UNIVERSITE DE STRASBOURG
Habilitation à diriger des recherches

On the physiology of group-living and its evolutionary consequences

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“Crawling at your feet”, said the Gnat, “you may observe a Bread-and-Butterfly”
“And what does it live on?”
“Weak tea with cream in it.”
A new difficulty came into Alice’s head. “Supposing it couldn’t find any?” she suggested.
“Then it would die, of course”
“But that must happen very often”, Alice remarked thoughtfully
“It always happens”, said the Gnat

Lewis Carroll
Through the looking glass and what Alice found there (1871)

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Research activities

Social stress as an important determinant of individual phenotype

I. Theoretical framework

A) On the social environment in relation to stress

From an evolutionary perspective, group living is classically viewed as a balance between the advantages earned and the costs suffered from aggregating with conspecifics. Its evolution, including in men, has typically been considered under the lights of predation pressure, resource competition, kin selection, habitat suitability, shared-information, and cooperation, to name but a few[1-6]. Whereas some species may aggregate simply because of habitat optimality (such as has been proposed to explain the evolution of coloniality in seabirds[7,8]), living in groups foremost poses the issue of interacting (passively, cooperatively, or competitively) with others[9-15]. Whether amicably or agonistic, such interactions have potent effects on individuals. Unravelling the interrelationships between the social environment and the expression of individual phenotypes (encompassing individual behaviour, physiology and health) offers a rich field of research that, only today, are we starting to fully grasp.

Besides well-known advantages (e.g. protection from predators, shared information on resources, thermoregulation) and constraints (e.g. competition, cuckoldry, transmission of parasites), group living also has more subtle effects on individual phenotypes. On one end of a cost-benefit continuum, studies have shown that social factors[a] may have adverse effects on individual fitness by affecting phenotypic traits such as energy expenditure[16,17], oxidative stress[18], stress hormone levels[9,19,20], immunity[21] and overall health[22-25]. On the other end, social factors may have positive outcomes, for instance acting as important buffers to reduce individual stress with positive consequences on health and fitness[20,26] (Fig. 1). As an example, epidemiological evidence in humans highlights the importance of social support in mitigating the occurrence of cardio-vascular disease[27], or positive effects of social support on immune function[28,29]. Other studies have revealed positive effects of social support on neuroendocrine function[20,26], e.g. lower salivary cortisol or plasma and urinary catecholamine levels[30-33] consistent with social effects on cardiovascular function. In other animal species, benefitting from the presence of social conspecifics to alleviate individual stress may also arise from buffering predation stress[34,35] through dilution or shared-vigilance mechanisms, buffering intra-specific competition through coalitional support or kin selection[36-38], or buffering nutritional/environmental stress by sharing information on resources[39], such as foraging sites or habitat quality.

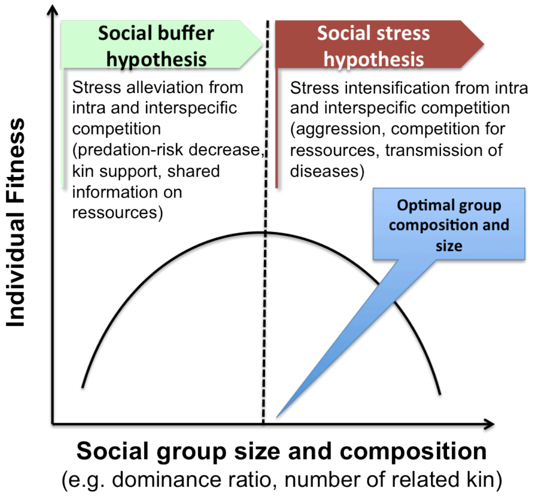

Fig 1. Simple theoretical model for the relationship between social stimuli and individual fitness. Both advantages and constraints accrue from living with social conspecifics. From a physiological point of view, this may have both positive and negative outcomes on individual stress; the downstream consequences of individual stress themselves being pathological or adaptive in nature (see main text).

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[a] I define social factors as any property of the social environment that may be experienced and/or acted on by an individual. This might include social interactions, social signals, or psychosocial emotional states. Social factors may have positive, negative or neutral consequences on phenotypic traits and fitness. They may be directly (e.g. social aggression) or indirectly (e.g. social density) perceived by an individual, and may have immediate and/or long-lasting consequences.

Despite decades of work in this field, our understanding of the intricate relationships between social factors and phenotypes still remains in its infancy, and hinge upon our understanding of evolution and how exactly natural selection operates. For instance, moving away from solely gene-centred views of evolution, contemporary shifts in evolutionary paradigms have set non-genetic inheritance[40–42] and *(nuclear) gene x (mitochondrial) gene x environment interactions*[43] as important sources of phenotypic variability. This of course sheds new lights on the importance of social environments in affecting individual phenotypes both in early-life and in adulthood, sometimes with surprising trans-generational consequences[44]. For instance, recent studies show that increased parental stress due to social environments may result in adaptive programming of the offspring organism (inter-generational effect) to face later social competition. This is the case in red squirrels[45] where maternal stress due to social competitiveness during pregnancy leads to adaptive offspring growth. Similarly, exposure to stress *in ovo* or *in utero* has been shown to affect future offspring social behaviour or functioning of the stress axis both in mammals and in birds[46,47]. Taken together, these results pave the way to a better understanding of how social stimuli in vertebrates may positively or negatively affect individual stress with mixed consequences (pathological or adaptive) on adult and offspring phenotype and fitness. The functional relationships, i.e. exact social and physiological mechanisms, by which social environments (positively or negatively) affect individual stress, health, and ageing; and the ultimate fitness consequences that result remain open and exciting evolutionary questions to address across animal taxa.

B) On the signalling of social attributes in relation to stress

Amongst the various aspects of social living, perhaps one of the most important is social communication, i.e. the (active/passive) transmission of information between conspecifics, and more specifically, the transmission of information about self-attributes. Social signals may be used in the context of both sexual selection (facilitating access to reproduction), or in the wider context of social selection (facilitating access to other types of resources, e.g. food patches, high quality habitats). Examples of social signalling include signalling aggressiveness[48], parasite load and immunity[49,50], parental care[51], resistance to oxidative stress[52], or the ability to maintain vital cellular processes[53].

Social theory predicts that social signals mediate social interactions between conspecifics by advertising information on the health and condition of their bearer (behavioural and physiological attributes), in sexual or other social contexts[54–57]. Because the signal strength of social signals is often tightly associated with social aggression[48,58], and because social signals of individual quality are likely the result of cumulative physiological responses to environmental challenges, there is an intuitive appeal to studying physiological stress as an underlying mediator of signal honesty[59]. However, whereas physiological processes may well underlie the development and maintenance of social signals, a more nuanced view is one of interaction, whereby social signals may also affect physiological state of the individual, given that most signals are dynamic and likely to be influenced by social interactions (see Fig. 2, adapted from[60]). When addressing the relationships between physiology and signals, researchers often opt for a unidirectional view where physiological processes determine the level of signalling, and only few studies have considered opposite relationships[58,61]. Yet, how social signals might evolve and to which extent social interactions are mediated by and/or constrain signal evolution requires an integrative experimental approach manipulating physiological traits on the one hand, and social factors on the other.

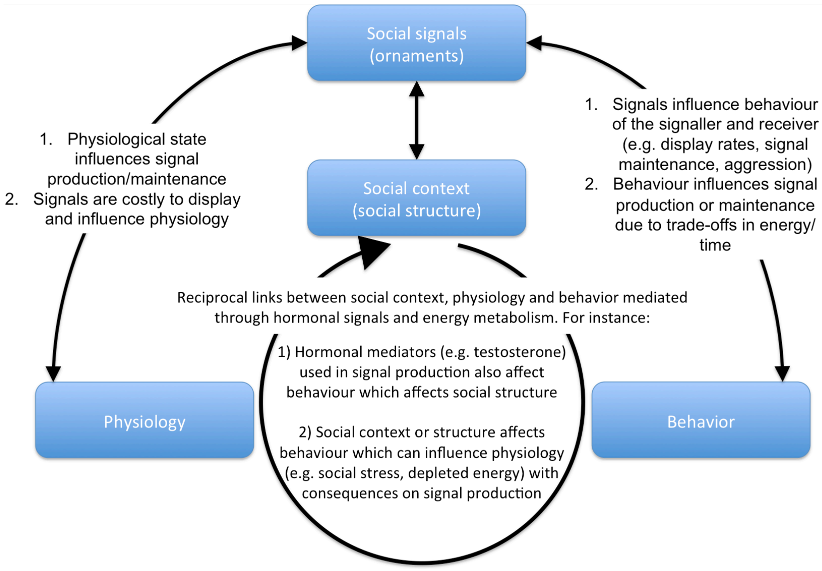


Fig 2. Forces shaping social signal evolution: multidirectional view of the relationships between social signals, the physiological processes underlying their development and the behavioural traits they are related to.

My past research has tackled the relationships between social stimuli and individual phenotypes both from a mechanistic and ultimate perspective. To do so, I have relied on colonial species of birds and mammals to address the relationships between social aggression and (1) individual energetics, or (2) individual stress. Further, I have investigated the physiological attributes that guaranteed the honesty of ornamentation in a monomorphic colonial seabird (see below), focusing on ornamental signals that are known to be important in the context of mate choice[62–66] (*i.e.* sexually selected signals), and that may also play an important role in social contexts[48,67] (*i.e.* more broadly socially selected signals).

All of this work has been carried out in natural environments and has relied heavily on a life history, mostly correlative, approach where heterogeneity in social environments has been explored in terms of variation in individual physiological traits. The rationale for working on colonial seabirds and colonial mammals stems in the heterogeneity of their social organization and the breadth of questions that this allows to address: my main models of research have been colonial king penguins (*Aptenodytes patagonicus*; Aves, Sphenisciformes) and Columbian ground squirrels (*Urocitellus columbianus*; Mammalia, Rodentia).

II. Past work on the relationships between social stimuli and individual physiology

1. King penguins | A model for studying the effects of social aggression on individual stress and energetics

The social system of colonial king penguins can best be described as a vast aggregation of individuals coming together during the breeding season for the sole purpose of reproduction. King penguins are long-lived seabirds that breed on-land in large colonies of several thousands of individuals (up to 500,000 pairs[68]!). While on-land, they have to cope with high-energy constraints, as the various stages of their yearly life cycle (moulting, breeding, extended chick-growth) are all associated with prolonged periods of fasting, for which those animals have adapted using numerous metabolic, physiological and behavioural adjustments[69-82]. In addition, king penguins have a dual-life, alternating those extended periods of fasting on-land with periods of intensive foraging and deep-diving at sea at several hundreds of kilometres of their breeding grounds[83,84], during which energy-conserving metabolic adjustments are also known to occur[85]. Finally, while breeding on-land, king penguins may be subject to inclement weather conditions[82,86], an extremely aggressive social environment[87], and on-land based predation, mostly of their offspring[87,88]. Thus, the phenotypic traits of those colonial seabirds are expected to be under strong influence of heterogeneity in both abiotic and biotic environments[82,89].

My previous work on this model system (since 2008) has shown that physiological and behavioural traits in adults are associated with variability in the social environment[14], specifically with social density[15,82], and likely have strong consequences on offspring development[90,89]. Indeed, my collaborators and I have found that higher social density around breeding adults is associated with higher energy expenditure at rest[82] and higher baseline stress levels[15], possibly due to the stress of breeding close to highly aggressive neighbours (i.e. bystander effects)[14]. Briefly, we used heart rate (Fig. 3) as a tool to monitor acute stress responses and estimate energy expenditure in response to changes occurring in the social environment.

Fig 3. Heart rate monitoring of breeding penguins in their natural environment. The transmitter of the HR–logger is taped to the feathers in a mid–dorsal position to prevent hindering movements from the bird and to be out of reach of the animal. The receptor is attached to a plastic flipper–band, loosely secured to the animal's flipper (left panel), or attached to a metal pole placed close to the incubating/brooding bird (right panel). When visible, the digital display allows monitoring HR (175 bpm in this case) from a distance, using binoculars. Taken from[91].

First[14], we found that breeding birds mounted strong heart rate responses during aggressive interactions, both when directly implicated in an aggressive event (actors, Fig. 4), or when simply at rest observing aggressive events occurring between neighbours (bystanders, Fig. 4). Different heart rate responses were associated with different levels of risk in aggressive interactions (Fig. 4), and depended on the level of implication of an individual bird (i.e. whether an actor initiated or was the recipient of an aggressive interaction), highlighting that penguins are highly sensitive to their social conspecifics and that some form of risk-assessment is implicated in modulating acute heart rate responses to stress (see[92,93] for risk-dependent modulation of heart rate from non-social stimuli).

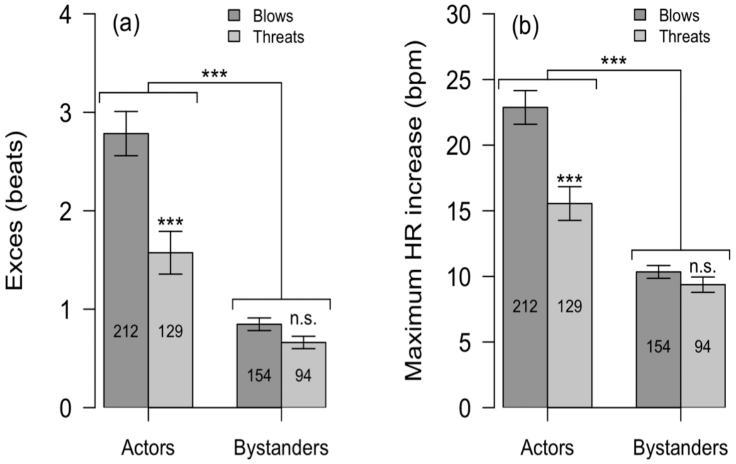


Fig 4. Heart rate (HR) responses to agonistic interactions (actors or bystanders, physical blows or threat displays) in breeding king penguins. (a) HR excess caused by the agonistic interaction (in beats). (b) Maximum HR increase between pre- and post-interaction baseline values (in bpm). Values are given as means ± SE. Number of agonistic interactions is figured in the bars. ***$P < 0.001$, n.s., non-significant. ***Behavioral Ecology (2012) 85: 1179-1185***

With the knowledge that penguins were highly sensitive to their social neighbours, we considered the physiological consequences of breeding in high-density colonies (up to 500,000 breeding pairs[68]) of highly aggressive conspecifics[87]. Indeed, king penguins are remarkably territorial birds, with threat displays between neighbouring individuals reaching rates of roughly 100 threats/h during the chick-brooding season[87]. The fact that there are 2 distinctive breeding peaks in the season[94], with social density differing greatly between those periods (Fig. 5), make king penguin a remarkable model for investigating how changes in the social environment are related to individual physiology. For instance, by comparing the energy expenditure (estimated by heart rate[95]) of males of similar reproductive status, but breeding under different social conditions[82]. We found that early in the season, males breeding under initially low but sharply increasing social density conditions experienced a substantial increase in their resting metabolic rate with progressively increasing colony density at the start of breeding (courtship and first incubation shift) (Fig. 5 box). This was not observed in late breeding males that experienced little changes in colony density (high and stable) at the same timing of their breeding cycle (Fig. 5 box). Those results suggested that males might pay an additional energy cost to breeding, even at rest. A particularly interesting result here, is not only that late breeders did not show an increase in their resting daily heart rate, but especially that their resting heart rate levels started where those of early breeders levelled-off (at high density). Thus, it may well be that the nature of the social environment (numerous aggressive conspecifics, densely packed and all defending territories) late in the season prevented birds from decreasing their level of both daily and resting energy expenditure at that time. Interestingly, the fact that resting heart rate was affected (and not only daily mean heart rate[82]), suggests an effect of the environment not simply mediated through physical activity but that could well be related to individual (socially-experienced) stress.

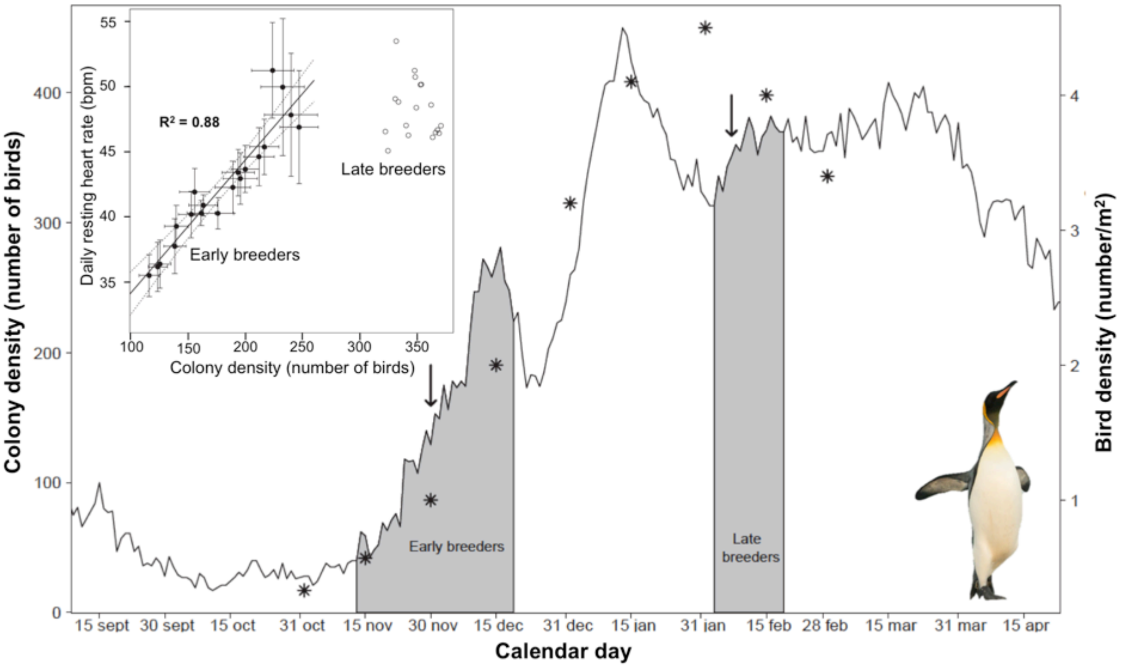


Fig 5. Changes in colony density over the 2008–2009 reproductive season for king penguins breeding in the Baie du Marin, Possession Island, Crozet Archipelago. Breeding density (stars): number of breeding birds per square meter in the study area. Colony density index (continuous line): number of transponder-tagged breeding birds present in a nearby sub-colony of fixed area (see text). Shadowed zones under the density index curve indicate time periods during which early and late breeders were monitored, with arrows showing the respective average laying dates. The date of the first observed laid egg in the study area was November 10. Box: Influence of colony density (number of birds) on resting heart rate (rHR, bpm) in breeding male king penguins. Significant regression line (solid line) and 95% confidence intervals (dashed lines) are given for early breeders (rHR = 24.0± 1.8 + 0.1±0.01 x density). Values are daily means for 3–14 (early breeders) or for 3–10 (late breeders) birds from 3 days before egg laying onwards (early breeders, n = 20 days), or throughout the whole monitoring period (late breeders, n = 18 days). For clarity, SE (bars) are presented only for early breeders. ***Functional Ecology (2014) 28: 621-631***

Naturally, the above results led to considering whether differences in local breeding density were indeed associated with variation in bird stress physiology. Thus, we questioned whether penguins breeding in socially dense environments were chronically stressed[15]. For this, we used the natural heterogeneity of king penguin colonies and compared the basal glucocorticoid hormone levels (corticosterone, the main stress hormone in birds) of birds breeding at high density at the centre of the colony, or at low density on the outskirts. Controlling for breeding timing, breeding status, fasting duration, and weather conditions, we revealed substantial differences between central and peripheral breeders in basal stress levels[15] (Fig. 6). Increasing density (increasing PC1, Fig. 3) positively explained 40% of the variance observed in baseline total corticosterone levels. It was interesting to note that the oxidative status (chronically stressed birds may be in a situation of oxidative stress[96]) of birds breeding at high density was similar to that of birds breeding at low density, suggesting that compensatory mechanisms (e.g. up-regulated antioxidant defences) may have been operational, though I would advocate caution in view of the limited sample size available for oxidative stress measurements.

