes a deadly burning trap. Our descriptive results correspond with this hypothesis: Lodge-building species occur in arid areas with low fire risk. Lodge building is a conspicuous behaviour, but worldwide only 20 myomorph rodent species (4% of studied species) have been reported to build lodges. However, when controlling for phylogeny, neither aridity nor fire severity remained as a significant predictor for the evolution of lodge building. This is probably due to the fact that most lodge species belong to one single genus, the pack rats (*Neotoma* spp.), reducing the number of independent evolutionary origins to only six. Two evolutional pathways for lodge building did not associate with low aridity, which were species building lodges nearby water, as is also known for several species of another rodent suborder, the Castorimorpha (Beavers; Baker & Hill, 2003).

Wildfires directly threaten the survival of a variety of animals (Jolly et al., 2022). Small mammals cannot run away from wildfires but seek protection in shelters (Ford et al., 1999). Observations suggest that not many rodents can escape from wildfires unless protected by underground burrows (Howard et al., 1959). Wildfires can kill rodents directly and reduce their survival probability after fires. As fire destroy above ground shelters, they additionally increase predation risk (Pastro, 2013). Lodges are usually made of dry plant material in environment with low humidity and are thus vulnerable to fire. Fire vulnerability has been observed in pack rats (*Neotoma* spp.), which are reluctant to vacate their lodges and likely die under fire event (Howard et al., 1959; Simons, 1991). Although some lodge-building species can dig burrows underneath their lodges, this cannot protect their expensive and flammable lodges from being burnt down. A burning lodge would likely kill the rodent hiding in it, and even if it survives, it would loss its protecting shelter.

Our study points to two strategies for lodge-building species to avoid fire. Three semi-aquatic species build lodges near water, making fire unlikely to ignite their wet lodges. Similar tactics are observed in non-myomorph rodents such as the two species of beavers (*Castor spec.*), which construct lodges near waters with sticks and branches (Baker & Hill, 2003). Most lodge-building species (17 of 20) in Myomorpha habituated in arid environments, based on the hot weather with low humidity, they face a relatively high theoretical fire sensitivity. However, the actual fire risk was very low for lodge-building species, probably because their arid environments had little fuel available to support wildfires. Many arid environments are associated with low plant productivity (Miranda et al., 2009;