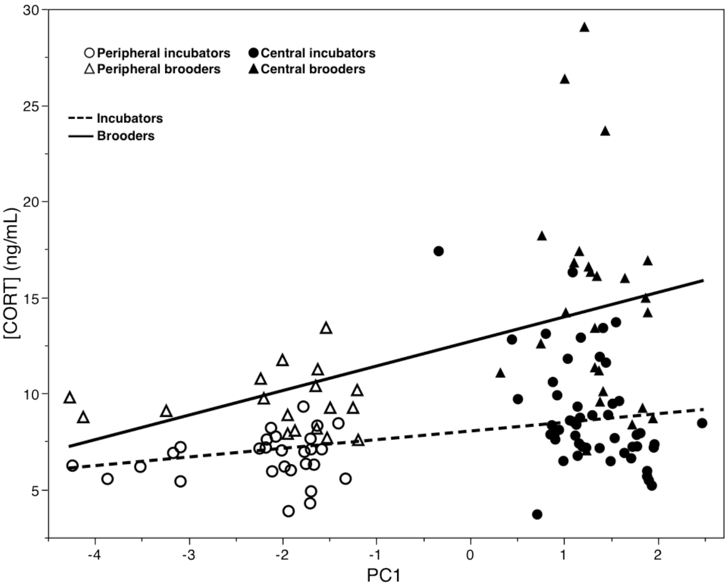


Fig 6. Influence of a principal component (PC1) describing local social density conditions on total baseline corticosterone (CORT) levels (ng/mL) in king penguins holding central or peripheral breeding territories in the Baie du Marin colony, Possession Island (Crozet Archipelago). Regression lines based on the best model are given for incubating and brooding birds. ***Oecologia (2014) 175: 763-772***

Taken together, those results suggest that social conspecifics may have substantial effects on breeding adults affecting both their stress metabolism and energy expenditure. This is surprising for a colonial breeder that relies mostly on stored energy reserves to sustain most of its reproduction[74]. Perhaps this is one of the prices to pay for the benefits of reproducing in vast colonies (avoidance of predators, transmission of information, availability of partners)[7]. Nonetheless, it raises the intriguing question of what the adaptive *vs.* detrimental consequence of elevated stress levels may be. For instance, we recently found that the phenotype of king penguin chicks shortly after hatching could be determined (at least partly) by maternal/early environmental effects[89]. King penguin chicks hatched late in the season had higher corticosterone, higher oxidative stress levels, shorter telomere lengths, and suffered from higher mortality than chicks hatched early in the season. Although late chicks clearly started with a disadvantage, those with higher corticosterone levels presented higher survival rates than those with low corticosterone, suggesting an adaptive function of high glucocorticoids in those individuals (Fig. 7). Interestingly, late chicks that have higher plasmatic corticosterone levels shortly after hatching are also incubated and raised during the period where colonial density is highest. Thus, it is possible that their phenotype is modulated in part by early environmental effects such as social density or parental stress, as has been recently shown experimentally in red squirrels[45]. This suggestion however, remains to be tested.

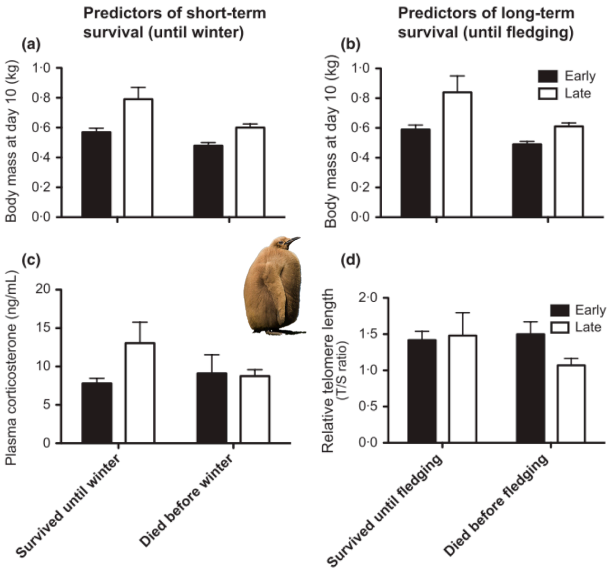


Fig 7. Phenotypic predictors (mean ± SE) at day 10 of short (until winter, a/c) and long-term (until fledging, b/d) survival of king penguin chicks. (a) Body mass at day 10 of chicks that survived vs. died before winter. (b) Body mass at day 10 of chicks that survived vs. died before fledging. (c) Plasma corticosterone concentration at day 10 of chicks that survived vs. died before winter. (d) Blood cell telomere length at day 10 of chicks that survived vs. died before fledging. ***Functional Ecology (2014) 28: 601-611***

The research presented above required 3 field seasons (totalling roughly 15 mo. of field work) of data collection on the sub-Antarctic island of Crozet (French Austral Territory). During that time, I co-supervised 3 different field assistants in the establishment of protocols and collection and processing of data in the field (N Malosse 2009, M Kauffmann 2010, B Gineste 2011). I was also responsible and co-supervised 2 Master students (V Valette 2010, A Smith 2011) in the analyses and processing of data, and in the writing of their Thesis that later yielded 3 publications[14,92,93].

2. Columbian ground squirrels | A model for studying the effects of social buffers on inter-individual aggression and energetics

The social system of Columbian ground squirrels can best be described as one of matrilineal philopatry. They are a hibernating rodent species with a short (3-4 mo.) active season during which females come into oestrus for only a single day[97]. Both males and females aggressively defend individual territories, male territoriality being highest during the mating season (a few weeks between mid-April and early May[98,99]). During the reproductive period, females cluster into contiguous home ranges <1,000 sq. meters[100], which are established around individual nest burrows in which they raise a litter of approximately 3 young[101,102]. Although lactating females are individually territorial[103], territorial overlap with neighbours may be high[100]. Dominance in males is age dependent, with younger 2-3 year olds being subordinate[98] and males become subordinate to females after the mating season[98,103]. Mothers maintain individual nest burrows in which they raise the young, occurring in philopatric matrilines (groups of ~0-4 co-breeding kin females in close spatial proximity) that likely allows them monopolizing favourable burrow systems and resources (Fig. 8). This heterogeneity in kin structure experienced both between females (inter-individual differences on a yearly basis) and within females (intra-individual differences over lifetime) provides an opportunity to investigate consequences of the social environment both from a proximate (stress, energetics) and the ultimate (fitness) point of view.

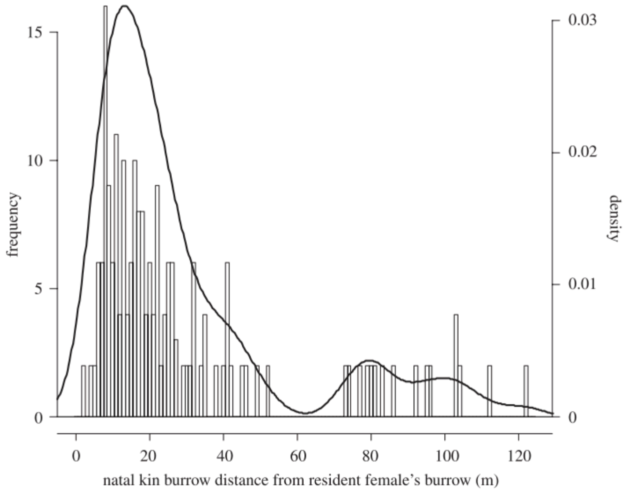


Fig 8. The distance between natal nest-burrow locations for adult females that were natal kin and reproduced concurrently on the study area from 1992 to 2007. A histogram of the frequency distribution and a density function (viz. a kernel density plot) are shown. ***Proceedings of the Royal Society B (2010) 28: 601-611***

From an ultimate point of view, my collaborators and I questioned the fitness benefits of co-breeding in the presence of kin individuals[3]. We investigated the potential causal paths (Fig. 9) by which the presence of kin might act on individual fitness, applying an individual fitness approach to a 16-year study of female ground squirrels. We examined variance in the individual fitness of females, and compared this with the average number of kin present for each female over her lifespan. The analyses revealed direct fitness benefits associated with matriline establishment via kin selection in those animals. Females with higher close kin numbers (averaged per year) achieved higher fitness over their lifetime[3]. This difference was owed to a direct effect of kin on litter size at weaning, possibly arising as a consequence of female kin sharing greater spatial proximity[3,104,105] and being more tolerant (less aggressive) towards one another[106] (genial neighbours).

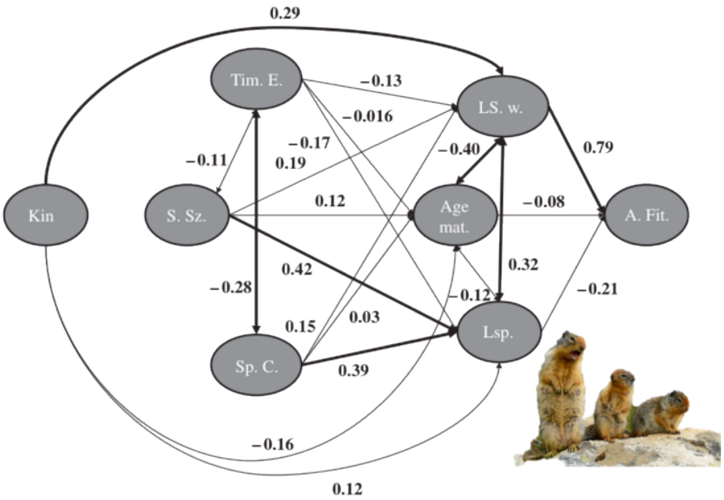


Fig 9. Influence of kinship on female fitness: overall path diagram with path coefficients. Variables: Kin, mean number of kin present over lifetime; Sp. C., mother's spring body condition; S. Sz., mother's structural size; Tim. E., timing of emergence; LS. w., litter size at weaning; Lsp., mother's lifespan; Age mat., age at maturity; A. Fit., adjusted fitness. Significant paths ($p < 0.05$) appear in bold. Single headed arrows indicate causality, whereas double-headed arrows indicate correlations ($n = 70$). ***Proceedings of the Royal Society B (2010) 28: 601-611***

Expanding on those results, we then studied aggressive behaviour during the breeding season to test whether females were indeed more tolerant of kin in this model system. Using a social network approach[107] (Fig. 10), we found that network measures characterizing received aggression (in-strength, in-degree) decreased as individuals aged, whereas network measures characterizing elicited aggression (out-strength, out-degree) peaked at prime reproductive age before decreasing in older individuals. More importantly, we found that aggressive behaviour directed to non-kin was twice as high as that directed to kin (Fig. 11), indeed confirming that breeding female ground squirrels were more tolerant to kin individuals.

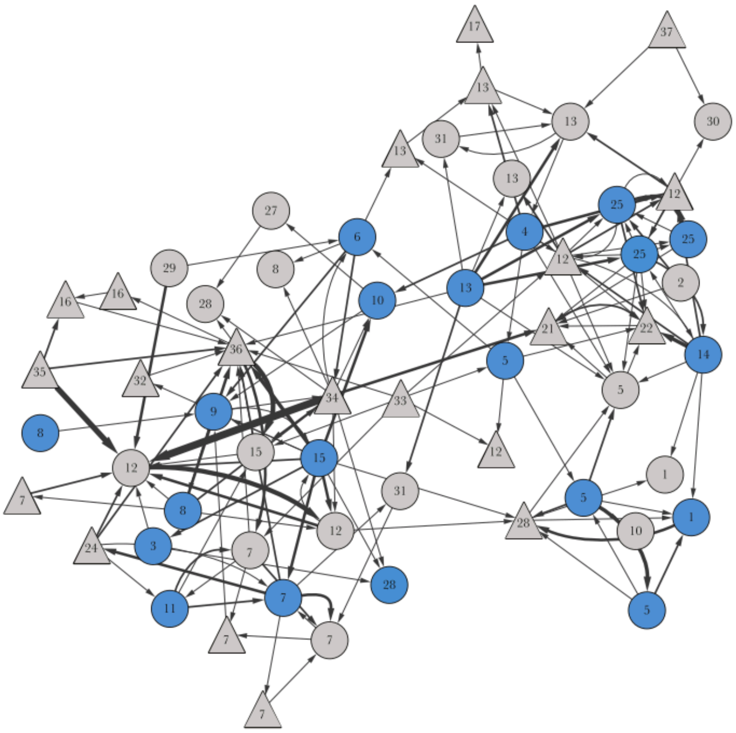


Fig 10. Directed, weighted, social network of aggressions during lactation in Columbian ground squirrels (*Urocitellus columbianus*). Females are symbolized by circles, males by triangles. Kin individuals (regardless of sex or age) sharing the same mother are depicted by the same number. A directed aggression between 2 individuals is symbolized by an arrow pointing from the initiator toward the recipient. Arrows are weighted according to the number of aggressions exchanged. Breeding females are depicted in blue. ***Behavioral Ecology (2016) 27: 1716-1725***

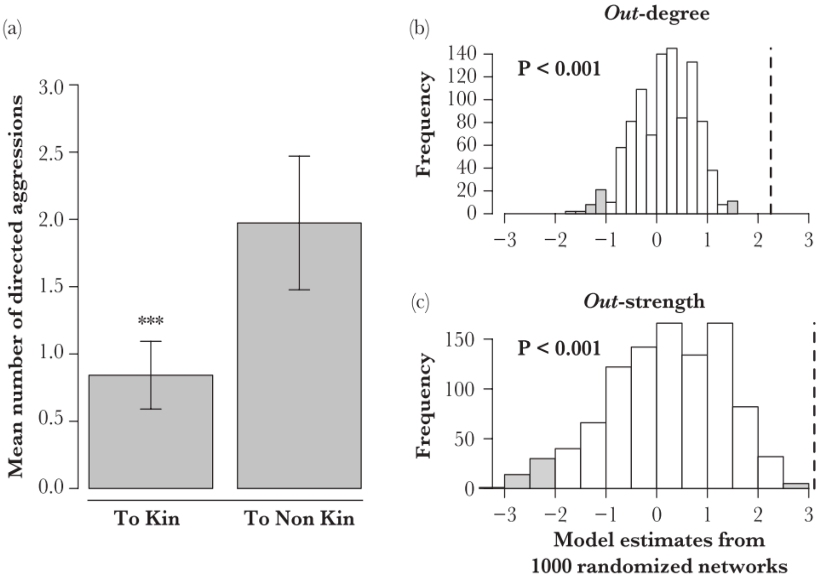


Fig 11. Aggressions directed toward kin or non-kin within a social network of aggressions in Columbian ground squirrels (*Urocitellus columbianus*): (a) the mean number of female–female aggressions directed to kin versus non-kin; (b) and (c) the distributions of model estimates obtained from 1000 randomized networks. The true estimates from the original model are figured by dashed lines. Effects falling outside the 95% CI, that is, in the gray bars, are considered significant. ***P < 0.001. ***Behavioral Ecology (2016) 27: 1716-1725***

Genial neighbour benefits via differential aggressiveness towards kin could arise because of different risks of infanticide for pups[108,109]. Alternatively, differential aggressiveness between kin and non-kin is likely to affect female energetics by modulating the amount of energy females can allocate to lactation vs. territorial defence, affecting their success at weaning. We tested this hypothesis by investigating the effect of female kin on energy allocation strategies over a 26 year period[38]. Controlling for female age, we showed that the number of co-breeding kin a female had during the season significantly affected her balance between somatic and reproductive mass allocation (Fig 12).

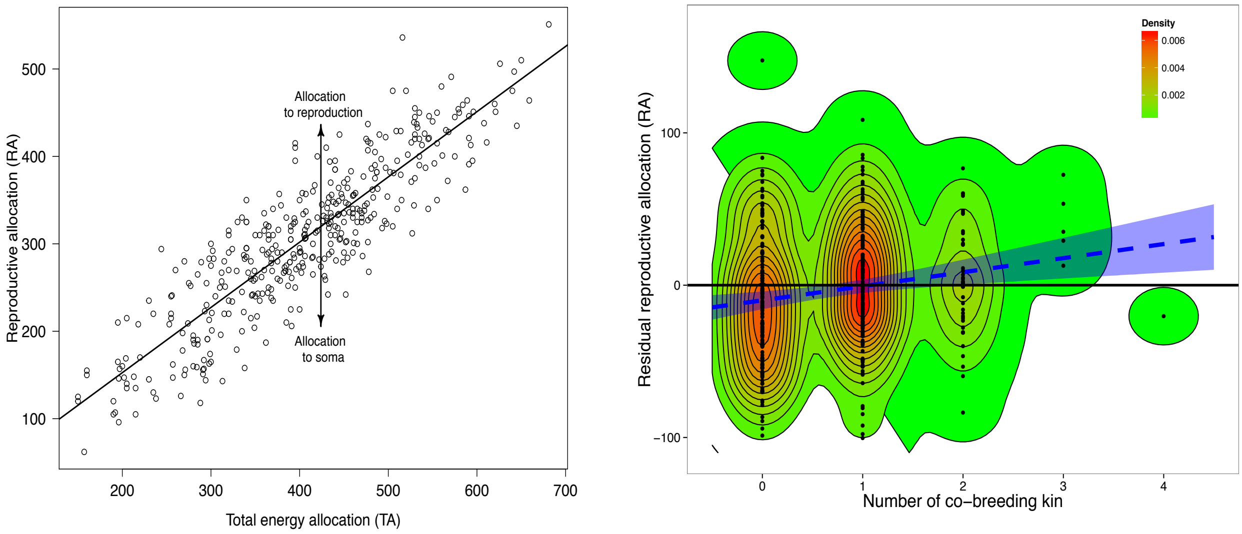


Fig 12. (Left panel) Relationship between reproductive (RA) and total (TA) allocation in female Columbian ground squirrels. Reproductive allocation is calculated as offspring mass gain (in g) from birth to weaning. Somatic allocation SA is calculated as female mass gain (in g) from emergence of hibernation to offspring weaning. Total allocation is the sum of reproductive and somatic allocations TA = SA + RA. Residuals from the regression line (residual RA) represent the balance of allocation between reproductive and somatic functions. Positive residuals represent higher allocation to reproduction and negative residuals higher allocation to the soma. (Right panel) Effect of co-breeding kin numbers on the balance between somatic and reproductive allocation. Positive values of residual RA (above the horizontal line) indicate an allocation bias towards reproduction, whereas negative values (below the horizontal line) indicate an allocation bias towards the soma. The prediction is figured by a dashed line with its 95% confidence interval. Kernel densities are figured for illustration purposes. ***Journal of Animal Ecology (2016) 85: 1361-1369***

Females with more co-breeding kin significantly biased their allocation of energy towards offspring production (LMM; estimate = 8.35 ± 2.87; t = 2.91; P = 0.004, n = 359, N = 138), supporting the hypothesis that breeding females were able to allocate more energy into reproduction when kin are present. In turn, the increased energy allocation had positive effects on litter size at weaning and thus female fitness.

The above results highlight important social effects on individual fitness, likely mediated through (1) greater tolerance and lower aggression from female kin, with likely lower risks of infanticide and greater protection of territorial boundaries[108,109], and (2) marked effects on individual energy allocation strategies. All those factors are likely to have strong effects on individual stress (e.g. energy mobilization and utilisation is mediated by glucocorticoid stress hormones), and this model system thus appears ripe for further research on the consequences of the social environment and social structure on social stress and its consequences on individual health and offspring phenotype in the wild (see current and future research).

The research presented above builds upon a long-term (>25 years) field study on Columbian ground squirrels, which require yearly 3-4 mo. field seasons in the Canadian Rocky Mountains to collect. I am one of the Principal investigators in this project, and have contributed to data collection in 2008, 2013, 2014, 2016, 2017, 2018 – ongoing (totalling roughly 18 mo. of field work to date). Over that time, I have co-supervised and trained 6 different field assistants (C Bordier 2013, AM van der Marel 2013, I Serrano-McGregor 2014, C Klaus 2013-2014, T Fraychak 2014, E Harscouet 2018) and one post-doc (M Tissier 2017) in the establishment of protocols and collection and processing of data in the field. I have been responsible and co-supervised 3 Master students (E Billy 2015, J Rabdeau 2016, T Barra 2018) in the analyses and processing of data, and in the writing of their Thesis. I have further co-supervised one Canadian BSc student (C Petel-Langevin 2014-18) and one American MSc student (K Rubach 2013-16) on separate life history projects, and I am currently involved in the supervision of a PhD student working on host-parasite interactions (JD Roth, 2016-ongoing). Finally, I have collaborated with 2 post-doctoral fellows (C Pasquaretta 2016 and C Récapet 2017) on various aspects of the project. This research has so far led to 8 publications[3,38,107,110–115]. I am part of an international effort for monitoring these populations in the wild (for more information, please visit https://animalbehaviour.wixsite.com/mountainmammalres) and actively collaborating with a private company expert in designing specific bio-logging tools for ecological research (Sextant Technology Ltd).

III. Past work on social signals as honest indicators of individual physiology

The central role of mate choice in sexual selection was early emphasized by Fisher[116] in 1934. As males and females may have different interests concerning reproduction[117], an imbalance of investment between partners (often leading females to invest more into the offspring than their partners) is likely to arise, laying the grounds for sexual conflict[118]. Typically, whereas sexual selection may optimize males' secondary sexual traits to outcompete one another over reproductive advantages associated with mating, females may benefit from being choosy, picking out the best male possible to father their offspring for instance in terms of parental care or genetic quality[119,120]. Accordingly, selection might act on sexual traits, providing mating individuals with a means to choose between a diversity of potential mates on the market, ultimately aiming at finding the best mate possible. Ornamented males may advertise individual quality to choosy females, who may then choose the best mates possible according to honest signals. It is important to note that the above relies on the assumption that sexual signals should be costly[121]. Only the best males should be able to bear them, and for selection to act upon sexual ornaments, the proximate (physiological) costs of being 'strong and sexy' must be high. In red grouse (*Lagopus lagopus scoticus*) for instance, males exhibit supra-orbital red combs whose size depend on circulating testosterone levels. Males with higher testosterone levels have larger combs, but this comes at a cost in terms of cell-mediated immunity (testosterone immuno-depressing effects). Comb size thus appears as an honest signal of male immune competence[122].