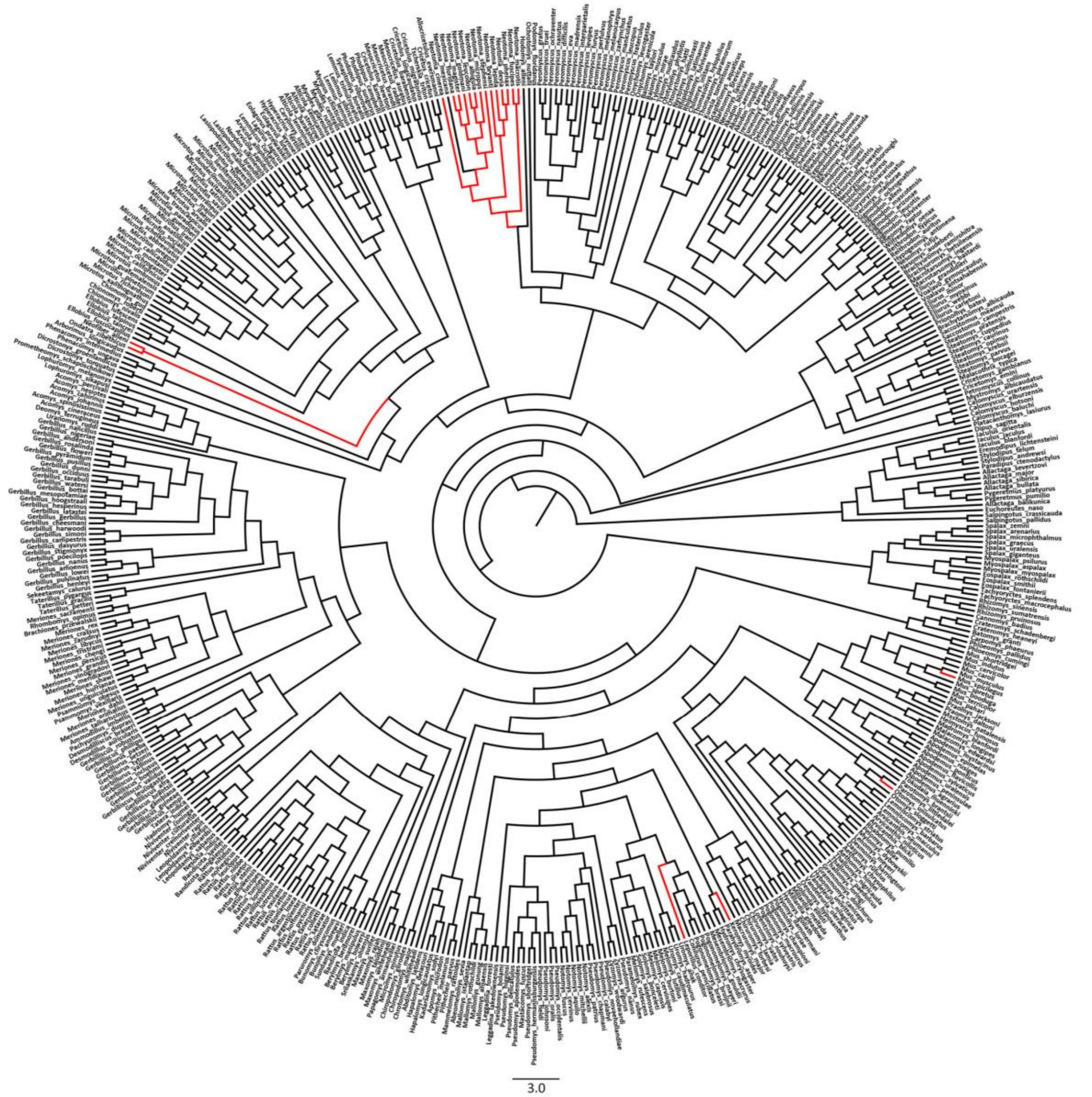

Figure 3 Phylogeny of 532 Myomorpha species and the occurrence of lodge building. Red branches represent the lodge-building species.

Turner & Randall, 1989; Yue et al., 2020), which does not only provide a lot of natural shelters but also makes fires unlikely to spread: If a fire starts, it simply runs out due to patches without any burnable material (McLaughlin & Bowers, 1982; Pausas & Keeley, 2021). For example, the bush Karoo rat (*Otomys unisulcatus*) occurs in the arid and hot Succulent Karoo of South Africa, where wildfires cannot spread as there is not sufficient plant material, but it does not occur in South African savannah habitat, where wildfires occur regularly (Kruger et al., 2006).

The dataset we used to calculate fire risk was based on daily observed fires with threshold 100 × 100 m (by hectare) for a period of 20 years, such that fires that occur in intervals longer than 20 years were not represented. The dataset does allow for

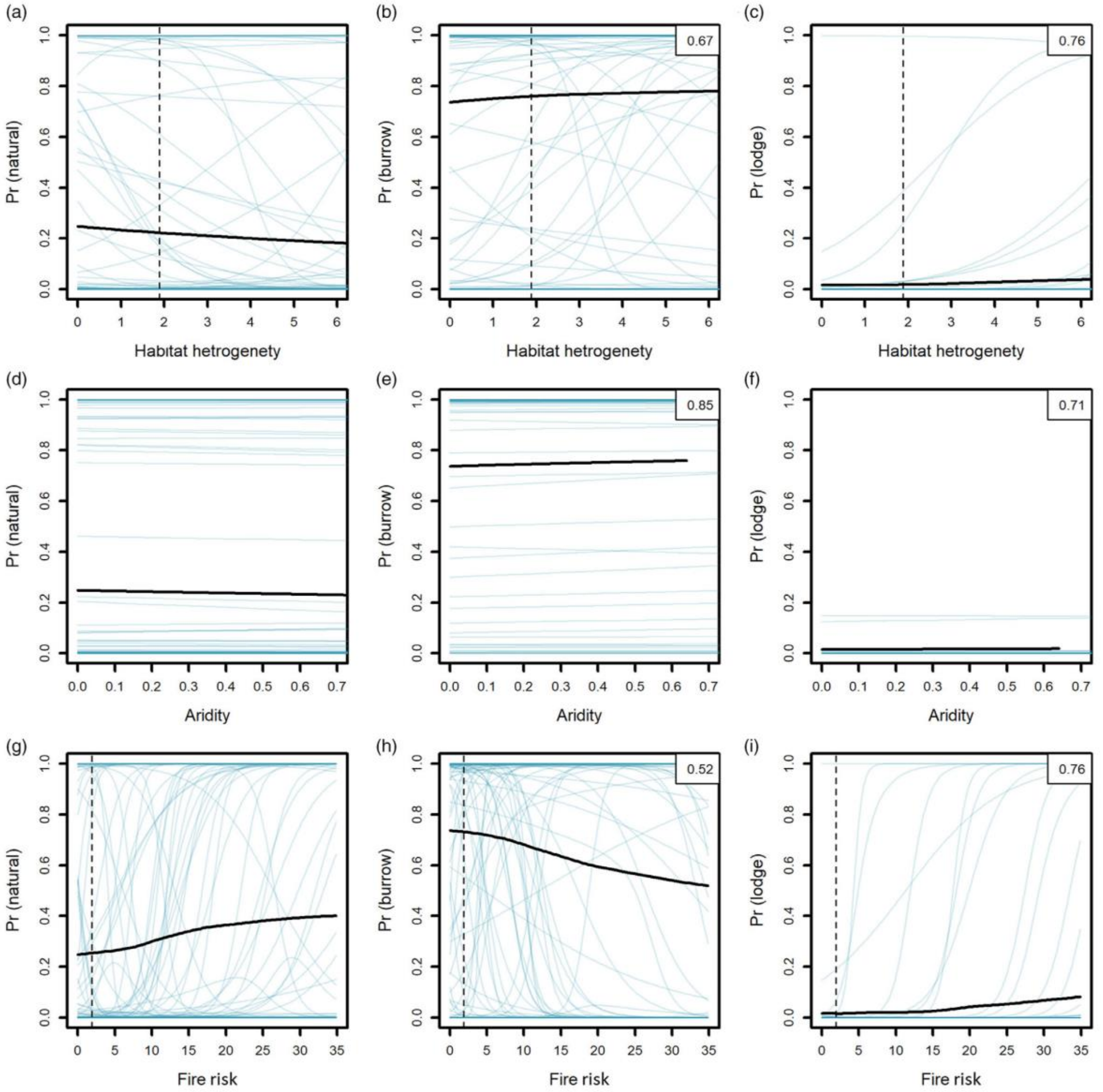

Figure 4 Illustration of evolutionary transitions in sheltering habit as a function of the predictors. Columns show (from left to right) the probability of natural shelter, burrows and lodge, while rows show (from top to bottom) predicted changes in those probabilities as a function of number of habitat (a–c), aridity (d–f) and fire risk (g–i). The numbers in the legends are the posterior probabilities (PP), that is, the proportion of the posterior distribution that supports a given association; these were not available for natural shelter, as this was the reference category. Within each row, all other predictors were held at their baseline value. Solid black lines are the predicted means, thin coloured lines are 100 random samples drawn from the posterior to illustrate uncertainty.

the detection of relatively small fires, however, fires with burnt areas smaller than 1 ha were not represented. Even in areas with a high fire risk, there might be pocket areas that were less burnt, and in areas with low fire risk, small fires might occur in patches with sufficient fuel. Whether such local environmental characteristics influence species distribution would be interesting to study, especially to understand the variation in distribution of a species within its distribution range.