A large body of research on sexually selected traits has focused on sexually dimorphic species investigating female mate choice and the honesty of male ornamental signals[123–128], *i.e.* species where the investment between males and females into reproduction is likely to strongly differ. In comparison, less has been done on mutual mate choice, and little is known on what could maintain the honesty of female ornaments[129,130], as in most species studied so far, females are generally regarded as dull, displaying little colourful ornaments, if any at all. In this regard, monomorphic species provide a challenging system for the study of mate choice and an important unexplained pattern for evolutionary biology. Monomorphic species are expected to occur when individual fitness strongly relies on shared parental care, and so, on reciprocal selection[131,132]. Mate choice then becomes critical for both sexes, and by honestly signalling individual quality, morphological signals may help males and females in their pairing decisions. However, because males and females often have differing physiological constraints it is unclear what proximate physiological pathways could guarantee the honesty of male and female ornaments. Differing physiological constraints between males and females, may indeed lead to differing associations between physiology and sexual signals, between physiology and fitness, and between sexual signals and fitness in both males and females.

King penguins | A monomorphic model for studying the physiological determinants of ornamentation

King penguins offer an interesting model for investigating the honesty of social ornamentation. As previously mentioned, king penguins have a long and complex breeding cycle[69,94]. The energy commitment to reproduction is particularly high for both sexes [74], as reproduction occurs on land, but parents are committed to cooperate on the long term (> 1 year to fledge a single offspring !), alternately foraging at sea to restore their body condition and provision their chick. The selection of a high quality partner might then be particularly important in such a slow breeding species and mutual mate choice is likely to be exacerbated. Indeed, annual divorce rates are as high as 81% [133], and mutual mate choice during ritualized courtships appears to be a central component of the breeding cycle [76,79,133]. In addition, recent evidence points out that ornaments in this species may also be used in social contexts not directly related to mate acquisition. King penguin display yellow-orange ear feather patches on either side of the head, and the size of those patches has been associated with bird aggressiveness[48]. Birds with larger patches are more aggressive in territorial disputes and are able to secure more central territories in the colony[67], suggested to be of higher quality[134] (but see[15,135]). Thus, ear feather patches may act as badges-of-status signalling individual aggressiveness in territorial dispute contexts.

At the time (2012) my colleagues and I started working on the physiological determinants of ornamentation in king penguins, the physiological traits conveyed by ornaments used in mate choice largely remained an open question. It was more than likely that one specific ornament signalled a combination of traits[136] which may have pertained to parental quality[137], genetic advantages[120,138], or other proxies of individual quality (such as anti-oxidant defences[139], immuno-competence[122], parasite load[140], or stress status[141]). Of the various colourful ornaments displayed by adults birds (see Fig. 13), the size of the auricular feather patches and the yellow-orange and ultra-violet component of beak spot colour appeared like important ornaments used in social communication[62–66,142].

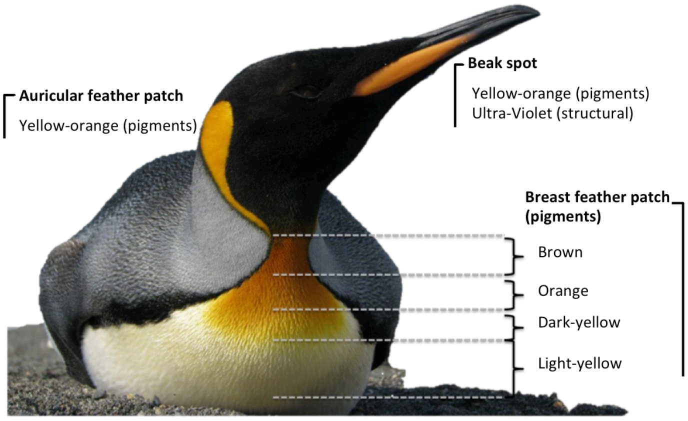
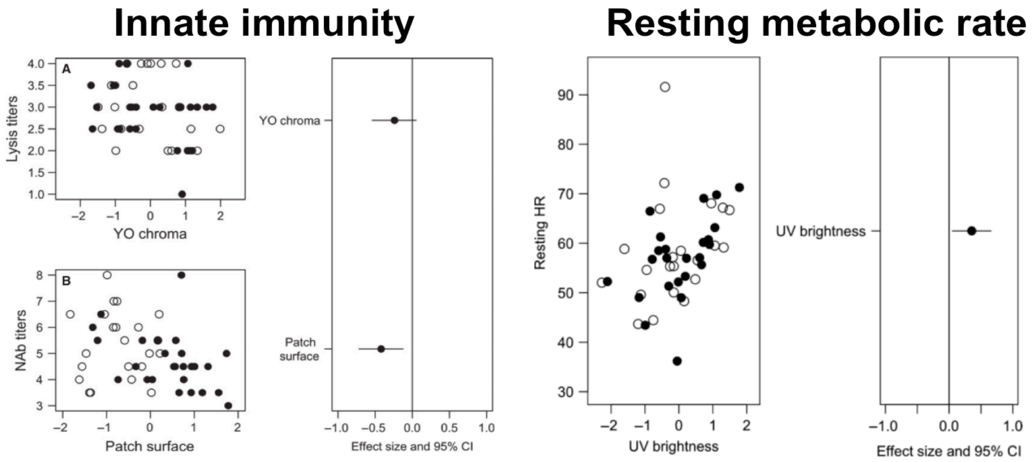


Fig 13. The conspicuous colour ornaments displayed by king penguin. When analysed by spectrophotometry, the keratin beak spot is composed of 2 distinct colours: a yellow-orange hue originating from pigments, and an ultraviolet hue resulting from cellular structure. The yellow-orange to brown colours of the auricular patch and breast feathers originate from pigments. Figure adapted from Q Schull 2016[143].

Thus, we started by questioning the physiological correlates that may be associated with variation in those ornaments in 31 freely breeding penguin pairs[144]. We focused on key physiological mediators known to show important associations with fitness including body condition, immunity, parasite loads, stress hormones, heart rate responses and energy status. Over an extensive set of variables, results confirmed the conveyance of honest information on physiological quality by color ornaments in both sexes. Beak coloration or auricular patch size were honest signals of innate immunity, the ability to mount a stress response in answer to an acute disturbance (capture), and resting metabolic rate (as estimated by heart rate) in both sexes (Fig. 14). The interesting finding however, is that body condition and oxidative stress were signaled by beak coloration in opposite directions for both sexes, likely highlighting differing physiological constraints and varying selection pressures in males and females (Fig. 15). Yet, ascertaining which physiological determinants may guarantee the honesty of information requires an experimental approach where the consequences of variation in individual's physiological status on bird ornamentation can be directly tested.



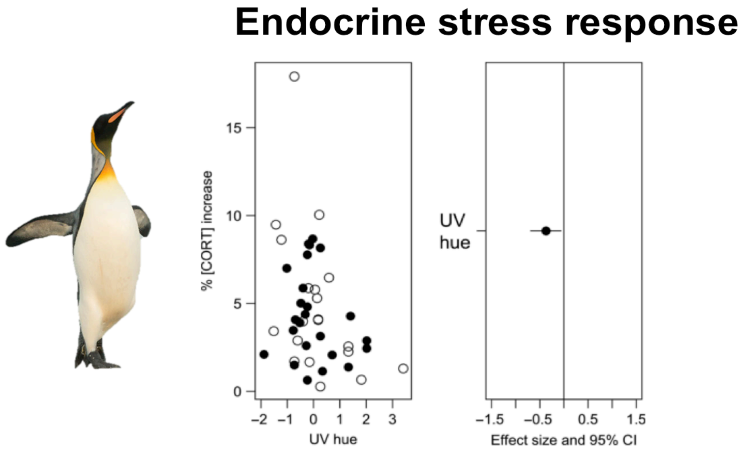


Fig 14. Relationships between beak coloration, auricular patch surface and physiological proxies of individual quality in king penguin (males full circles, females open circles). Standardized effect sizes (z-transformed r) and their associated 95% confidence intervals are given. ***Biological Journal of the Linnean Society (2016) 118: 200-214***

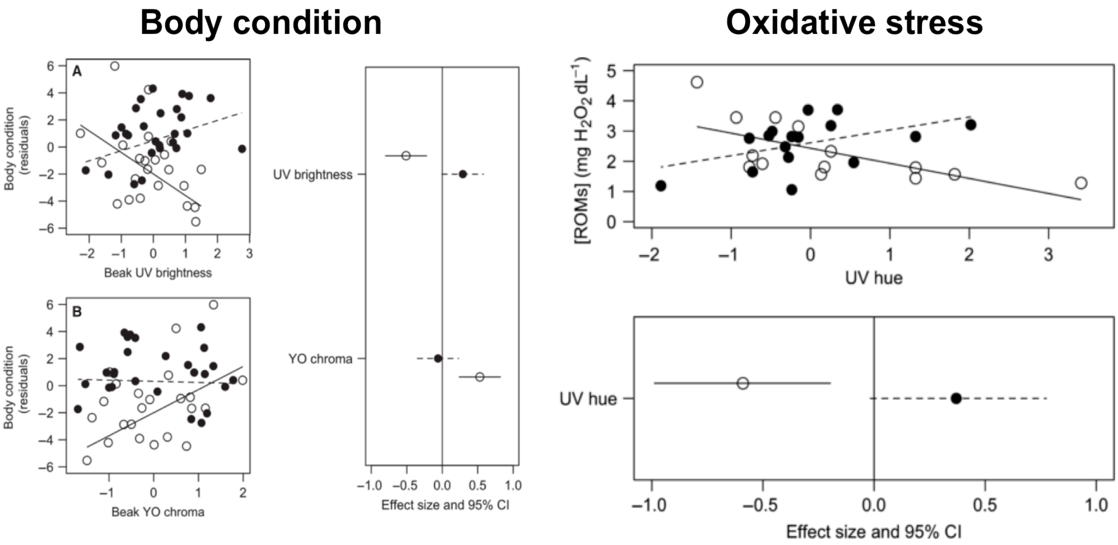
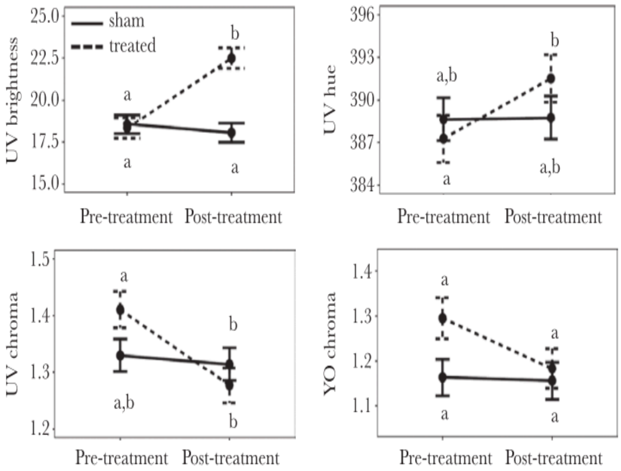


Fig 15. Contrasting information signalled by beak coloration on body condition and oxidative stress in male and female king penguin (males full circles, females open circles). Standardized effect sizes (z-transformed r) and their associated 95% confidence intervals are given. The solid line depicts the relationship for females, the dashed line the relationship for males. ***Biological Journal of the Linnean Society (2016) 118: 200-214***

We turned to this approach in the framework of Quentin Schull's PhD thesis. First, we focused on bird immunity by working on ectoparasite loads (namely ticks; *Ixodes uriae*) and by experimentally removing the constraints of parasites in a group of free-living breeding birds[145]. Our results showed that beak coloration responded rapidly to a relief in parasite load, indeed confirming an existing trade-off between resources invested into immunity and resources invested into ornamental colors (Fig. 16). Further, beak coloration (UV brightness and yellow-orange chroma) appeared to dynamically signal changes in fasting status[145], a physiological trait of critical importance to successful reproduction in penguins[77].

Fig 16. Effects of an experimental anti-parasitic treatment on the beak coloration of breeding adult penguins. Changes in beak brightness, hue and chroma were assessed using LMMs, with bird ID specified as a random variable, the treatment (treated vs. control), the time period (pre-treatment vs. post-treatment) and the interaction between those factors specified as independent variables. Sex was tested in the models but was not significant. Least-Square (LS) means are presented. Values not sharing a common letter are significantly different for P < 0.05. ***Behavioral Ecology (2016) 27: 1684-1693***



Second, we questioned to which extent bird's physiological status prior to molt determined the production of ornamental signals. Indeed, adult king penguins undergo a dramatic yearly molt over a period of 3–4 weeks ashore during which they renew their entire plumage and their yellow– orange keratin beak spot[146,69], providing a perfect opportunity to test for ornamental production costs by manipulating individual physiology at that time (Fig. 17). We did this by experimentally manipulating bird stress, either subjecting them to chronically high glucocorticoid hormones (via subcutaneous implants, Fig. 18) or subjecting them to an immune challenge (lipopolysaccharide injection, Fig. 19).

Fig 17. During the molt, king penguins renew their entire plumage (left panel) and their beak spot on each side of the beak (middle panel). The old keratin- based beak spots are shed (right panel). Reproduced from Schull et al. 2018[147] ***Ecology & Evolution (2018) 8: 1084-1095***

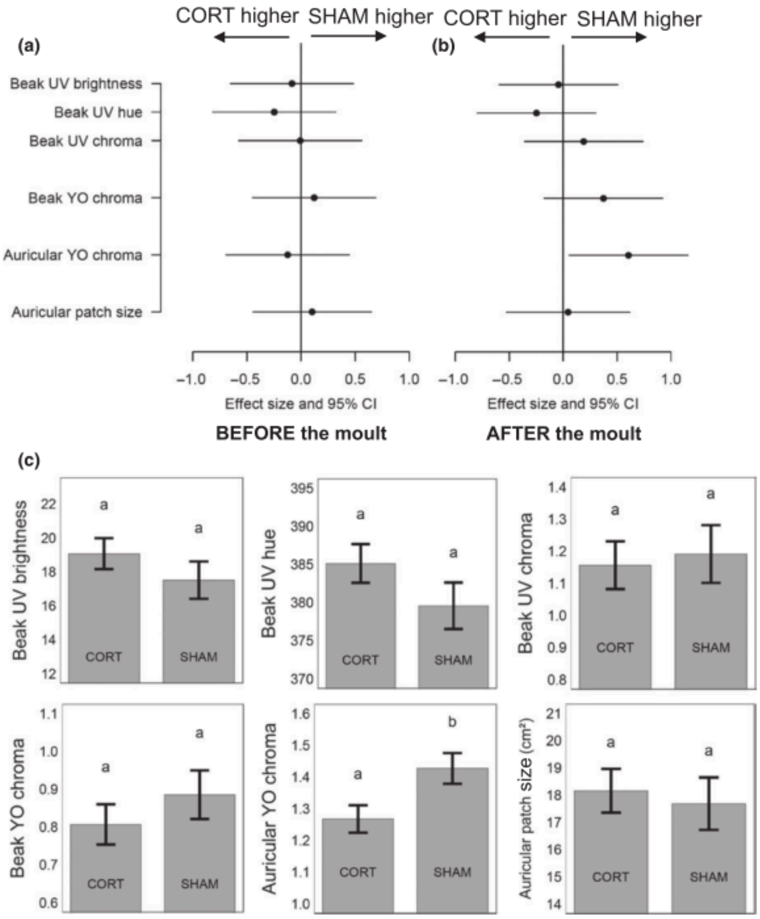


Fig 18. Pre- (panel a) and post- (panel b) molt comparison of beak and auricular patch color variables (controlled for body condition at the beginning of the molt), and auricular patch surface (controlled for structural size and body condition) in king penguins (Aptenodytes patagonicus) treated at molt initiation with a corticosterone (CORT) or sham implant. Panel c represents marginal means (±SE) of color variables measured after the molt. ***Ecology & Evolution (2018) 8: 1084-1095***

Our results revealed the existence of both condition dependent and condition-independent aspects of ornamentation related to stress in adult penguins. For instance, birds subjected to physiological stress (increased glucocorticoids) molted auricular feather patches that had lower yellow-orange chroma than sham-treated birds (Fig. 18), suggesting less deposition of pigments in those structures. Similarly, subjecting birds to an immune challenge led to a decreased in the purity of the yellow-orange auricular feathers (low chroma) also suggesting a re-allocation of pigments to immune functions (Fig. 19). Interestingly, the immune challenge also appeared to affect beak coloration (ultraviolet chroma) highlighting a cost in the production of this structural component as well (Fig. 19).

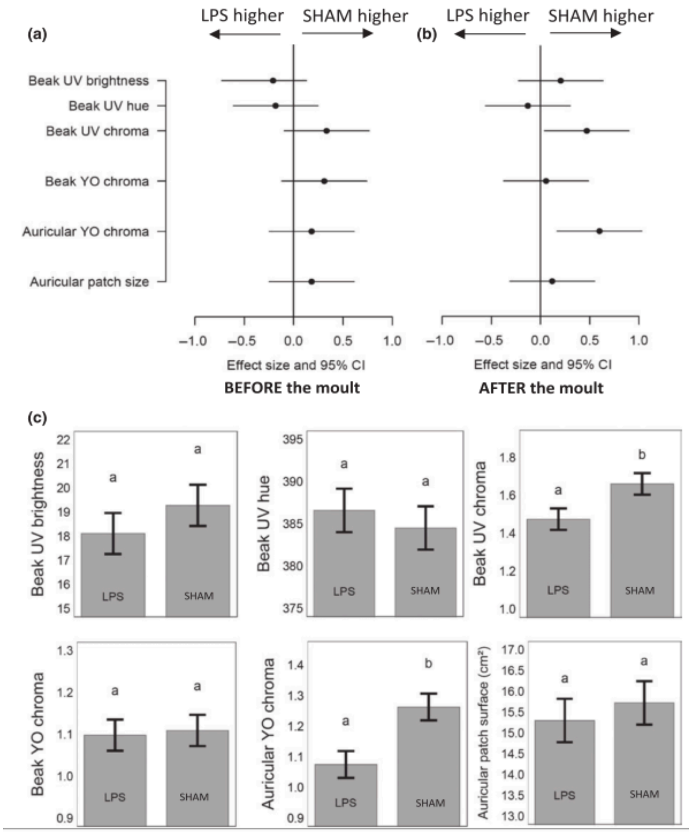


Fig 19. Pre- (panel a) and post- (panel b) molt comparison of beak and auricular patch color variables (controlled for body condition at the beginning of the molt), and auricular patch surface (controlled for structural size and body condition) for king penguins (Aptenodytes patagonicus) treated at molt initiation with lipopolysaccharide (LPS) or physiological serum (sham). Panel c represents marginal means (±SE) of color variables measured after the molt. ***Ecology & Evolution (2018) 8: 1084-1095***

In contrast, other aspects of ornamentation appeared not to react to our treatments, and were highly correlated before and after the molt[147]. This was for instance the case for the surface of bird auricular patches and beak ultraviolet hue (the position of the UV peak), suggesting that these aspects of ornamentation may be genetically constrained, or alternatively, enforced by social mediation (i.e. ornaments should mirror social status and be constantly assessed during competitive interactions).

The above research on social ornamentation is an on-going project, which I started together with collaborators Pierre Bize (University of Aberdeen), Jean-Patrice Robin (IPHC, CNRS) and F Stephen Dobson (Auburn University) in 2012. It has so far spanned 8 field seasons (including the current one), during which I participated in the training and supervision of 8 overwintering field assistants (S Pardonnet 2012, L Durand 2013, E Lefol 2014, H Saadaoui 2015, E Voisin 2016, D Michaux 2017, C Gerard 2018, S Avril 2019). Apart from an initial exploratory study that I led on the relationships between ornamentation and individual physiology[144], the work presented above has constituted the bulk of a thesis defended by my first PhD student Quentin Schull[143] (2013-2016), co-supervised with Jean-Patrice Robin and Pierre Bize. As a collaborative team, we are now continuing to expand on the above questions with another PhD student (T Hammer) just starting her thesis for the period 2018-2021 on the impact of social and environmental pressures on king penguin quality and fitness.