Our descriptive results agree with the hypothesis that lodge-building species are more likely distributed in arid environments with low fire risk, but these effects were not significant when controlled for phylogeny. Phylogenetically controlled models take the evolutionary relatedness of species into account (Hadfield & Nakagawa, 2010), and the 20 lodge-building species fall into seven genera (two of them closely related) of two (seven in total) myomorph families. Most (14 of 20) of the lodge-building species are pack rats (*Neotoma* spp.), such that their data are phylogenetically dependent, representing only one independent evolutionary transition. While only approximately one third of myomorph species had data on shelter usage, the use of lodges is very conspicuous and our data source has probably reported for most species that do build lodges. Thus, it is unlikely increase the statistical power of our analysis by including more species that build lodges. In summary, our result suggests lodge-building species often distribute in areas characterized by low fire risk, during evolutional processes, they may have persisted in areas with less incidence of large and intense fires, possibly due to low fuel loads.

Two evolutionary transitions to lodge building occurred in species living in wetlands and along waterways. These species (*Neofiber alleni, Ondatra zibethicus* and *Xeromys myoides*) live in regions with an overall three times higher fire risk compared to the other lodge-building species (0.63 vs. 0.21, see Appendix S1, column 'fire risk'). However, within these habitats they choose aquatic niches for lodge building which significantly reduces the likelihood of their lodges being burnt down. Therefore, these species suggest another possibility for the evolution of lodge building. The vulnerability of lodges to fire could be reduced by either (1) the environment being too wet to allow lodges to ignite, or (2) the environment has low primary productivity and does not produce sufficient fuel to maintain fires.

Based on the result of this study, we suggest future studies on lodge-building rodents should focus on specific species to test whether aridity combined with low fire risk is associated with the limitation of their distribution range, for example, this would predict that the range of lodge-building species ends where fire risk increases, or that in these areas, they use different shelters than lodges. In addition, studies on specific species also help capturing the effect of short and patched fires with smaller spatial and time scales, which are likely underestimated in studies conducted in global scale. Most lodge-building species are folivores (*Otomys, Leporillus*, many species of *Neotoma*), some eat seeds and fruits (*Mus spicilegus* and *Neotoma phenax*) and some even eat invertebrates (*Xeromys myoides*; see Appendix S1, column 'Diet'). The main folivores diet is consistent with their sheltering habit as lodges are mainly constructed with plant material and thus also offer a food source directly at the shelter. Our descriptive results suggested that lodge-building species have larger body size (body mass/length ratio) than those living in natural shelters or burrows, which may bring advantages for them to construct and defend their lodge against other rodents (Schradin, 2005; Schradin & Pillay, 2005). As these descriptive results are not controlled by phylogeny, we cannot determine to what extent the association is biased by their phylogenetic relatedness. It would be interesting to have further investigation on the natural history traits commonly shared by lodge builders and the potential interaction with ecological factors, for example, if lodge-builders becomes larger when faces high interspecific competition for their lodges. Therefore, studies comparing the body size between lodge-building species with sympatric non-lodge-building rodent species would be useful to test this potential association.

Conclusions

Our study investigated possible associations between ecology, natural history and sheltering habits in mouse-like (myomorph) rodents. The descriptive result suggests that lodge-building species are mostly herbivorous, tend to have larger body size than those who live in burrows or natural shelters and are more likely to occur in arid environment with low fire risk. However, lodge-building remains a rare sheltering strategy for mouse-like rodents (3.7% of species), and the high relatedness between those species makes it difficult to test these associations in phylogenetically controlled studies. In sum, the associations found in our study should be tested rather on a species than comparative level. For example, a previous study on bush Karoo rats suggested that their distribution was limited by wildfire (Kerley & Erasmus, 1992). We suggest to study lodge-building rodents such as the South African bush Karoo rat or the Australian stick-lodge rat to test the predictions: (1) lodge builder are larger than other sympatric rodents, and (2) lodge builders have a species distribution range restricted by aridity (species distribution more arid than area around it) and (3) fire risk.

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Author contributions

J. Qiu collected and analysed the data, designed methodology and led the writing of the paper. C. Schradin conceived the ideas and designed methodology. All authors contributed critically to the drafts and gave final approval for publication.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Dataset of sheltering habit and fire risk of Myomorph.

Appendix S2. Calculation of fire risk.

Appendix S3. Descriptive result of ecological and natural history factors.

Appendix S4. Phylogenetic models.