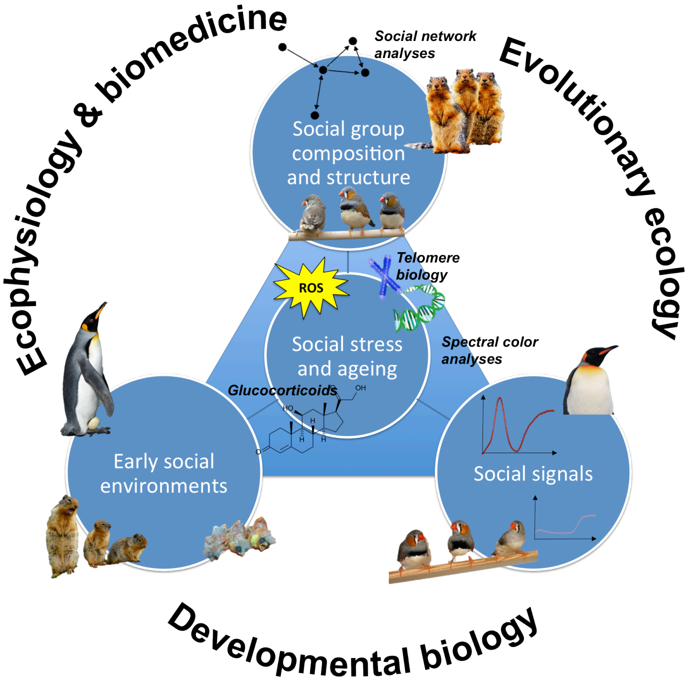
Research activities

Current and future research projects

I. Overall rationale

Environmental variation in social contexts may influence individual stress through changes early in life or at any later stage. Rearing conditions, social competition or social support either early or later in life, might influence individual stress and how stress "get's under the skin" in group-living individuals. In turn social stress might have pronounced effects on individual health, reproduction and survival, through its effects on vital organismal processes such as the management of energy stores, immunity, oxidative stress, and cellular senescence. Additionally, the ability to limit/cope with stress and its consequences may be both inherited and under the influence of other extrinsic factors, with varying consequences depending on the individual, and social stressors early in life may lead to adaptive programming of the offspring phenotype, preparing it for future social challenges. Finally, physiological processes including energy trade-offs and individual stress are likely to mediate bi-directional relationships between the social environment and morphological features used as signals in social interactions.

My current research projects aim at uncovering the mechanistic links relating the social environment to individual phenotype both in the young organism and adulthood by addressing the following questions: **(a)** Is social stress a major cause of oxidative stress in group-living vertebrates? **(b)** Does social stress increase telomere attrition rates and cellular ageing? **(c)** Is individual's susceptibility and ability to cope with stress heritable? **(d)** How do genetics and early life experience shape individual stress and phenotypes later in life? **(e)** Does social stress conditions affect ageing early in life? **(f)** Do socially stressed parents adaptively program offspring phenotype to face future social challenges? **(g)** Does social support alleviate the effects of social stress, oxidative stress and cellular senescence and ageing? **(h)** Do social interactions and social stress constrain, or are they mediated by, social signal evolution?



In an attempt to shed light on some of those questions, I have chosen to use a somewhat comparative approach keeping my focus on several colonial species of mammals and birds. The objective is not to provide comparative phylogenetic analyses, but rather to make use of the existing variation in social environments in various colonial vertebrates, to test whether selection has generated similar responses. In addition to the Columbian ground squirrel (mammal) and king penguin (bird) models presented above, I have also started experimental work on colonial zebra finches (*Taeniopygia guttata*) in controlled laboratory conditions.

II. Unravelling the effects of social environments on individual stress, health and ageing

As presented above, my previous work in Columbian ground squirrels highlights the importance of social kin for breeding females, allowing them to increase both their energy allocation[38] to reproduction and reproductive success[3,38,113]. Thus kin individual likely acts as a social buffer against aggressive conspecifics[107], which may have marked consequences on individual stress. To investigate whether kin presence is an important determinant of female stress (glucocorticoid hormones, oxidative stress) during reproduction with potential consequences on ageing (telomere attrition rates), the present project uses a social network (SN) approach. SN analysis is used to identify patterns of social interactions (including how they change over time) allowing insights into the key components of social relationships. In a variety of species, studies have linked social centrality (regardless of the relatedness between group members) to aspects of individual fitness[148-151]. SNs model the individuals of a social group as nodes in a social network diagram and their social interactions as "edges" (lines that connect nodes). SNs include information on the directionality, frequency, intensity, and order in which social interactions take place. From this, a social web including all relationships (unrelated, close and distant kinship) around individuals, with information on identity and frequency of contacts and the nature of the ties that bind them can be constructed[152]. Although the application of SN to physiological/health investigations has been somewhat limited, recent work has used network analyses to explain patterns of obesity[153,154], depression[155] and smoking probability[156] in humans, revealing strong effects of social links in the spread of epidemics, and highlighting the interdependency of health status in socially connected networks[157]. Recently, studies from the biomedical literature have highlighted the use of SN analyses to study telomere dynamics in humans[158], and experimental manipulations of GC in birds have revealed effects on the structure of SNs[46]. Thus SNs appear as promising and powerful tools for investigating the social mechanisms linking sociality, stress and ageing in group-living vertebrates.

In my current research project, the MamTag project, both all-occurrence behavioural observations[159] and small custom-made spatial proximity detection collars are used to establish SNs based on social contacts during reproduction. Behavioural observations allow building separate directed SNs based on aggressive and amicable behaviours (as we have previously done in this species[107]), whereas contact collars allow measuring individual associations continuously over prolonged periods (the entire active season) and obtaining more complete social networks, including the component of under-ground behaviour not available to the observer (Fig. 20).

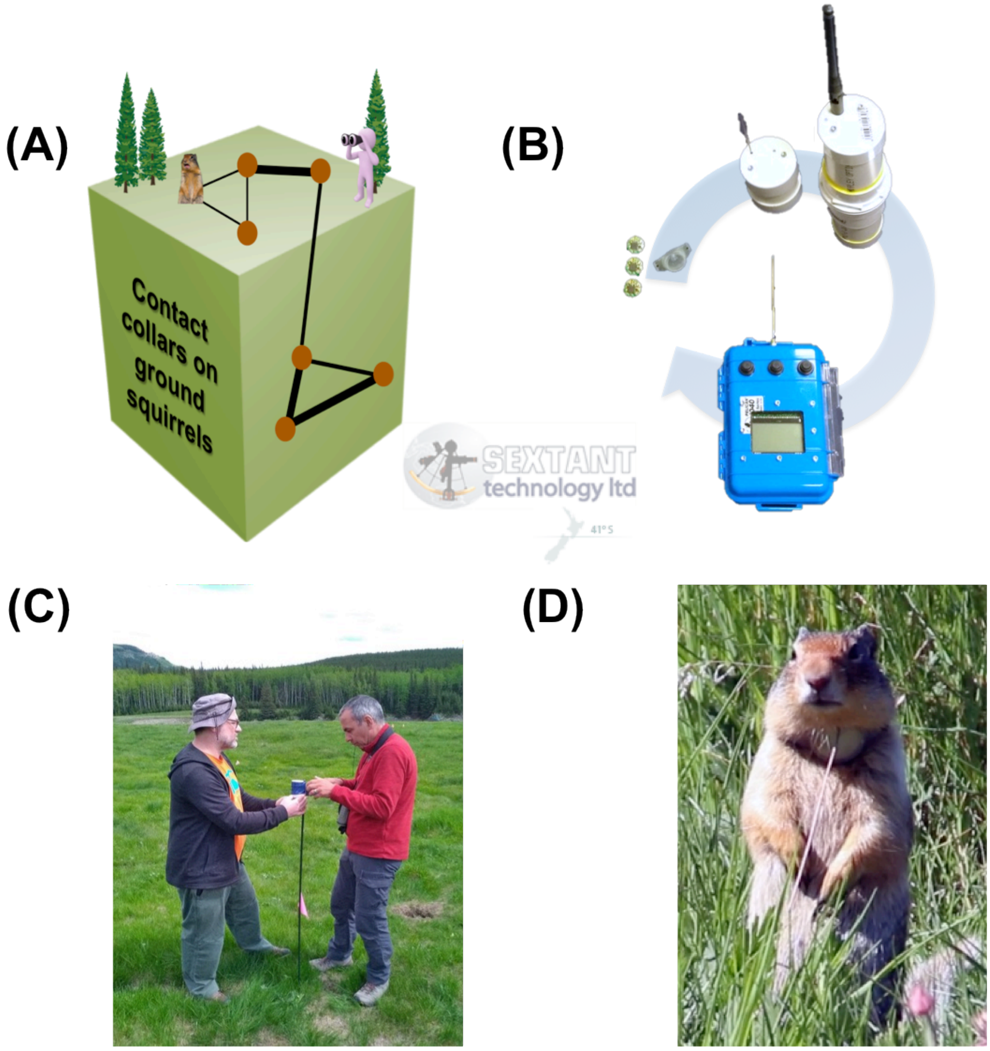


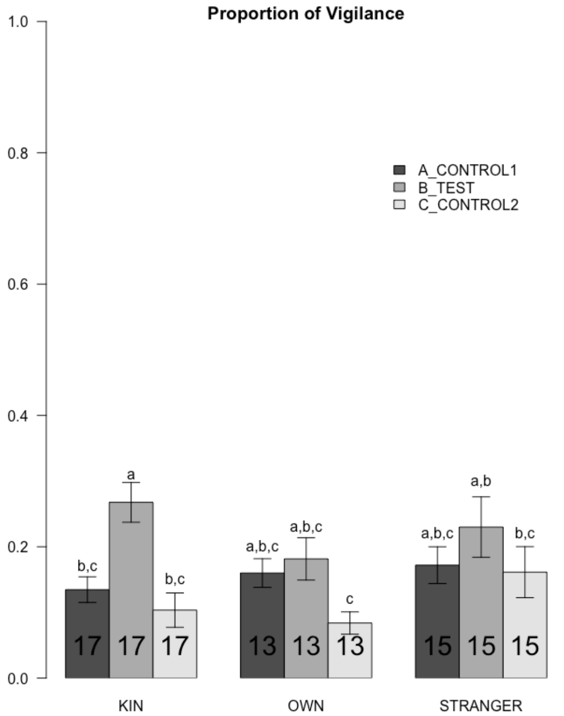
Fig 20. The MamTag system is developed by a private engineering company based in New-Zeland (Sextant technology Ltd.). It is specifically designed and tailored for Columbian ground squirrels, and allows (A) to track inter-individual contacts both above and below ground using radiofrequency contact collars. (B) The system uses 4 different components (clockwise): *i)* contact loggers coupled with accelerometers and magnetometers that are placed on a collar around the animal's neck and record social contacts and body acceleration; *ii*) short- and *iii*) long-range beacon antennas which function is to both continuously synchronize all deployed collars to the GPS date stamp and to record and relay information about collar location, battery and memory status; and finally *iv*) a portable remote allowing to start/stop the system, to manually trigger collar synchronisation, and to locate individual collars in the field. (C) Short-range beacons are set approximately 1.5m off the ground and record the occurrence of collars within a 10m radius. (D) Ground squirrels appear to habituate to the collars within a few hours of fitting, i.e. normal behavioural activities are resumed (foraging, territorial behaviour, grooming, alarm calling, etc.).

The MamTag project relies on combining the continuous behavioural tracking of individuals *via* daily observations and the use of contact collars, in conjunction with experimental designs aimed at manipulating perception of the social environment. For instance, social cues are manipulated by simulating an invasion of unrelated females from neighbouring colonies onto territories of breeding females using odour-based cues (scent-marking) known to be an important mechanism of social (including kin) recognition and monitoring in ground squirrels[160–162]. Polymer cubes are used to collect scent from the scent glands of unfamiliar females, in order to simulate the invasive presence of foreign females and stimulate a response by resident females (Fig. 21). Cubes are deployed for a week during lactation for females to habituate to their presence before scents are collected. The scent of a kin or unfamiliar individual is then acutely exposed to resident lactating females (deposited around their nest burrow) to simulate a territorial invasion. The number of unrelated scents that are presented can vary, allowing identifying relevant thresholds where the presence of unfamiliar individuals may be considered an important threat. Scent cubes are changed daily from a stock kept in the fridge in airtight containers to ensure the scent remains fresh.

Fig 21. Scent collection in the Columbian ground squirrels. Female territorial scents are collected by rubbing an odourless polymer cube against the oral scent glands (squirrel's oral angles) of the animal. A clear greasy streak is left on the cube and a characteristic odour confirms that the cube is marked.

A 'control group' of females is provided with a cube bearing their own scent mark. If kin are an important buffer to social stress, then an increase in female stress levels should occur in stranger vs. kin or self-odour groups, which can be monitored through increased glucocorticoid levels both in plasma and in faeces (breakdown glucocorticoid products). In addition, females having received unfamiliar scents are expected to spend more time in vigilance behaviour and/or exploring territorial boundaries and smelling cubes during the test. This is expected to lead to fewer contact rates between females and a modification in the structure of the social network. Down stream consequences of social stress on individual physiology are expected to occur both on individual oxidative stress, possibly directly due to glucocorticoid effects on oxidative stress[96,163] or indirectly via modulations of animal metabolism, and ageing processes such as telomere attrition rates known to be highly susceptible to oxidative stress[164].

In 2017 (repeated in 2018 but not yet analyzed), we launched a first field campaign to test the effects of odor cubes on female vigilance behavior. We deployed cubes in the morning before females got up from their burrows, and recorded behavior for 30 minutes. Surprisingly, females increased the proportion of vigilance in their behavioral time budget when exposed to the scent of a female kin, but not to the scent of a stranger from a different population (Fig. 22). One possible explanation resides in the fact that females might be more concerned about familiar individuals in their immediate environment – and our next step will be to test if females show the same behavioral response when exposed to non-kin individuals from the same population (familiar non-kin individuals).



	propVIG		
	B	*CI*	*p*
Fixed Parts			
(Intercept)	0.13	0.08 – 0.19	<.001
GROUPOWN	0.03	-0.06 – 0.11	.561
GROUPSTRANGER	0.04	-0.04 – 0.12	.373
TREATMENTB_TEST	0.13	0.06 – 0.20	<.001
TREATMENTC_CONTROL2	-0.03	-0.10 – 0.04	.378
GROUPOWN:TREATMENTB_TEST	-0.11	-0.22 – -0.01	.040
GROUPSTRANGER:TREATMENTB_TEST	-0.07	-0.18 – 0.03	.149
GROUPOWN:TREATMENTC_CONTROL2	-0.04	-0.15 – 0.06	.403
GROUPSTRANGER:TREATMENTC_CONTROL2	0.02	-0.08 – 0.12	.691
Random Parts			
σ^2		0.011	
$\tau_{00, ID}$		0.003	
N_{ID}		45	
ICC_{ID}		0.240	
Observations		135	
R^2 / Ω_0^2		.520 / .485	

Fig 22. Effect of the exposure of kin, stranger or own-scents on the vigilance behaviour of lactating female Columbian ground squirrels. Values not sharing the same letters are significantly different for P < 0.05. The cubes were exposed in 3 time periods: Control 1 (cubes with no scent), test (cubest with scent) and control 2 (cubes with no scent following scent exposure). Statistics were obtained from a Linear Mixed Model with group (kin, own, stranger), treatment (control1, test, control2), and their interaction specified as independent variables – and female ID specified as a random factor. Effect sizes for fixed and random parts are given in the table.

Combining experimental designs where social cues are manipulated, together with an ecophysiological approach where individual stress (in the broad sense) is repeatedly assessed, and with a behavioral approach where individual social behavior is continuously monitored is likely to prove a powerful approach to unraveling the exact role of social kin in regards to buffering social aggressiveness. Manipulating one modality of social communication (odor) is of course somewhat limited, and my future plans of research aim at expanding this to multiple modalities such as by manipulating acoustic cues (e.g. via playbacks), or visual, acoustic and olfactory cues by temporarily removing individuals altogether. With this said, teasing apart the respective contribution of those different modalities and their importance in social communication is likely to prove a challenging task!

This research project is supported by a grant obtained from the Fyssen Foundation, a grant obtained from the University of Strasbourg Institute for Advanced Sciences, and an international collaboration grant obtained from the CNRS. The project involves a post-doctoral fellow that I will supervise (S Sosa 2018-20), an expert engineer in electronics (Dominique Filippi, Sextant Technology Ltd, New Zealand), and long-term collaborators F Stephen Dobson (Auburn University), Rudy Boonstra (University of Toronto), Peter Neuhaus (University of Calgary), François Criscuolo (IPHC CNRS).

II. Unravelling the early effects of stress on individual social phenotype

Understanding the evolution of group living requires defining the inter-generational effects of sociality, *i.e.* gathering information on how the social environment early in life shapes individual phenotype later in life. Indeed, a bad start in life may be related to long-term changes in adult morphology, physiology, fecundity and lifespan[165–167]. For instance, human epidemiological studies noticed that populations exhibiting catch-up growth after a bad start in life also suffered adverse long-term outcomes in terms of cardiovascular diseases, blood pressure or type 2 diabetes[168–170]. Although cellular ageing occurs throughout lifespan, most of telomere loss takes place during the growth period, early in life[171]. In birds for instance, recent studies have shown that early (*in ovo*) exposure to high glucocorticoid levels increase oxidative stress and lead to higher telomere loss when measured later in life[172]. In this regard, social stress early in life may have long term effects via precocious ageing, and social animals may have developed specific adaptations to cope with it. Further, the ability to limit and cope with ROS production[173,174] and/or telomere length[175,176] may be partly heritable, influencing the balance between oxidative stress and telomere loss differently depending on the individual. Finally, whereas most studies investigating early life social effects on offspring phenotype have focused on detrimental consequences later in life, few studies have considered whether early social adversity may allow the adaptive programming of offspring phenotype to face social competition, such as by promoting rapid offspring growth[45] (see[46,177] for positive effects of early exposure to stress hormones on offspring social learning or independence from parents). Thus, there is a need to better understand how social environments influence life stress during critical developmental stages of early life, what the adaptive vs. detrimental consequences of such variation may be, and given variation in environmental and genetic background, whether some individuals may have a better start than others.

King penguins are an ideal model system for addressing this question. Spatial heterogeneity in breeding territories is associated with marked variation in behavioural, physiological, and fitness characteristics of breeding birds. Central breeding territories offer increased protection from detrimental weather conditions and high predation rates on the outskirts, and should be of higher quality. However birds in central territories also have to contend with numerous aggressive neighbours, and thus the benefits *vs*. costs of breeding centrally are unclear. As mentioned above, we recently uncovered marked differences in the GC levels of birds breeding on central *vs*. peripheral colony territories[15]. Birds on central territories had higher GC levels, which were significantly explained by social characteristics of their environment, namely higher conspecific density and aggression[38,39], with likely consequences on their energy expenditure during fasting[82]. However, it remains unclear whether high GC levels are a cause for, or a consequence of, breeding on central territories. In addition, we have found higher GC levels to enhance chick survival in specific environmental circumstances, which might be related to being reared in different social conditions[89]. The present project addresses those questions and aims as disentangling the effects of social environment on individual stress and ageing *vs*. effects of individual stress on social behaviour.

Effects of the social environment on the ontogeny of stress: Together with collaborators from our 119 IPEV French Polar Program, we used a cross-fostering design to study the ontogeny of the stress response in king penguin chicks raised in varying colonial conditions. We swapped freshly laid eggs between 120 penguin pairs breeding at high or low social densities at the start of reproduction. Parent physiological condition was assessed (GC and oxidative stress levels, telomere length, body condition), as well as chick condition (same parameters) and growth (body size, mass) throughout their yearly development (days 10, 35, 105 and a year later at fledging). In addition, social aggressiveness in high and low densities was measured by behavioural scan sampling throughout the breeding season including studied individuals and their surrounding neighbours. This design allows relating chick parameters to the stress condition of biological and foster parents to understand how social *vs.* genetic backgrounds affect the ontogeny of stress in young individuals, and its consequences on ageing rates. This data is currently being analyzed: samples remain to be processed in the lab for GCs and telomere length (oxidative stress done) and statistical analyses of results to be done.

Effects of individual physiology on social competitiveness: adaptive vs. detrimental effects of high glucocorticoids in early life: To determine adaptive vs. detrimental effects of early stress on individual phenotype, this research aims at experimentally manipulating glucocorticoid concentrations in young king penguin chicks. Circulating glucocorticoid levels in overwintering chicks are manipulated to investigate the effects of high glucocorticoid levels on bird competitiveness and spatial position in the colony. Two groups of increased (N = 25) and SHAM (N = 25) chicks are created. Sample size is chosen based on survival rates of early-born penguin chicks (65%), to insure that a minimum of 10-15 chicks in each group survives the winter[89]. Chicks are implanted with subcutaneous corticosterone (CORT) or placebo implants (Innovative Research of America, Sarasota, FL, USA) within natural physiological range as routinely done in penguins[178,179], including king penguins[143]. Implants are chosen to diffuse a concentration of approximately 12 $ng.mL^{-1}$, which corresponds to an increase of 50% in baseline CORT concentrations relative to that of early chicks shortly after birth[89], and increase of 40% relative to that of chicks captured just before moult onset, after the winter period[180]. Thus, circulating CORT concentrations will present a substantial increase relative to normal circulating baseline levels, while remaining well within biological significance (maximum CORT levels observed in chicks following an acute stress are > 100 $ng.mL^{-1}$)[180]. Both CORT and SHAM chicks will be monitored over the winter period and their behavioural time budget (aggressiveness, sleeping, comfort, etc.) will be established using scan-sampling[159]. Activity loggers (Actical ® Phillips, Respironics)[82] are used to assess the overall physical activity of CORT and SHAM chicks. In addition, the social position of CORT and SHAM chicks relative to the edge of the 'crèche' (both in terms of number of chicks separating it from the edge, and in terms of distance) is measured twice a day (morning and afternoon). This allows investigating chick movement into the 'crèche' and its dynamics over time. If higher CORT underlies chick competitiveness, high CORT-chicks should be more aggressive[181] and secure more central position in crèches affording them protection against predators and inclement weather conditions[182,75]. We will then monitor chick growth patterns, oxidative stress, and telomere length as above, sampling blood at 10-days, 35, 100 and 130 days post-hatching.

III. Unravelling the feedbacks between social signals and stress

When addressing the relationships between physiology and signals, researchers often opt for a unidirectional view where physiological processes determine the level of signalling. Yet, physiological processes are highly dynamic traits that are known to quickly respond to environmental changes, allowing organisms to adjust their behaviour and metabolism to the new prevailing environmental conditions. Because social signals are expected to elicit a behavioural response from conspecifics that may in turn affect individual physiology, the directionality of the relationship between social signals and individual physiology is unclear.

The aim of this on-going research project is to test the physiological costs of wearing a social signal in breeding penguins, which is an ideal study system due the fierce competition among breeders for securing a central territory within the colony. As mentioned earlier, breeders bearing larger auricular patches have been reported to behave more aggressively and to be more likely to secure central territories in the colony[48,87]. Our recent results also show accumulating evidence of tight relationship between auricular patch size and physiological status[143]. In the present project, my collaborators and I have been using a protocol where we experimentally manipulate 3 groups of penguins: we either experimentally reduce the auricular patch size of breeding males (N = 20) or females (N = 20) from different breeding pairs, or leave auricular patch size untouched (i.e. N = 20 control males and 20 control females).

We reduce auricular patch size by ca. 20% by applying a black non-toxic dye along the edges of the orange plumage patch (Fig. 22), and also apply the dye to an equivalent area on the heads of control breeders, but on black plumage surrounding the auricular patch, thus actively controlling for any unknown effects of the marker.

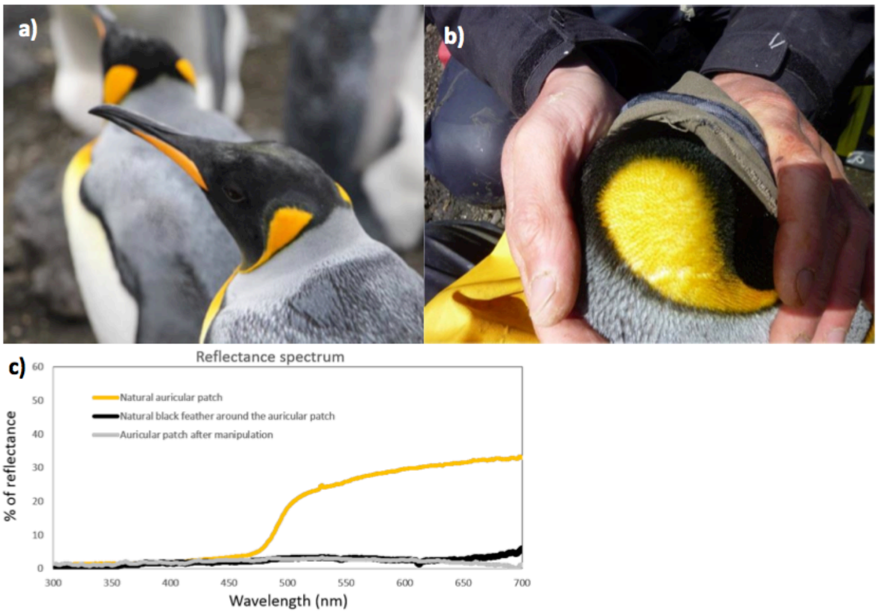


Fig 22. Experimental manipulation of auricular patch size in (a) naturally breeding king penguins (b) using black hair dye. The reflectance spectrum presented in (c) shows the efficiency of the treatment in removing the yellow-orange colour that is then no different from the natural black colour of the feathers surrounding the ear patch. Figure taken from Schull 2016[143].

Our protocol aims at treating males and females at a similar stage of incubation (3 days after the start of their first incubation shift), and monitoring them from a distance in the days preceding and following the experimental manipulation of their patch size to determine their behavioural time budget during incubation using scan sampling[159]. In addition, a first blood sample is collected on the day of the auricular patch size manipulation and a second sample is collected 10 days later to determine both total plasma glucocorticoid levels and corticosteroid-binding globulin[96], which will allow assessing the fraction of free (biologically active[96]) glucocorticoids. In between the two blood sampling, birds are equipped with an activity logger (Actical ® Phillips, Respironics) to record their overall physical activity, and with an external cardio-frequency meters (Polar ® model RS800, Polar Electro Oy, Kemple, Finland) to record their heart rate[82,75]. Together with the follow-up of focal birds, two to four randomly chosen neighbours are monitored for behavioural time budget and changes in blood parameters.

This experimental approach allows (i) testing for retrograde effects on the behaviour and physiology of a social badge status as well as (ii) exploring effects of badge status on the behaviour and physiology of neighbours. If the size of the ear patch interacts with condition, we predict that in comparison to before the experimental treatment, birds with reduced ear patches should show increased aggression and decreased measures of physiological condition, whereas control birds should not. During these experiments, we also monitor colour traits, particularly the UV reflectance of the beak spot, which has been shown to dynamically signal bird condition at other times of the year[143,145,183,184].

IV. Social stress buffering through self-medication: an experimental project in zebra finches

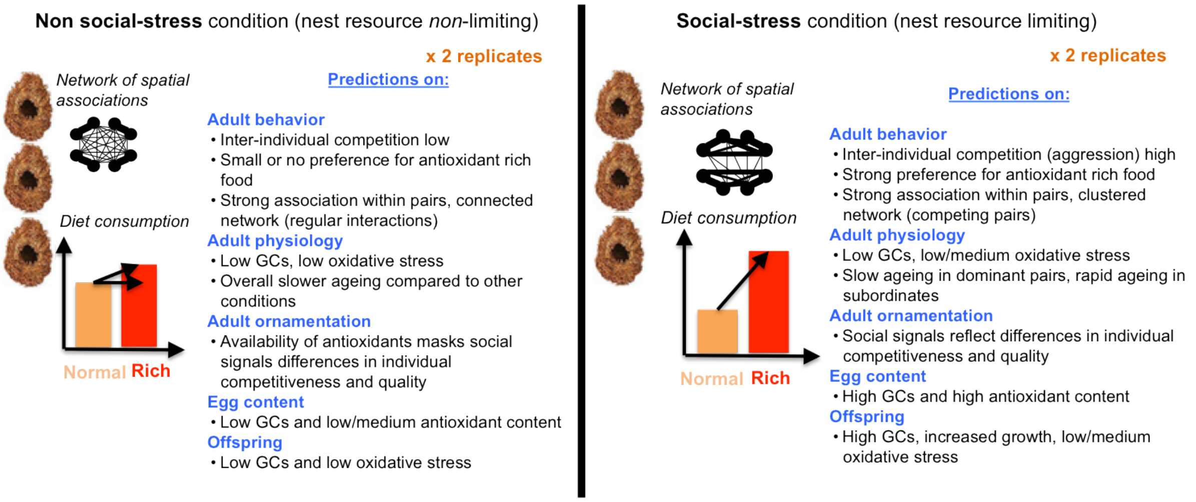
Our understanding of the consequences of social stress and its deterministic effects on the development of the young organism would strongly benefit from knowledge on species that have naturally evolved to cope with social stressors and where robust experiments allow drawing causal inferences. In particular, few studies have investigated adaptive modulations of offspring phenotype to cope with social competition later in life (for an example in mammals, see[45]), or adult self-medication facing social stress. Here, using the colonial zebra finch as a model, we propose an experimental project on social stress with joint examination of the consequences of social competition on adult (including social ornamentation) and offspring phenotype – and test the capacity of adults to self-buffer potentially detrimental effects of social stress.

Zebra finches | An experimental model for studying social stress

Zebra finches represent a model of choice for implementing an experimental design on social stress and maternal effects since much background work related to these questions has been done over the past decades using Zebra finches. In those social birds (groups of around 50 individuals during breeding season), bidirectional effects of the social environment on individual stress physiology and individual stress physiology on social behavior are known. Zebra finches are highly sensitive to their social conspecifics and pair disruption is for instance known to increase individual stress[185,186], with trans-generational consequences on offspring: increased female offspring growth, decreased offspring stress sensitivity (glucocorticoid response to stress) and delayed male offspring plumage development[187]. In addition, recent studies indicate that the future social behavior of young individuals is affected by early developmental stress, with early post-hatching exposure to GCs promoting early independence from parents in social networks[46], and improving performance in foraging tasks[188] (see also[189,190]). Although pre-hatching maternal effects of yolk content modulation on future offspring phenotype have been widely studied[191], alterations of yolk GC content in response to social stress are inconclusive[187], and the link between maternal stress and levels of yolk GC remains mostly untested[191] (but see[187]). Further, studies investigating adaptive modulations of offspring phenotype to cope with social competition later in life are lacking (for an example in mammals, see[45]). Of interest are the findings that variation in the dietary intake of antioxidants affects maternal deposition of antioxidants in egg yolk[192], important for embryonic growth, hatching success and chick development and survival[193]. Because increased stress hormone levels may lead to a disruption of oxidative balance[163,172], one important question is whether maternal investments in egg yolk under social stress are conditioned by the availability of dietary antioxidants. Given the above, this model system appears to be ripe for research into the consequences of (non-pair) social competition on adult stress, oxidative physiology and telomere attrition rates, and trans-generational consequences on offspring phenotype (growth rates, oxidative stress, telomere attrition rates, social behavior).

With this in mind, the objectives of this project are to unravel the mechanistic and evolutionary consequences of social stress using a controlled experimental paradigm in highly social zebra finches. Specifically, we will experimentally test the following hypotheses: (1) Perceived (psychosocial) stress from the social environment influences oxidative stress via modulation of stress hormones (glucocorticoids, GC) accelerating organism ageing (measured via the loss of telomeres)[164,194]; (2) The pro-ageing consequences of social stress may be actively buffered by selective foraging on antioxidant-rich[195–197] resources, a form of self-medication[195]; and (3) socially stressed mothers adaptively program offspring phenotype to cope with increased social competition for resources later in life by depositing different levels of hormones/antioxidants in yolk[193,192,198]. To address these questions, we are creating 1 experimental and 1 control group of breeding pairs of ZFs (equilibrated male/female sex ratio), each housed in separate aviaries (1 m^3); studied in 2 replicates (see Fig. 23). Birds of known (and similar) breeding age, to avoid any confounding effect of age and breeding experience on stress physiology, are monitored from pair bonding to the independence of the chicks produced. First, birds are held at a similar social density for 10 days, before increasing social density in one group (social stress condition) and decreasing density in the other (non-social stress condition). In the social stress condition, social density is twice that of the control group. More importantly, the availability of nest sites is similar in the two conditions. Thus, we aim to create a paradigm where social competition for limiting nest site resources should occur.

Each aviary is equipped with 2 sources of different seeds that vary in their antioxidant content: either yellow ("antioxidant poor") or red millet ("antioxidant rich"). Preliminary measures of total antioxidant content conducted in 2017 in collaboration with the *CAMBA* chemistry group of the IPHC shows that red millet has twice the antioxidant content of yellow millet. Bird behaviour is analysed via continuous camera recording to determine networks of spatial associations and aggressive behaviour, and individual time budget spent at the nest (and nests visits by others) and at given foraging sources. Adults are measured for mass (nearest g), structural size (wing, tarsus and bill length, nearest mm) and colour ornaments (see III. Unravelling the feedbacks between social signals and stress below) using an Ocean Optics JAZ Spectrophotometer: (1) before changes in social density, (2) after changes in social density at offspring hatching, and (3) at offspring independence. A blood sample (150 µL) is be taken each time to determine antioxidants and oxidative stress markers in plasma, as well as telomere length (only for the first and last sample) and microsatellite marker (pedigree analysis) from red blood cells nucleated in birds. Measures of doubly-labelled water allowing to estimate energy expenditure are done before and after changes in social density. We will determine glucocorticoid levels in feathers, an integrative measure of the stress during the entire period of feather growth (ca. 3 weeks)[199], the same feather being collected before and after each experimental trial. Clutch size and individual egg mass and volume is determined in each clutch (twice to test for potential brood reduction in stressed groups). One egg per clutch is sacrificed to measure glucocorticoid and antioxidant content. We aim to study the development of the offspring produced in each aviary. ZFs are monogamous and, in the wild, exhibit low levels of extra pair paternity[200]. However, it might be different in captivity, especially in a context of social stress. Thus we will determine the paternity of all chicks by genetic analyses. Birds will be monitored until the independence of the offspring (ca. 50 days[201]). Chicks are monitored for mass and size growth: measures at day 4, at fledging (day 17-22) and at independence (~day 50). Blood samples and feathers are collected to measure antioxidant, markers of oxidative stress, telomere length, microsatellite and glucocorticoid levels. Predictions are summarized in the figure.



Non social-stress condition (nest resource *non*-limiting)

x 2 replicates

Predictions on:

Adult behavior
- Inter-individual competition low
- Small or no preference for antioxidant rich food
- Strong association within pairs, connected network (regular interactions)

Adult physiology
- Low GCs, low oxidative stress
- Overall slower ageing compared to other conditions

Adult ornamentation
- Availability of antioxidants masks social signals differences in individual competitiveness and quality

Egg content
- Low GCs and low/medium antioxidant content

Offspring
- Low GCs and low oxidative stress

Social-stress condition (nest resource limiting)

x 2 replicates

Predictions on:

Adult behavior
- Inter-individual competition (aggression) high
- Strong preference for antioxidant rich food
- Strong association within pairs, clustered network (competing pairs)

Adult physiology
- Low GCs, low/medium oxidative stress
- Slow ageing in dominant pairs, rapid ageing in subordinates

Adult ornamentation
- Social signals reflect differences in individual competitiveness and quality

Egg content
- High GCs and high antioxidant content

Offspring
- High GCs, increased growth, low/medium oxidative stress

Fig 23. Experimental paradigm for testing the consequences of social competition on stress in zebra finches with joint attention to adult and offspring physiology, ornamentation and behaviour.

The above research is just starting – and is led in collaboration with Josefa Bleu (IPHC, University of Strasbourg). Together, we are co-supervising one PhD candidate (Martin Quque 2017-20) and one Master student (Charly Ferreira 2019) on this topic. Further, we are just starting an international collaboration led by Dr. Neeltje Boogert (Exeter University) and involving Dr. Damien Farine (Max Planck) directly related to this research, and which aims at testing the consequences of social instability on the physiology and senescence of those highly social birds.

Concluding remarks

As humans, the idea that the social environment is a strong modulator of our health and well-being seems like a blatant fact of life. We live in a stressful world and we have all experienced positive (eustress) and negative (distress) effects of interpersonal relationships with our bosses, employees, colleagues, spouses, parents, children and siblings. Social stresses and how we handle them are some of the most important aspects of our lives, and have major influences on our health status and lifespans as adults, so that both the quality and length of our life are impacted[158,24,25,202,203]. Even more so, social stresses may have in utero repercussions shaping the development and future life of our children (e.g. mood disorder, depression, metabolic syndromes), due to trans-generational consequences through maternal or epigenetic effects[47,202,204–207].

What we don't realize – or often think about – is that social stress is a property of our biology, and it's something that we share with species that, like us, live and interact in a social environment. This means other primates, to be sure, but other mammals and birds as well. In fact, it is well known that the hormonal mechanisms that are part of our responses to stress are widely shared among vertebrates. Extending beyond purely correlative or epidemiological studies in humans, our understanding of the consequences of social stress and its deterministic effects on the development of the young organism will strongly benefit from knowledge on species that have naturally evolved to cope with social stressors and where robust experiments allow drawing causal inferences can be done. The work I have presented here is hopefully, a small step in this direction. Moving further afield will prove challenging – I believe it will require studying past and present variation in social systems and how such variation may have coevolved not only with specific life history traits and life cycles, but more generally with all aspects of animal phenotypes, including physiological stress and ageing.

In the foreword to Dawkin's first edition of *The Selfish Gene* (1976), Robert L. Trivers wrote:

"Darwinian social theory gives us a glimpse of an understanding symmetry and logic in social relationships which, when more fully comprehended by ourselves, should revitalize our political understanding and provide the intellectual support for a science and medicine of psychology. In the process it should also give us a deeper understanding of the many roots of our suffering."

We still have a long way to go.

Curriculum vitae

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Professional trajectory

2017-	Researcher (CRCN CNRS)	Institut Pluridisciplinaire Hubert Curien (UMR 7178 CNRS)
2014-16	Associate researcher (CDD)	Institut Pluridisciplinaire Hubert Curien (UMR 7178 CNRS)
2012-14	AXA Post-Doctoral Fellow	Centre d'Ecologie Fonctionnelle et Evolutive (UMR CNRS)
2011-12	FYSSEN Post-Doc. Fellow	Université de Lausanne
2010-11	Teaching assistant	Faculty of Psychology, Université de Strasbourg
2008-11	PhD candidate	Institut Pluridisciplinaire Hubert Curien (UMR 7178 CNRS)

Distinctions/bonus

2017	Bonus: Prime d'encadrement doctoral et de recherche from CNRS
2012	Speaker for PhD Graduation Ceremony of the University of Strasbourg
2012	PhD dissertation award by the *Fondation Université de Strasbourg*
2010	PhD student award. Best oral contribution. Graduate school day, University of Strasbourg
2010	PhD student award. Highly commended poster. 1st World Seabird Conference

Research contracts

(Acquired either as PI or co-PI on the project)

2018-20	**University of Strasbourg Institute for Advanced Sciences**. Alleviating social stress: effects of social buffers on ageing in wild mammals. 200 000 € (*Co-PI with F. Stephen Dobson*)
2018-19	**The Royal Society. International Exchange Grant.** Reproduction and ageing in times of social turmoil. £ 6 000 (*Co-PI with Neeltje Boogert, University of Exeter*)
2017-18	**Fondation Fyssen.** Effects of the social environment on individual stress and ageing: an approach using social network analyses in Columbian ground squirrels. 33 505 €
2016-18	**CNRS. Projet International de Cooperation Scientifique**. Understanding the oxidative and pro-ageing consequences of social stress in natural populations. 22 000 €
2015-19	**French Polar Institute.** Mediators of individual quality : proximate aspects and fitness consequences ~200 000 € (*Co-PI with Jean-Patrice Robin*)
2012	**AXA Research Fund.** Postdoctoral research grant. Social stress and its oxidative and pro-ageing consequences: an ontogenic and evolutionary approach in birds and mammals. 120 000 €
2011-15	**French Polar Institute**. Ashore living strategies of penguins: physiological adaptations and evolutionary trade-offs ~200 000 € (*Co-PI with Jean-Patrice Robin*)
2011	**Fondation Fyssen.** Mate choice and individual quality in breeding king penguin. 24 600 €

Main research themes

- Studying the bidirectional links between social stimuli and individual phenotypes
- Studying individual life history trajectories in the light of energy constraints
- Studying the role of kin selection in the evolution of philopatry

Scientific output

36 A-rank publications

582 citations, h-index = 14 (google scholar statistics)
28 contributions (15 talks, 12 posters) in national and international conferences
10 invited oral contributions (seminars, workshops, conferences)

Publications
(Full texts available at https://animalbehaviour.wixsite.com/vincentviblanc/publications)

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2. Lemaire BS, Viblanc VA, Jozet-Alves C. Sex-specific lateralization during aggressive interactions in breeding king penguins. *Submitted to Proceedings of the Royal Society B*
1. Stier A, Schull Q, Bize P, Lefol E, Haussmann M, Roussel D, Robin JP, Viblanc VA. Naturally equipped to resist stress? Oxidative stress and mitochondrial responses to acute and chronic stress exposure in breeding king penguins. *Submitted to Journal of Experimental Biology*

Book chapters

- Dobson FS, Viblanc VA. 2018. Fitness. Encyclopedia of Animal Cognition and Behavior, Eds. Vonk J, Shackelford TK. Springer.

Conference proceedings

- Stier A, Schull Q, Viblanc VA, De Margerie E, Zahn S, Handrich Y, De Buffrenil V, Erbrech A, Guerin N, Martrette J-M, Groscolas R, Criscuolo F, Bize P, Robin JP. 2015. How do adults and chicks of king penguins (Aptenodytes patagonicus) face nutritional constraints while breeding or growing? Acta physiologica 214: 87.
- Viblanc VA, Stier A, Reichert SE, Handrich Y, Massemin S, Criscuolo F, Bize P, Robin JP. 2014. Reproduction in the king penguin: constraints imposed by colonial breeding and a long chick-raising period. 26th International Ornithological Congress, Tokyo (Japan). Ornithological Science 13 (Supplement): 447.

Published data sets

- Schull Q, Dobson FS, Stier A, Robin J, Bize P & Viblanc VA (2016) Data from: Beak colour dynamically signals changes in fasting status and parasite loads in king penguins. Dryad Digital Repository doi:10.5061/dryad.5j40q.
- Viblanc VA, Saraux C, Murie JO & Dobson FS (2016) Data from: kin effects on energy allocation in group-living ground squirrels. Dryad Digital Repository doi:10.5061/dryad.50hk0.
- Bordier C, Saraux C, Viblanc VA, Gachot-Neveu H, Beaugey M, Le Maho Y, Le Bohec C (2014): Data from: Inter annual variability of fledgling sex ratio in king penguins. figshare

Conferences

- 3e Colloque d'Ecophysiologie Animale : 2017 (& Symposium Chair)
- Congrès de Physiologie et Biologie Intégrative: 2015
- International Ornithological Congress: 2014
- Journées Scientifiques du CNFRA: 2014, 2015
- University of Toulouse, Laboratory of Evolution and Biodiversity: 2017 (invited)

- University of Toronto, Department of Biological Sciences: 2013 (invited)
- University of Bern, Institute of Ecology & Evolution, Switzerland: 2012 (invited)
- Centre for Functional and Evolutionary Ecology: 2012 (invited)
- International Penguin Conference: 2010, 2013, 2016
- Québec Society for the Biological Study of Behavior: 2012
- Social systems: demographic and genetic issues, Paimpont, France: 2010
- World Seabird Conference: 2010, 2015 (invited & Symposium Chair)
- European Ornithologist Union: 2009, 2011, 2015 (invited)
- Behavior and Ecology Meeting SERL: 2011, 2012, 2015
- French Society for the study of Animal Behavior: 2011
- University of Bern, Adelboden, Use of vertebrate model systems to study social evolution: 2009
- Mammal Research Institute, Białowieża, Poland: 2009 (poster)
- Phillip Island Nature Parks Reseach Station, Australia: 2009 (invited)

Referee activity

- Review Editor for Frontiers in Behavioral and Evolutionary Ecology since 2013
- Reviewing activity on Publons
- Grant proposal: The National Science Centre Poland
- Book chapter: The social life of greylag geese (Cambridge University Press)

Thesis referee/jury member

2018	Referee	2 MSc theses for the Master's program in Ecophysiology and Ethology, University of Strasbourg
2018	Committee member	PhD advisory committee member for Juliette Rabdeau at the Centre d'Etude Biologique de Chizé. PhD project on the impact of anthropogenic activities on the behaviour and life history traits of Montagu's harrier (*Circus pygargus*)
2017	Referee	2 MSc theses for the Master's program in Ecophysiology and Ethology, University of Strasbourg
2016	Jury member	PhD defence of Quentin Schull: Sexual selection, social selection and individual quality: underlying mechanisms and ultimate consequences of ornamentation in a monomorphic species, the king penguin (Aptenodytes patagonicus)
2016	Mentor	Early Career Scientist Workshop. International Penguin Congress, Cape Town, SA
2016	Referee	2 MSc theses for the Master's program in Ecophysiology and Ethology, University of Strasbourg
2015	Jury member	Final exam for Master's program in Ecophysiology and Ethology, University of Strasbourg
2015	Referee	3 MSc theses for the Master's program in Ecophysiology and Ethology, University of Strasbourg
2015	Referee	7 student presentations. 2nd World Seabird Conference, Cape Town, SA
2014	Jury member	Final exam for Master's program. Ecole Sup. Agro-développement international (ISTOM), Cergy
2012	Jury member	Animal Ecophysiology final exam

Teaching appointments

2010-11	Lecturer	Introduction to Ethology	Faculty of psychology, University of Strasbourg

2010-11	Lecturer	Evolution of hominids & anthropology	Faculty of psychology, University of Strasbourg

Main collaborators

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- Alberta Parks
- Alberta Fish & Wildlife
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Supplement 1

Students, fellows and assistants co-advised from 2008 to 2021

Postdoctoral fellows

- *Sebastian Sosa* (2018-20): Social networking in the Columbian ground squirrel: a bio-logging approach linking animal behaviour to individual health and ageing. Currently selecting applicants.
- *Charlotte Récapet* (2016): Social modulation of the tradeoff between offspring number and quality in Columbian ground squirrels.
- *Cristian Pasquaretta* (2016): Social networks of aggression in the Columbian ground squirrel.

PhD students

- *Tracey Hammer* (2018-present): The impact of social and environmental pressures on king penguin quality and fitness. PhD candidate at the University of Strasbourg.
- *Martin Quque* (2017-present): The coevolution of sociality and longevity in animal societies. PhD candidate at the University of Strasbourg
- *Jeffrey D Roth* (2016-present): An experimental approach on costs of parasitism in Columbian ground squirrels. PhD candidate at Auburn University, USA.
- *Quentin Schull* (2013-16): Sexual selection, social selection and individual quality: underlying mechanisms and ultimate consequences of ornamentation in a monomorphic species, the king penguin (Aptenodytes patagonicus). PhD Thesis defended October 2016 at the University of Strasbourg.

MSc and undergraduate

- *Charly Ferreira* (2019): Physiological and behavioural consequences of an experimental social competition paradigm in captive zebra finches. Master candidate at the University of Strasbourg.
- *Thibaut Barra* (2018): Local resource competition, maternal investment, and skewed sex ratios: testing sex allocation models in the Columbian ground squirrel. Master Thesis defended August 2018 at the University of Strasbourg.
- *Thibaut Barra & Nina Cossin-Severin* (2017): Establishment of an accelerometer-based ethogram in king penguins. Master 1 short research project at the University of Strasbourg.
- *Mélanie Crombecque & Marie Pfister* (2017): Discrimination of anti-oxidant rich diets in zebra finches. Master 1 short research project at the University of Strasbourg.
- *Catherine Petel-Langevin* (2017): Modulation of the trade-off between reproductive and somatic allocation in a colonial rodent species, the Columbian ground squirrel. BSc at the Université du Québec à Montréal. Defended April 2017.
- *Iris Prinet* (2016): Variability of nest-defence behaviour over lifespan and fitness consequences in the Alpine swift. Master Thesis defended June 2016 at the University of Paris Saclay.
- *Juliette Rabdeau* (2016): Variability of risk taking behaviour in Columbian ground squirrels: effects of extrinsic and intrinsic factors and fitness consequences. Master Thesis defended June 2016 at the University of Strasbourg.
- *Emeline Billy* (2015): Tactics of energy allocation between somatic and reproductive effort in the Columbian ground squirrels and fitness consequences. Master Thesis defended June 2015 at the University of Strasbourg.
- *Claire Périé* & Maud Marty (2014): Modulation of heart rate responses to live predator encounters in king penguin chicks. Engineer (C Périé) and BSc (M Marty) research project. SupAgro Montpellier (C Périé) and Université Paris Sud (M Marty).
- *Lucile Bovet & Laure Cattin* (2012): Sexual selection in a monomorphic species: do color ornaments reflect physiological quality in a show-breeding seabird, the king penguin? Master 1 short research project at the University of Lausanne.
- *Andrew Smith* (2011): Heart rate responses to anthropogenic disturbances in breeding king penguin. Master Thesis defended June 2011 at the University of Strasbourg.
- *Victorien Valette* (2010): Heart rate as an indicator of sensitivity to social stress in king penguin. Master Thesis defended June 2006 at the University of Strasbourg.

Field assistants

Penguins

- *Sandra Avril* (2019)
- *Caroline Gérard* (2018)
- *Denis Michaux* (2017)
- *Emanuelle Voisin* (2016)
- *Hédi Saadaoui* (2015)
- *Emilie Lefol* (2014)
- *Laureline Durand* (2013)
- *Sylvia Pardonnet* (2012)
- *Benoit Gineste* (2011)
- *Marion Kauffmann* (2010)
- *Nelly Malosse* (2009)

Columbian ground squirrels

- *Erwan Harscouet* (2018)
- *Thibaut Barra*, MSc (2018)
- *Pierre Uhlrich*, TCE (2018, 2017, 2016)
- *Mathilde Tissier*, post-doc (2017)
- *Juliette Rabdeau*, MSc (2016)
- *Catherine Petel-Langevin* (2014)
- *Isabel Serrano-McGregor* (2014)
- *Taylor Fraychak*, MSc (2014)
- *Carrie Klase*, MSc (2013, 2014)
- *Kristen Rubach,* MSc (2013, 2014)
- *Anne-Marie van der Marel* (2013)
- *Célia Bordier* (2013)

Supplement 2

Abstracts of publications

PROCEEDINGS OF THE ROYAL SOCIETY B

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Kin selection in Columbian ground squirrels (*Urocitellus columbianus*): littermate kin provide individual fitness benefits

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Since W. D. Hamilton's seminal work on the evolution of sociality, a large body of research has accumulated on how kin selection might explain the evolution of cooperation in many group-living species. Our study examined the evolutionary basis of philopatry and cooperation; specifically, whether individuals benefit from the presence of close kin. We applied an individual fitness approach to a 16-year study of Columbian ground squirrels (*Urocitellus columbianus*) to investigate potential causal paths by which the presence of kin might act on individual fitness. Our results indicate that individual fitness benefits resulted from associations of philopatric female kin, and support the hypothesis that increased tolerance of proximity of kin is a proximate mechanism for these benefits. The major life-history influence of kin on individual fitness was through improved reproductive success, and this benefit may have been owing to philopatric settlement of kin that were recognized through familiarization in the natal burrow. Thus, we demonstrated an evolutionary basis necessary for ongoing kin-selected cooperation in Columbian ground squirrels, though the mechanism of familiarity may determine which kin individuals benefit from cooperative behaviours.

Keywords: individual fitness; philopatry; kin recognition; kin selection; path analysis; *Urocitellus columbianus*

1. INTRODUCTION

Since W. D. Hamilton's early discussion of the genetic evolution of social behaviour (Hamilton 1964), many advances have been made in our understanding of how kin selection might promote the evolution of cooperation and sociality (West-Eberhard 1975; Wilson 1975; Oli 2003; Bshary & Bergmüller 2008). Kin selection is likely to operate whenever the benefits of helping a relative reproduce overcome any fitness costs of the helping behaviour (Komdeur 1992; Komdeur *et al.* 1995; Oli 2003). For kin selection to favour cooperation, individuals with kin present should have enhanced fitness compared to individuals without kin. This expectation has seldom been tested with an appropriate fitness measure, though many studies have examined nepotism associated with just a few fitness traits (e.g. MacColl *et al.* 2000; Pope 2000; reviewed in primates, Silk 2007).

The individual fitness approach (McGraw & Caswell 1996; Oli 2003; Oli & Armitage 2008) should provide an alternative for testing whether kin presence is beneficial to fitness. Individual fitness can be estimated for animals that live together and have different degrees of kinship. An association of presence of kin and greater individual fitness would show that philopatry is adaptive, and that heritable behaviours associated with kinship might evolve through kin selection. While indirect, this expectation provides a test of whether kin selection could favour helping or cooperation within a population.

We investigated philopatric maternal kin in a local population of Columbian ground squirrels (*Urocitellus columbianus*). These ground squirrels are hibernating rodents with a short active season of three to four months (Dobson *et al.* 1992). They are relatively long lived (up to about 10 years old), and generation overlap (both spatial and temporal) allows for the presence of matrilineal kin and the occurrence of nepotistic behaviours (King & Murie 1985; King 1989*a*). Female philopatry produces kin associations that may result in both competition and cooperation among relatives (Dobson *et al.* 1997; Dobson 1998; for a review, Lawson Handley & Perrin 2007). Females exhibit territoriality (Murie & Harris 1978, 1988) and kin-differential behaviours, namely reduced aggressiveness and increased tolerance of close maternal kin (King 1989*b*). Such observations raise the question of whether fitness benefits are associated with cohabitation with kin.

We performed a detailed analysis of causal influences by which the presence of kin might increase individual

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Kin selection in Columbian ground squirrels: direct and indirect fitness benefits

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Abstract

Empirical and theoretical studies have supported kin selection by demonstrating nepotism or modelling its conditions and consequences. As an alternative, we previously found that female Columbian ground squirrels had greater direct fitness when more close kin were present. Extending those results, we used population matrix methods to calculate minimum estimates of individual fitness, estimated direct and indirect components of fitness, estimated inclusive fitness by adding the direct fitness (stripped of estimated influences of the social environment) and indirect fitness components together, and finally looked for inclusive fitness benefits of associations with close kin who seem to be 'genial neighbours'. We examined the estimated fitness of a sample of 35 females for which complete lifetimes were known for themselves, their mothers and their littermate sisters. Six of these females had no cosurviving adult close kin, and their direct fitness was significantly lower than 29 females with such kin ($\lambda = 0.66$ vs. $\lambda = 1.23$). The net fitness benefit of the presence of close kin was thus 0.57. The estimated indirect component of fitness through benefits to the direct fitness of close kin was 0.43. Thus, estimated inclusive fitness for females with cosurviving close kin ($\lambda = 1.09$) was significantly greater than that for females without surviving close kin (viz., $\lambda = 0.66$). The presence of closely related and philopatric female kin appeared to result in considerable fitness benefits for female ground squirrels, perhaps through the behavioural mechanisms of lowered aggression and other forms of behavioural cooperation.

Keywords: cooperation, direct fitness, group-living, inclusive fitness, indirect fitness, individual fitness, kin selection, matrix models, *Urocitellus columbianus*

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Introduction

Hamilton (1964) developed the theory of kin selection to explain what appeared to be cases of altruistic helping behaviour, in which some individuals in a population forgo personal fitness components (e.g. reproduction in the case of sterile ant workers) in favour of aiding another individual's fitness (e.g. the reproduction of the 'queen' colonial ant). Hamilton solved the seeming dilemma by formalizing genetic nepotism, analogous to cases in which close human relatives (kin) or friends are favoured via the gift of position with little or no regard for merit. The basic idea is that traits that promote kin might be favoured by natural selection because close relatives have a high probability of sharing genes underlying 'kin promotion' through descent. Hamilton provided an accounting procedure for dealing with the influence of the social environment in terms of fitness, including the ideas of indirect and inclusive fitness. Of course, the benefits and any costs of such helping behaviour are important, and these were incorporated into 'Hamilton's inequality': $rb > c$, where r is the coefficient of relatedness, b the benefit of helping behaviour and c the cost of helping, both b and c measured in fitness terms. When the

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ORIGINAL PAPER

Male reproductive tactics to increase paternity in the polygynandrous Columbian ground squirrel (*Urocitellus columbianus*)

Shirley Raveh · Dik Heg · Vincent A. Viblanc · David W. Coltman · Jamieson C. Gorrell · F. Stephen Dobson · Adele Balmer · Peter Neuhaus

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Abstract In polyandrous and polygynandrous species where females mate with multiple partners, males are expected to maximize their fitness by exhibiting an array of reproductive behaviors to ensure fertilization success, such as competing for the best mating order within a mating sequence, optimizing their investment in copulation, and mate guarding. Though there is genetic evidence of a first-male precedence in siring success for many mammalian species, the causes of this effect are poorly understood. We studied influences on first-male precedence in Columbian ground squirrels (*Urocitellus columbianus*). We found that the time a male spent consorting and mate guarding declined with his mating order (both the highest for the first male to mate). Mate guarding by the first male significantly reduced, but did not exclude, the number of additional males a female accepted. Later mating males reduced the time spent consorting, suggesting a perceived decreased chance of fertilization success. Consortship and mate guarding durations were positively related to the male's siring success and to each other, suggesting that males adjusted these behaviors strategically to increase their chances of fertilization success. Our results suggest that besides being the first male to consort, first-male sperm precedence is further enhanced through longer mating bouts and by suppressing the chances and/or efforts of later mating males.

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Active territory defence at a low energy cost in a colonial seabird

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Aggressive behaviour associated with the defence of a territory is thought to impose substantial energy costs and thus to represent a trade-off with other energy-demanding activities. The energy costs of aggressive behaviours, however, have rarely been estimated in the wild, and the overall contribution of territorial defence to daily energy expenditure has never been determined. We studied the activity budget of breeding king penguins, *Aptenodytes patagonicus*, equipped with heart rate data loggers to estimate the energy costs associated with territory defence in this colonial bird exhibiting very high rates of agonistic interactions. We also assessed whether threat displays imposed lower energy costs than attacks with body contact. During territorial defence (i.e. threats and physical attacks combined), energy expenditure averaged 1.27 times resting metabolic rate. Defence accounted for 13% of the daily time budget and contributed to 2.7% of the total daily energy expenditure. Interactions with body contact cost three times more than threat displays, but accounted for only 16% of the aggressive behaviours recorded. Neither did body mass, body size, penguin sex or breeding stage affect the cost of aggressiveness. Our results are consistent with previous research reporting that fighting imposes significant metabolic costs. However, we found that aggressive behaviour in king penguins was not an expensive activity compared to the total energy budget. Because king penguins go without food and are sleep deprived while breeding, they may have developed behavioural strategies (e.g. lower rates of attacks with body contact) allowing them to defend their territory efficiently at a low energy cost.

In many animal species, individuals perform aggressive behaviours to gain access to limited resources, such as food, territories or mates, which can improve their fitness (Cutts et al. 1999; Hagelin 2002; Logue & Gammon 2004). Usually, however, individuals will limit their use of aggressive behaviours because they often incur short-term costs in terms of time, energy demands or risk of injuries (Hack 1997; Neat et al. 1998; but see Riechert 1988), and these proximate costs can result in fundamental long-term fitness costs (Hagelin 2002; Langkilde et al. 2005). They may also increase predation risk as a result of reduced vigilance during fights (Jakobsson et al. 1995; Brick 1998). Nevertheless, the benefits of defending a resource are generally higher than the costs associated with aggressive behaviours, so that agonistic interactions among individuals are common (Maynard Smith 1982).

Based on trade-offs between expected benefits and costs of fighting, different strategies and decision rules have evolved for resolving conflicts (Maynard Smith & Parker 1976; Enquist & Leimar 1983). As physical aggression is associated with a greater risk of injury than threat displays (Clutton-Brock et al. 1979), most animals typically assess the fighting ability and motivation of their opponent before escalating into a fight with body contact (Payne 1998; Jonart et al. 2007). Animals may therefore assess correlates of resource-holding power (RHP), a measure of the probability of winning an escalated contest (Parker 1974; Maynard Smith & Parker 1976). Resource-holding power is largely determined by individual characteristics such as body size and condition (Marden & Rollins 1994; reviewed in Huntingford & Turner 1987). In addition to RHP, fighting success may also depend on the individual's motivation to fight (Elwood et al. 1998; reviewed in Enquist & Leimar 1987), which in turn depends on its willingness to expend energy or to risk injuries (Enquist & Leimar 1987). Such motivation may be estimated by determining whether the individual is the initiator or the receiver in a fight (Arnott & Elwood 2007; Briffa & Sneddon 2007).

Although aggressive behaviours are expected to impose substantial energy costs (Parker 1974; Riechert 1988), only a few

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It Costs to Be Clean and Fit: Energetics of Comfort Behavior in Breeding-Fasting Penguins

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Abstract

Background: Birds may allocate a significant part of time to comfort behavior (e.g., preening, stretching, shaking, etc.) in order to eliminate parasites, maintain plumage integrity, and possibly reduce muscular ankylosis. Understanding the adaptive value of comfort behavior would benefit from knowledge on the energy costs animals are willing to pay to maintain it, particularly under situations of energy constraints, e.g., during fasting. We determined time and energy devoted to comfort activities in freely breeding king penguins (*Aptenodytes patagonicus*), seabirds known to fast for up to one month during incubation shifts ashore.

Methodology/Principal Findings: A time budget was estimated from focal and scan sampling field observations and the energy cost of comfort activities was calculated from the associated increase in heart rate (HR) during comfort episodes, using previously determined equations relating HR to energy expenditure. We show that incubating birds spent 22% of their daily time budget in comfort behavior (with no differences between day and night) mainly devoted to preening (73%) and head/body shaking (16%). During comfort behavior, energy expenditure averaged 1.24 times resting metabolic rate (RMR) and the corresponding energy cost (i.e., energy expended in excess to RMR) was 58 kJ/hr. Energy expenditure varied greatly among various types of comfort behavior, ranging from 1.03 (yawning) to 1.78 (stretching) times RMR. Comfort behavior contributed 8.8–9.3% to total daily energy expenditure and 69.4–73.5% to energy expended daily for activity. About half of this energy was expended caring for plumage.

Conclusion/Significance: This study is the first to estimate the contribution of comfort behavior to overall energy budget in a free-living animal. It shows that although breeding on a tight energy budget, king penguins devote a substantial amount of time and energy to comfort behavior. Such findings underline the importance of comfort behavior for the fitness of colonial seabirds.

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Introduction

Maintenance behaviors (i.e. allo- and autogrooming, allo- and autopreening, bathing, scratching, stretching, etc.) serve a variety of purposes and are widespread throughout the animal kingdom (e.g. in mammals [1–3], in birds [4–6], in fish [7], in crustaceans [8], and in insects [9–10]). Studies that have considered the adaptive significance of maintenance behaviors (referred to as comfort behavior in birds [11]) have suggested both proximate (i.e. bodily) and more ultimate (i.e. social) functions such as the maintenance of good corporeal condition (e.g. parasite control, thermal insulation or muscle condition [2,5,12–14]) or the maintenance of sexual ornaments [6,15–16]. Maintenance behaviors have also been suggested to be facilitated by social contexts [17], and accredited to play a role in social relationships [3,18–19].

In birds, comfort behavior is usually referred to as a set of activities concerned with the care of the integument and the maintenance of a functional body structure, i.e. by increasing proprioceptive sensitivity and circulation in the muscles for instance [4–5,11]. Several studies have previously shown that birds spend a substantial amount of time in comfort behavior. Indeed, a meta-analysis over 62 different avian species, revealed that birds devoted 9.2% of their daily time budgets to comfort activities [20] (92.6% of which was preening), and figures close to 15% have been reported in several species (15% in gulls [21], 14% in Japanese quail [22], 14.9% in peacocks [6]). Obviously, the time devoted to comfort behavior must trade with that devoted to other activities, which could incur some costs, including indirect energy costs. For example, individuals allocating a higher proportion of time into comfort may face a reduction in resting time, decreased

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Original Article

Coping with social stress: heart rate responses to agonistic interactions in king penguins

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In colonial breeders, agonistic interactions between conspecifics are frequent and may have significant physiological implications. Physiological responses (e.g., increased heart rate) to such social stressors may be determined by the potential costs of agonistic interactions, such as personal injury or risk of breeding failure, and by the motivation of the individuals concerned. The latter may vary according to individuals' reproductive status or willingness to engage in agonistic interactions. In this study, we investigated heart rate responses to aggressive interactions in a breeding colony of king penguins *Aptenodytes patagonicus*. From heart rate (HR) and behavior recorded in 20 adults at various stages of the breeding season, we investigated how king penguins reacted to aggressive neighbors. A total of 589 agonistic interactions, 223 in which birds were actors and 366 in which birds remained bystanders (i.e., witnesses that were not involved in interactions), were characterized. We found that HR increased during agonistic interactions, both in actors and bystanders. The intensity (threat displays or physical attacks), duration, and rate of aggressive events (number of threats/blows per unit time) of an interaction significantly influenced the HR response in actors. For bystanders, however, only the duration of interactions seemed to matter. Our results also suggest a role for individual motivation, as initiators of agonistic interactions displayed higher HR increases than responders, and as increases were not constant throughout the reproductive season. We conclude that individual risk assessment and motivation modulate physiological responses to social stressors in group-living animals. *Key words:* aggressive behavior, colonial breeding, context assessment, heart rate modulation, motivation, stress. *[Behav Ecol]*

INTRODUCTION

Reaping individual fitness benefits from clustering with conspecifics has paved the road for the evolution of group-living and animal sociality (Alexander 1974; Wilson 1975; Baglione et al. 2002; Viblanc et al. 2010; Dobson et al. 2012). However, sociality comes with costs. Individual requirements must be compromised with those of other group members for animal groups to retain their integrity (West-Eberhard 1979; Armitage and Schwartz 2000; Sueur et al. 2010). The social environment hence has strong effects on individual behavior (Boissy and Le Neindre 1997) and physiology (Cacioppo 1994), including hormone secretion (Creel 2001; Oliveira et al. 2001; Goymann and Wingfield 2004), neurotransmitter secretion (Edwards and Kravitz 1997), immune function (Bartolomucci 2007), and regulation of the autonomous nervous system, as reflected by changes in heart rate (HR) (Berntson and Boysen 1989; Aureli et al. 1999; Wascher et al. 2008a).

Evidence that social interactions may strongly affect stress responses in free-living animals is accumulating (Oliveira et al. 2001; Wascher et al. 2008a,b; Wascher et al. 2009; Mouterde et al. 2012, see Cacioppo 1994, Kemeny 2003), and how stress responses may be shaped depending on social context and associated risk (Wascher et al. 2009; Mouterde et al. 2012) is of central interest to our understanding of the *pros* and *cons* of group-living. For instance, in a series of studies considering social interactions in greylag geese (*Anser anser*), Wascher and colleagues (2008a,b, 2009) recently showed that the individual's HR response to stress was subject to both the nature and intensity of the social context, as well as to the identity of those involved. The authors argued that such differences in physiological responses might reflect differences in individuals' motivation depending on the social context (Wascher et al. 2009).

The case of aggressiveness and agonistic interactions is of particular relevance for social contexts. Intraspecific competition is ubiquitous and agonistic interactions are commonly performed when individuals defend undividable resources such as territories, food, or mates. The fitness benefits of defending a resource must outweigh the costs associated with its defense for agonistic behaviors to evolve and persist (Maynard-Smith 1982; Maynard-Smith et al. 1988). The costs of agonistic interactions may come in many forms, including physical injury, time and energy investment, and physiological costs. Of particular interest is the finding that such physiological effects may also be experienced by bystander individuals: social group members who are only witnesses to such interactions (Oliveira et al. 2001; Wascher et al. 2008b). There is thus little doubt that specific social contexts, such as agonistic interactions differing in risk for instance, may elicit varying physiological responses in different individuals, and how important these responses may be in terms of physiological investment merits further consideration.

In this study, we investigated HR responses of free-living, colonial king penguins (*Aptenodytes patagonicus*) to agonistic interactions, which were bouts of either threat displays or physical attacks with body contact. HR is a highly sensitive physiological parameter that may be used to investigate individuals' reactivity to the social environment (Nakagawa et al. 2001; Wascher et al. 2008a) and responsiveness to

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BMC Ecology

RESEARCH ARTICLE Open Access

Coping with continuous human disturbance in the wild: insights from penguin heart rate response to various stressors

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Abstract

Background: A central question for ecologists is the extent to which anthropogenic disturbances (*e.g.* tourism) might impact wildlife and affect the systems under study. From a research perspective, identifying the effects of human disturbance caused by research-related activities is crucial in order to understand and account for potential biases and derive appropriate conclusions from the data.

Results: Here, we document a case of biological adjustment to chronic human disturbance in a colonial seabird, the king penguin (*Aptenodytes patagonicus*), breeding on remote and protected islands of the Southern ocean. Using heart rate (HR) as a measure of the stress response, we show that, in a colony with areas exposed to the continuous presence of humans (including scientists) for over 50 years, penguins have adjusted to human disturbance and habituated to certain, but not all, types of stressors. When compared to birds breeding in relatively undisturbed areas, birds in areas of high chronic human disturbance were found to exhibit attenuated HR responses to acute anthropogenic stressors of low-intensity (*i.e.* sounds or human approaches) to which they had been subjected intensely over the years. However, such attenuation was not apparent for high-intensity stressors (*i.e.* captures for scientific research) which only a few individuals experience each year.

Conclusions: Habituation to anthropogenic sounds/approaches could be an adaptation to deal with chronic innocuous stressors, and beneficial from a research perspective. Alternately, whether penguins have actually habituated to anthropogenic disturbances over time or whether human presence has driven the directional selection of human-tolerant phenotypes, remains an open question with profound ecological and conservation implications, and emphasizes the need for more knowledge on the effects of human disturbance on long-term studied populations.

Keywords: Stress, Heart rate, Habituation, Selection, Seabird, Human disturbance, Long-term monitoring

Background

Whereas considerable knowledge in ecology and animal behaviour has been gained from scientific research on wild animal populations (*e.g.* [1-17], reviewed in [18]), continuous exposure to humans can have profound effects on the biology of wild species, *e.g.* [15,19-21]. Thus, a crucial aspect of ecological research is to investigate and identify those effects (especially that of chronic disturbance), in order to understand and account for potential biases when deriving conclusions from the data yielded by studies in the wild [17]. Several authors have questioned how the exposure to anthropogenic disturbance might affect the biology of species under study [19-21]. For instance, some species have been shown to habituate to (*i.e.* tolerate) [22] frequent human disturbance (*e.g.* marine iguanas, *Amblyrhynchus cristatus*; [19]; Magellanic penguins, *Sphenicus magellanicus*; [20,23]; Jackass penguins, *Spheniscus demersus*; [24]). In contrast, other species have been shown to sensitize to human stressors (*e.g.* Yellow-eyed penguin, *Megadyptes antipodes;* [25]), and others still have been shown to exhibit different responses depending on their developmental stage

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Functional Ecology

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Energetic adjustments in freely breeding-fasting king penguins: does colony density matter?

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Summary

1. For seabirds that forage at sea but breed while fasting on land, successful reproduction depends on the effective management of energy stores. Additionally, breeding often means aggregating in dense colonies where social stress may affect energy budgets.

2. Male king penguins (*Aptenodytes patagonicus*) fast for remarkably long periods (up to 1·5 months) while courting and incubating ashore. Although their fasting capacities have been well investigated in captivity, we still know very little about the energetics of freely breeding birds.

3. We monitored heart rate (HR, a proxy to energy expenditure), body temperature and physical activity of male king penguins during their courtship and first incubation shift in a colony of some 24 000 freely breeding pairs. Males were breeding either under low but increasing colony density (early breeders) or at high and stable density (late breeders).

4. In early breeders, daily mean and resting HR decreased during courtship but increased again 3 days before egg laying and during incubation. In late breeders, HR remained stable throughout this same breeding period. Interestingly, the daily increase in resting HR we observed in early breeders was strongly associated with a marked increase in colony density over time. This finding remained significant even after controlling for climate effects.

5. In both early and late breeders, courtship and incubation were associated with a progressive decrease in physical activity, whereas core body temperature remained unchanged.

6. We discuss the roles of decreased physical activity and thermoregulatory strategies in sustaining the long courtship–incubation fast of male king penguins. We also draw attention to a potential role of conspecific density in affecting the energetics of breeding-fasting seabirds, that is, a potential energy cost to coloniality.

Key-words: body temperature, energy expenditure, fasting, heart rate, physical activity, seabird, social density, stress

Introduction

Energy availability and its efficient use and management constrain many aspects of animal ecology, shaping life-history strategies and evolutionary trade-offs (Drent & Daan 1980; Martin 1987; McNamara & Houston 1996; Green *et al.* 2009). This is particularly true during reproduction, where parents not only have to allocate energy to their own maintenance but also need to meet the energy requirements of courtship, incubation and chick growth. Trade-offs can be even more challenging when resources become limiting, for example during prolonged periods of fasting. Accordingly, most seabirds forage at sea but breed while fasting on land (Lack 1968; Ricklefs 1983; Dobson & Jouventin 2007). Hence, their reproductive success is expected to rely on the efficient management of energy stores ashore, and critical depletion of these stores may result in breeding failure (Olsson 1997; Ancel, Fetter & Groscolas 1998; Gauthier-Clerc *et al.* 2001). Whereas the physiology of fasting seabirds (especially penguins) has been well studied under captive and non-breeding conditions (Cherel *et al.* 1988a; Cherel, Leloup & Le Maho

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Starting with a handicap: phenotypic differences between early- and late-born king penguin chicks and their survival correlates

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Summary

1. The exceptionally long (*c.* 11 months) growth period of king penguin chicks (*Aptenodytes patagonicus*) is interrupted by the Austral winter. As a consequence, penguin chicks born late in the breeding season have little time to build-up their energy reserves before the drastic energy bottleneck they experience during winter and face greater risks of mortality than early-born chicks.

2. Whereas it is well known that breeding adults alternate between early- and late-breeding attempts, little is known on the phenotype of early- and late-chicks, and on the potential existence of specific adaptive phenotypic responses in late-born individuals.

3. We investigated phenotypic differences between early- and late-chicks and tested their survival correlates both before the winter and at fledgling. Chicks were sampled 10 days after hatching to measure body mass, plasma corticosterone levels, oxidative stress parameters and telomere length.

4. Late-chicks were heavier than early-chicks at day 10. Late-chicks also had higher corticosterone and oxidative stress levels, shorter telomere lengths and suffered from higher mortality rates than early-chicks. For both early- and late-chicks, high body mass close to hatching was a strong predictor of survival up to, and over, the winter period.

5. In late but not early-chicks, high corticosterone levels and long telomeres were significant predictors of survival up to winter and fledging, respectively.

6. Our study provides evidence that late- and early-king penguin chicks showed marked phenotypic differences 10 days after hatching. We provide an integrative discussion on whether these differences may be adaptive or not, and to what extent they may be driven by active maternal effects, indirectly induced by environmental effects, or stem from individual differences in parental quality.

Key-words: corticosterone, early-life conditions, growth, individual quality, oxidative stress, phenotypic plasticity, reproductive timing, telomere

Introduction

In seasonal environments, breeding timing is key to the reproductive success of most animals. Food resources often decline as the breeding season advances, which conflicts with the good nutritional conditions required by offspring to reach a body condition that promotes their survival over the growth period and after independence (Roff 1980). As a consequence, the offspring of late-breeders typically suffer from higher mortality rates than those

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PHYSIOLOGICAL ECOLOGY - ORIGINAL RESEARCH

Stress hormones in relation to breeding status and territory location in colonial king penguin: a role for social density?

Vincent A. Viblanc · Benoit Gineste · Antoine Stier · Jean-Patrice Robin · René Groscolas

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Abstract Because glucocorticoid (stress) hormones fundamentally affect various aspects of the behaviour, life history and fitness of free-living vertebrates, there is a need to understand the environmental factors shaping their variation in natural populations. Here, we examined whether spatial heterogeneity in breeding territory quality affected the stress of colonial king penguin (*Aptenodytes patagonicus*). We assessed the effects of local climate (wind, sun and ambient temperature) and social conditions (number of neighbours, distance to neighbours) on the baseline levels of plasma total corticosterone (CORT) in 77 incubating and 42 chick-brooding birds, breeding on territories of central or peripheral colony location. We also assessed the oxidative stress status of a sub-sample of central vs. peripheral chick-brooders to determine whether chronic stress arose from breeding on specific territories. On average, we found that brooders had 55 % higher CORT levels than incubators. Regardless of breeding status, central birds experienced greater social density (higher number of neighbours, shorter distance between territories) and had higher CORT levels than peripheral birds. Increasing social density positively explained 40 % of the variation in CORT levels of both incubators and brooders, but the effect was more pronounced in brooders. In contrast, climate was similar among breeding territories and did not significantly affect the CORT levels of breeding birds. In brooders, oxidative stress status was not affected by local density or weather conditions. These results highlight that local heterogeneity in breeding (including social) conditions may strongly affect the stress levels of breeding seabirds. The fitness consequences of such variation remain to be investigated.

Keywords Coloniality · Corticosterone · Crowding · Population density · Glucocorticoids · Oxidative stress · Seabird · Stress · Territory location

Introduction

Glucocorticoid (GC) hormones, corticosterone (CORT) in birds, are products of the physiological stress response enabling vertebrates to cope adaptively with predictable and unpredictable changes in the environment (Wingfield and Romero 2001; Sapolsky 2002; Boonstra 2004). At baseline levels, they regulate the energy balance to meet the different energy demands associated with specific life history stages (Landys et al. 2006; Romero et al. 2009). In response to acute stressors, transient increases in GCs trigger physiological and behavioural changes aimed at increasing individual fitness (Wingfield et al. 1998). Given these critical functional roles, there is a need to understand the relationships between inter- and intra-individual GC

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RESEARCH ARTICLE

Modulation of heart rate response to acute stressors throughout the breeding season in the king penguin *Aptenodytes patagonicus*

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ABSTRACT

'Fight-or-flight' stress responses allow animals to cope adaptively to sudden threats by mobilizing energy resources and priming the body for action. Because such responses can be costly and redirect behavior and energy from reproduction to survival, they are likely to be shaped by specific life-history stages, depending on the available energy resources and the commitment to reproduction. Here, we consider how heart rate (HR) responses to acute stressors are affected by the advancing breeding season in a colonial seabird, the king penguin (*Aptenodytes patagonicus*). We subjected 77 birds (44 males, 33 females) at various stages of incubation and chick-rearing to three experimental stressors (metal sound, distant approach and capture) known to vary both in their intensity and associated risk, and monitored their HR responses. Our results show that HR increase in response to acute stressors was progressively attenuated with the stage of breeding from incubation to chick-rearing. Stress responses did not vary according to nutritional status or seasonal timing (whether breeding was initiated early or late in the season), but were markedly lower during chick-rearing than during incubation. This pattern was obvious for all three stressors. We discuss how 'fight-or-flight' responses may be modulated by considering the energy commitment to breeding, nutritional status and reproductive value of the brood in breeding seabirds.

KEY WORDS: Acute stress, Energy cost, Fasting, Heart rate, Penguin, Reproductive value, Risk assessment, Seabird

INTRODUCTION

Animals facing environmental disturbances respond by mounting a series of physiological and behavioral modifications known as the stress response (Romero, 2004). Those adaptive changes are intended to redirect energy resources towards increasing fitness, in a so-called 'emergency life-history state' (Wingfield et al., 1998; Boonstra et al., 2001). Because stress responses can be costly in terms of energy, health or missed breeding opportunities (e.g. McEwen and Wingfield, 2003), they are likely shaped to increase lifetime fitness according to the life-history characteristics of considered organisms and the risk associated with specific disturbances (Nephew et al., 2003; Boonstra, 2013). For instance, physiological responses to stress may depend on the energy reserves of the animal (Cyr et al., 2008) or mechanistically underlie parental decisions (Lendvai et al., 2007; Bókony et al., 2009; Goutte et al., 2011), considering a trade-off between the cost of missing a breeding opportunity versus the expected benefits of surviving to breed in the future (Williams, 1966).

In response to acute disturbances (e.g. predation events, sudden storms), an early and short-lived phase of the stress response involves a sympathetic discharge from the nervous system, increasing heart rate, muscle tone, mobilizing energy substrates (e.g. neoglucogenesis) and priming the body to action (Wingfield, 2003). This acute 'fight-or-flight' response occurs within seconds, and is controlled by central sympathetic command neurons (Jansen et al., 1995). Heart rate (HR) has been shown to increase with increased sympathetic input (Cyr et al., 2009), and can be used to investigate the fine tuning of 'fight-or-flight' responses to acute stressors of various nature. For instance, we recently found that the HR response of colonial king penguins (*Aptenodytes patagonicus*) to acute experimental stressors increases with stressor intensity (Viblanc et al., 2012). Similarly, several studies have documented stimuli-dependent modulations of HR responses to stress in other species (Nephew et al., 2003; Tarlow and Blumstein, 2007; Wascher et al., 2011), including other penguins (Giese, 1998; Holmes et al., 2005; Ellenberg et al., 2006, 2013). To our knowledge, however, whether acute stress responses are modulated according to life-history stages in interaction with stressor intensity is unknown. This study thus examined whether HR stress responses in king penguins were modulated by changes in energy and reproductive status throughout the breeding season, depending on stressor type and associated risk.

King penguins provide an interesting model to answer such questions. Their energy commitment to reproduction is especially high, because parents alternate between long-term fasting shifts on land to care for their single egg or chick and foraging trips at sea (Groscolas and Robin, 2001). Fasting shifts shorten with advancing reproduction (Weimerskirch et al., 1992) as efforts to provision the chick increase. The higher workload experienced while rearing young chicks is likely reflected in the higher glucocorticoid levels of the parents at that time (Viblanc et al., 2014a; Bonier et al., 2009). Chicks only fledge 14–16 months later, and birds that lose a chick can not replace it in the same season (Weimerskirch et al., 1992). Thus, the value of reproduction in a given season is expected to increase with advancing breeding shift (Winkler, 1987; Côté, 2000) and acute 'fight-or-flight' responses may be shaped accordingly. For instance, given that stress responses typically redirect behaviour and energy from reproduction to survival, HR responses associated with 'flight' initiation could be attenuated during later breeding stages to prevent chick desertion by the parents (Redondo and Carranza, 1989; Albrecht and Klvana, 2004). Alternatively, HR stress responses could increase with increasing investment in relation to chick defence, as penguin parents are more defensive of their breeding territory during chick-rearing (Côté, 2000) and exhibit heightened glucocorticoid levels at this time (Viblanc et al., 2014a). In addition, penguin pairs that breed successfully in a given

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Testing the reproductive and somatic trade-off in female Columbian ground squirrels

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Keywords
Capital breeding, Columbian ground squirrels, energy allocation, income breeding, reproductive allocation.

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Abstract

Energetic trade-offs in resource allocation form the basis of life-history theory, which predicts that reproductive allocation in a given season should negatively affect future reproduction or individual survival. We examined how allocation of resources differed between successful and unsuccessful breeding female Columbian ground squirrels to discern any effects of resource allocation on reproductive and somatic efforts. We compared the survival rates, subsequent reprodction, and mass gain of successful breeders (females that successfully weaned young) and unsuccessful breeders (females that failed to give birth or wean young) and investigated “carryover” effects to the next year. Starting capital was an important factor influencing whether successful reproduction was initiated or not, as females with the lowest spring emergence masses did not give birth to a litter in that year. Females that were successful and unsuccessful at breeding in one year, however, were equally likely to be successful breeders in the next year and at very similar litter sizes. Although successful and unsuccessful breeding females showed no difference in over winter survival, females that failed to wean a litter gained additional mass during the season when they failed. The next year, those females had increased energy “capital” in the spring, leading to larger litter sizes. Columbian ground squirrels appear to act as income breeders that also rely on stored capital to increase their propensity for future reproduction. Failed breeders in one year “prepare” for future reproduction by accumulating additional mass, which is “carried over” to the subsequent reproductive season.

Introduction

In order to survive and reproduce, animals must acquire energy from the environment and successfully allocate it to various metabolic needs (Brown et al. 2004). However, because energy resources are usually limited under natural conditions, life-history traits are seldom maximally expressed (Fisher 1930; Reznick 1985; Kunz and Orrell 2004). Resources allocated to one biological function often reduce availability for allocation to other biological functions, a type of life-history trade-off (Stearns 1992).

An assumption of life-history theory is the existence of “energy costs” associated with trade-offs with respect to survival and reproduction (Lack 1966; Williams 1966; Hirshfield and Tinkle 1975; Bell 1980; Stearns 1992). In iteroparous species (i.e., those that reproduce more than once), annual resource allocation can be divided into two primary biological functions: somatic and reproductive efforts (Hirshfield and Tinkle 1975). Resources can be allocated either to individual soma in the form of growth, personal maintenance, and survival, or to reproduction in the form of immediate offspring production and parental care. When environmental resources are acquired annually or when the annual energy budget is fixed, these two categories add up to the total energy resources available for allocation. If current reproduction requires a high

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Original Article

Aggression in Columbian ground squirrels: relationships with age, kinship, energy allocation, and fitness

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Matrilineal kin groups are common in social mammals and often exhibit cooperative behaviors. Social interactions in such groups may have varying consequences on fitness depending on the number of kin present. We used social network analysis to study which factors (including individual spatial distribution, sex, age, and kinship) affected patterns of aggressive interactions in Columbian ground squirrels during the important breeding period of lactation. In addition, we studied how patterns of aggressive interactions affected female reproduction and fitness. Received aggressions lessened as ground squirrels aged, likely reflecting greater dominance in older individuals. Outwards aggression peaked at prime reproductive age, but decreased in older individuals. In females, outwards aggressiveness was positively related to energy allocated to reproduction and annual fitness, suggesting that highly aggressive females were either of high intrinsic quality or were able to defend high-quality territories. Finally, female–female aggression was primarily targeted toward non-kin individuals, revealing the advantage for breeding adult females of having close kin neighbors that were also breeding. Thus, breeding females that were close kin appeared to be "genial neighbors" that benefited from increased fitness, highlighting the role of kin selection in mitigating the costs (e.g., injuries, stress) of aggression.

Key words: **aggressiveness, fitness, kin selection, philopatry, social network, territoriality.**

INTRODUCTION

Aggressive behavior between individuals is common in social groups, allowing individuals to gain access to important resources such as territories, food, or sexual partners (Clutton-Brock et al. 1979; Isbell 1991; Adams 2001). Besides obvious benefits, aggressive interactions also carry costs, in terms of energy expenditure (Rovero et al. 2000) and stress or injuries (Boonstra et al. 2001; Viblanc et al. 2012), which can influence survival (Moorcroft et al. 1996; Boonstra et al. 2001) and reproductive success (Lea et al. 2010; Betini and Norris 2012). Thus, aggressive interactions and territorial strategies often result from a cost/benefit fitness balance that depends on the individual attributes of opponents and the expected outcome of the conflict (Enquist and Leimar 1983, 1987). For instance, to avoid unnecessary injury costs associated with overt social aggression, animals may assess their opponents based on their likelihood of winning a contest (resource-holding power; Parker 1974; Enquist and Leimar 1983) before escalating into physical disputes (Maynard Smith and Parker 1976). Resource-holding power is often determined by resource value (Enquist and Leimar 1987), and individual attributes linked to social dominance and age (Haley 1994; Murray et al. 2007) or individual condition or quality (Clutton-Brock and Albon 1979; Mowles et al. 2010).

Individual social attributes, including aggressive behavior, might depend on the presence of kin. Specifically, kin selection

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Mutually honest? Physiological ‘qualities’ signalled by colour ornaments in monomorphic king penguins

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Mate choice is expected to be important for the fitness of both sexes for species in which successful reproduction relies strongly on shared and substantial parental investment by males and females. Reciprocal selection may then favour the evolution of morphological signals providing mutual information on the condition/quality of tentative partners. However, because males and females often have differing physiological constraints, it is unclear which proximate physiological pathways guarantee the honesty of male and female signals in similarly ornamented species. We used the monomorphic king penguin (*Aptenodytes patagonicus*) as a model to investigate the physiological qualities signalled by colour and morphological ornaments known to be under sexual selection (coloration of the beak spots and size of auricular feather patches). In both sexes of this slow-breeding seabird, we investigated the links between ornaments and multiple indices of individual quality; including body condition, immunity, stress and energy status. In both sexes, individual innate immunity, resting metabolic rate, and the ability to mount a stress response in answer to an acute disturbance (capture) were similarly signalled by various aspects of beak coloration or auricular patch size. However, we also reveal interesting and contrasting relationships between males and females in how ornaments may signal individual quality. Body condition and oxidative stress status were signalled by beak coloration, although in opposite directions for the sexes. Over an exhaustive set of physiological variables, several suggestive patterns indicated the conveyance of honest information about mate quality in this monomorphic species. However, sex-specific patterns suggested that monomorphic ornaments may signal different information concerning body mass and oxidative balance of males and females, at least in king penguins. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2016, **118**, 200–214.

KEYWORDS: body condition – king penguin – monomorphic seabird – mutual mate choice – ornament – oxidative stress – sexual selection – ultra-violet signals.

INTRODUCTION

The evolutionary explanation for conspicuous and similar ornaments in both sexes (i.e. in sexually monomorphic ornamented species) has been a long-standing quandary in evolutionary biology (reviewed by Kraaijeveld, Kraaijeveld-Smit & Komdeur, 2007). Two main hypotheses have been proposed to explain mutual ornamentation. The first suggests that female ornaments are non-functional, but arise as a

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Original Article

Beak color dynamically signals changes in fasting status and parasite loads in king penguins

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Dynamic ornamental signals that vary over minutes, hours or weeks can yield continuous information on individual condition (e.g., energy reserves or immune status), and may therefore be under strong social and/or sexual selection. In vertebrates, the coloration of the integument is often viewed as a dynamic ornament, which in birds can be apparent in the beak. King penguins (*Aptenodytes patagonicus*) are monomorphic seabirds that possess conspicuous yellow–orange (YO) and ultraviolet (UV) beak spots that are used by both males and females in mate choice. We studied the dynamicity of beak spot sexual traits, and to what extent they reflected changes in individual condition in fasting king penguins and in penguins treated with an anti-parasitic drug. We also describe the maturation of this colorful ornament during the yearly catastrophic moult. On a time-scale of days to weeks, beak spot coloration changed in response to fasting and experimental changes in parasite load. Beak spot UV brightness decreased over a 10-day fast in breeding birds. For birds caught during courtship and held in captivity YO chroma decreased after a 24-day fast. Birds that were treated with an anti-parasitic solution showed an increase in UV coloration after parasite removal. Altogether, our results show that beak spot coloration is a dynamic ornament that reflects multiple dimensions of changes in individual condition in breeding-fasting penguins.

Key words: **dynamic ornament, fasting, honest signal, king penguin, parasites, sexual selection.**

INTRODUCTION

Darwin's theory of sexual selection has been central to evolutionary biology, providing scientists with a framework for understanding mechanisms that might lead to the evolution of individuals selecting mates that produce fitter offspring (Darwin 1871). When assessing mate or competitor condition, animals often rely on ornamental signals that are costly to produce and/or maintain, and are therefore expected to honestly reflect individual quality (Zahavi 1975; Grafen 1990; Cotton et al. 2004; Walther and Clayton 2004). Mates may use such ornaments to assess the direct and/or indirect fitness benefits (e.g., paternal care, genetic benefits; Møller and Thornhill 1998; Mays and Hill 2004; Fromhage et al. 2009) that arise from mating with partners able to bear their cost.

In species where interactions with mates and/or social competitors occur repeatedly, there should be strong selection for dynamic signals that allow continuous tracking of changes in individual condition over extended periods of time (Velando et al. 2006; Ardia et al. 2010; Rosenthal et al. 2012). Dynamic changes in integument coloration have been reported in fish and amphibians (Sköld et al. 2013), reptiles (Weiss 2002), mammals (Stephen et al. 2009), and birds (Velando et al. 2006; Ardia et al. 2010). In birds, studies have suggested that beak coloration may serve as a dynamic signal of individual condition (Blount et al. 2003; Faivre, Grégoire, et al. 2003; Navarro et al. 2010; Rosenthal et al. 2012). In contrast to feathers that are replaced only during moult and constitute an inert (nonvascularized) tissue, the beak is a vascularized part of the integument (Lucas and Stettenheim 1972). Thus, rapid changes in beak coloration may reflect more dynamic changes than feathers in the deposition or mobilization of pigments (e.g., carotenoids; Alonso-Alvarez et al. 2004), or rearrangement of local microstructures (e.g., keratin; Dresp and Langley 2006) linked to modifications in individual condition over time.

One important trade-off shaping the evolution of honest signals is between sexual ornaments and immune function, and by extension resistance to parasites (Hamilton and Zuk 1982). Differential allocation of pigments to ornaments or immune function is thought

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Breeding status affects the hormonal and metabolic response to acute stress in a long-lived seabird, the king penguin

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ABSTRACT

Stress responses are suggested to physiologically underlie parental decisions promoting the redirection of behaviour away from offspring care when survival is jeopardized (e.g., when facing a predator). Besides this classical view, the "brood-value hypothesis" suggests that parents' stress responses may be adaptively attenuated to increase fitness, ensuring continued breeding when the relative value of the brood is high. Here, we test the brood-value hypothesis in breeding king penguins (*Aptenodytes patagonicus*), long-lived seabirds for which the energy commitment to reproduction is high. We subjected birds at different breeding stages (courtship, incubation and chick brooding) to an acute 30-min capture stress and measured their hormonal (corticosterone, CORT) and metabolic (non-esterified fatty acid, NEFA) responses to stress. We found that CORT responses were markedly attenuated in chick-brooding birds when compared to earlier stages of breeding (courtship and incubation). In addition, NEFA responses appeared to be rapidly attenuated in incubating and brooding birds, but a progressive increase in NEFA plasma levels in courting birds suggested energy mobilization to deal with the threat. Our results support the idea that stress responses may constitute an important life-history mechanism mediating parental reproductive decisions in relation to their expected fitness outcome.

1. Introduction

Because parents are limited both in the time and energy to invest into offspring, decision rules about breeding and parental care should be selected considering a trade-off between the relative value of current reproduction *vs.* that of expected future breeding opportunities (Williams, 1966; Trivers, 1972; Maynard-Smith, 1977). According to the reproductive value hypothesis, parents may invest more into parental care as the clutch or offspring age, because of the higher probability of progeny surviving until sexual maturity (Andersson et al., 1980; Clutton-Brock, 1991). Consistently, several studies have shown that parental investment may change with offspring age, i.e. with the relative reproductive value of the young (Andersson et al., 1980; Redondo and Carranza, 1989; Cézilly et al., 1994; Albrecht and Klvana, 2004). For instance, birds are known to increase the amount of parental nest defence as offspring age, both throughout the incubation (Sjöberg, 1994; Albrecht and Klvana, 2004; Osiejuk and Kuczynski, 2007) and chick-brooding (Redondo and Carranza, 1989) periods.

Mechanistically, stress responses have been suggested to physiologically underpin parental decisions by promoting the redirection of behaviour away from offspring care when survival is jeopardized. Stress responses allow animals to cope with unpredictable environmental challenges (i.e. labile perturbations, reviewed in Wingfield, 2003) by rapidly mounting a series of physiological and behavioural modifications. For instance, increases in glucocorticoid hormones (mainly corticosterone CORT, in birds) may promote the mobilization of energy substrates required to deal with impending threats (e.g. approaching predator, inclement weather). Breeding parents may then redirect their energy investment towards survival, thereby reducing or giving-up altogether on parental duties (Wingfield et al., 1998). The latter should especially apply to long-lived species for which lifetime reproductive success depends more on adult survival than seasonal fecundity, individuals behaving as 'prudent parents' (Drent and Daan, 1980; Stearns, 1992). However, when the value of the current breeding attempt is high relative to that of future reproductions, stress responses may be attenuated to ensure reproduction is not abandoned (Wingfield and Sapolsky, 2003).

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Kin effects on energy allocation in group-living ground squirrels

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Summary

1. The social environment has potent effects on individual phenotype and fitness in group-living species.

2. We asked whether the presence of kin might act on energy allocation, a central aspect of life-history variation.

3. Using a 22-year data set on reproductive and somatic allocations in Columbian ground squirrels (*Urocitellus columbianus*), we tested the effects of co-breeding and non-breeding kin on the fitness and energy allocation balance between reproduction and personal body condition of individual females.

4. Greater numbers of co-breeding kin had a positive effect on the number of offspring weaned, through the mechanism of altering energy allocation patterns. On average, females with higher numbers of co-breeding kin did not increase energy income but biased energy allocation towards reproduction.

5. Co-breeding female kin ground squirrels maintain close nest burrows, likely providing a social buffer against territorial invasions from non-kin ground squirrels. Lower aggressiveness, lower risks of infanticide from female kin and greater protection of territorial boundaries may allow individual females to derive net fitness benefits via their energy allocation strategies.

6. We demonstrated the importance of kin effects on a fundamental life-history trade-off.

Key-words: energy, kin selection, life-history trade-offs, matriline, philopatry, reproductive allocation, somatic allocation

Introduction

The social environment is known to strongly affect individual behaviour, physiology and fitness. For instance, social interactions, social status and the composition of the social environment may influence individual stress levels (Creel *et al.* 2013), oxidative stress (Beaulieu *et al.* 2014), immunity (Bartolomucci 2007), longevity (Silk *et al.* 2010), offspring production and survival (Silk, Alberts & Altmann 2003), and metabolic rate (Sloman *et al.* 2000). Despite these potent effects, including on energy expenditure (Viblanc *et al.* 2014), no study thus far has considered how the social environment might shape individual energy allocation decisions during reproduction, though some have considered how cooperation among individuals may allow alleviating workload in cooperative breeders (Reyer 1984; Komdeur 1994; Sharp, English & Clutton-Brock 2013). This is surprising given that (1) resources occur in limited amounts in nature (either in time, space or quantities), (2) energy trade-offs between functions are central to life-history theory and (3) social interactions often occur repeatedly within a season and over the years, leading to social heterogeneity in the nature and composition of social environment (e.g. age structure, nature of social bonds, number of kin) that might affect energy balance. Thus, understanding whether the social environment influences the optimal allocation of energy to the functions of growth, maintenance and reproduction appears central to an appraisal of life-history decisions in group-living species.

In particular, whereas the trade-off between somatic and reproductive functions has been long considered (Williams 1966; Hirshfield & Tinkle 1975; van Noordwijk

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Long-term field studies on rodents

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Long-term studies on rodents have been conducted for longer periods (up to 70 years) and more generations (up to 88 generations) than for most other mammalian taxa. These studies have been instrumental in furthering our understanding of ecophysiology, social systems, and population and community processes. Studies on African striped mice (*Rhabdomys pumilio*) revealed that basal blood glucose levels span a far greater homeostatic range than previously thought. Studies on American red squirrels (*Tamiasciurus hudsonicus*) demonstrated how endocrine pathways underlying phenotypic plasticity allow individuals to respond to different environments. Long-term studies on African striped mice, marmots (*Marmota*), tuco-tucos (*Ctenomys sociabilis*), and degus (*Octodon degus*) revealed that ecological constraints on dispersal are drivers of group formation in some species but not others. Social flexibility, when the social system of an entire population can change due to individuals changing their social tactics, has been demonstrated in striped mice. Long-term studies on prairie voles (*Microtus ochrogaster*) found that males and females often live in pairs, leading to subsequent studies of the neural mechanisms underlying social monogamy. Long-term studies on other arvicoline rodents contributed more to our understanding of the factors influencing population dynamics than studies on any other mammalian order. While food availability and predation have been identified as factors influencing population dynamics, no single factor alone drives population dynamics in any species. We encourage researchers to incorporate manipulative experiments into long-term studies and to take integrative approaches to inform cross-disciplinary theory.

Estudios de largo plazo en roedores se han realizado de manera más prolongada y abarcando un mayor número de generaciones comparado con estudios similares en otros taxa de mamíferos. Estos estudios han expandido nuestro conocimiento en ecofisiología, sistemas sociales, y procesos poblacionales y comunitarios. Estudios en el ratón rallado africano (*Rhabdomys pumilio*) han revelado niveles basales de glucosa en la sangre que abarcan un rango homeostático más amplio que lo conocido previamente. Estudios en la ardilla roja (*Tamiasciurus hudsonicus*) han demostrado cómo las vías endocrinas que median la plasticidad fenotípica permiten a los individuos responder a ambientes contrastantes. Estudios de largo plazo en el ratón rallado africano, tuco-tucos sociales (*Ctenomys sociabilis*) y degus (*Octodon degus*) han demostrado como las restricciones ambientales pueden gatillar la formación de grupos sociales en algunas especies pero no en otras. La flexibilidad social, donde el sistema social de una misma población cambia debido a cambios en las tácticas usadas por los individuos, también se ha demostrado en el ratón rallado africano. Estudios de largo plazo en ratones de la pradera (*Microtus ochrogaster*)

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ORIGINAL RESEARCH

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Experimental stress during molt suggests the evolution of condition-dependent and condition-independent ornaments in the king penguin

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Abstract

Sexual selection and social selection are two important theories proposed for explaining the evolution of colorful ornamental traits in animals. Understanding signal honesty requires studying how environmental and physiological factors during development influence the showy nature of sexual and social ornaments. We experimentally manipulated physiological stress and immunity status during the molt in adult king penguins (*Aptenodytes patagonicus*), and studied the consequences of our treatments on colourful ornaments (yellow-orange and UV beak spots and yellow-orange auricular feather patches) known to be used in sexual and social contexts in this species. Whereas some ornamental features showed strong condition-dependence (yellow auricular feather chroma, yellow and UV chroma of the beak), others were condition-independent and remained highly correlated before and after the molt (auricular patch size and beak UV hue). Our study provides a rare examination of the links between ornament determinism and selection processes in the wild. We highlight the coexistence of ornaments costly to produce that may be honest signals used in mate choice, and ornaments for which honesty may be enforced by social mediation or rely on genetic constraints.

KEYWORDS

Corticosterone, honest signal, Immunity, sexual selection, social selection

1 | INTRODUCTION

Understanding the evolution of conspicuous ornaments, often costly to produce and maintain, has been a long-standing focus of evolutionary biology (Andersson, 1994; Kuijper, Pen, & Weissing, 2012). Darwin (1871) laid the groundwork for this topic by observing that conspicuous ornaments could enhance access to sexual partners and reproduction, and that their evolution might be explained by sexual selection. In the second half of the twentieth century, researchers realized that ornaments could also be used in competition for nonsexual resources, such as access to food and territories outside reproduction (Tobias, Montgomerie, & Lyon, 2012; West-Eberhard, 1983). West-Eberhard (1983) pointed out in her theory of social selection that ornaments can evolve whenever they enhance gene replication due "to differential success in social competition, whatever the resource at stake" (West-Eberhard, 1983). Consequently, sexual selection can be viewed as a

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RESEARCH ARTICLE

Functional Ecology BRITISH ECOLOGICAL SOCIETY

Maternal oxidative stress and reproduction: Testing the constraint, cost and shielding hypotheses in a wild mammal

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Abstract

1. Oxidative stress has been proposed as a central causal mechanism underlying the life-history trade-off between current and future reproduction and survival in wild animals.
2. While mixed evidence suggests that maternal oxidative stress may act both as a constraint and a cost to reproduction, some studies have reported a lack of association between reproduction and maternal oxidative stress.
3. The oxidative shielding hypothesis offers an alternative explanation, suggesting that mothers may pre-emptively mitigate the oxidative costs of reproduction by increasing antioxidant defences prior to reproduction.
4. We tested the oxidative constraint, cost and shielding hypotheses using a longitudinal field study of oxidative stress levels in a species that breeds using daily energy income, the Columbian ground squirrel (*Urocitellus columbianus*).
5. Elevated maternal oxidative damage prior to reproduction was associated with higher maternal investment in litter mass at birth, but not at weaning.
6. Breeding females increased their antioxidant capacity and decreased their oxidative damage from birth to lactation, compared to non-breeding females measured at the same time periods. However, lower maternal oxidative stress during lactation was not associated with higher offspring survival or mass growth over this period.
7. Our results provide little evidence for maternal oxidative stress acting as a constraint on, or cost to, reproduction in Columbian ground squirrels, but partially support the idea that oxidative shielding occurred to buffer potential oxidative costs of reproduction.

KEYWORDS
antioxidant, body condition, cost of reproduction, life history, mammal, mitochondria, trade-off

1 | INTRODUCTION

Central to life-history theory, the "cost of reproduction" hypothesis predicts that breeding individuals should trade-off high investments into current reproduction with future survival or reproductive prospects (Hirshfield & Tinkle, 1975; Reznick 1985; Stearns, 1992; Williams, 1966). While fitness costs to reproduction have often been highlighted (Descamps, Boutin, McAdam, Berteaux, & Gaillard, 2009; Flatt, 2011; Koivula, Koskela, Mappes, & Oksanen, 2003; Lehto Hurlimann, Stier, Scholly, Criscuolo, & Bize, 2014; Linden & Møller, 1989; Nager, Monaghan, & Houston, 2001; Nur, 2002; Penn & Smith, 2007), the mechanisms responsible for such costs remain poorly understood, despite an

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