

REVIEW

Costs and benefits of solitary living in mammals

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solitary living; group living; social system; socio-ecology; thermoregulation; mammal.

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Email: lindelanimakuya@gmail.comEditor: David Hone
Associate Editor: Rebecca NagelReceived 26 July 2023; revised 14 October 2023;
accepted 4 December 2023

doi:10.1111/jzo.13145

Abstract

While for decades behavioural ecologists have studied the costs and benefits of group living, solitary living has received little attention. Instead, it was assumed to be the default stage from which sociality evolved. Mammals underwent around 200 million years of social evolution, with a few species evolving communal or cooperative breeding in harsh environments. Other mammal species are successful with solitary living in exactly the same and many other environments, indicating that solitary living is beneficial under many environmental conditions. Comparative studies on mammals indicate that solitary living might not be the ancestral but a derived state. Solitary living in mammals is less common than previously believed, occurring in 22% of the studied species. Here, we review costs and benefits of solitary living in mammals. We found very few studies that considered solitary living and show important future avenues of research based on the factors that are important for the evolution of group living. We also emphasize that a solitary form of social organization does not imply an unsocial lifestyle: solitary mammals typically have non-random but individualized social interactions with their neighbours, indicating important social structure.

Introduction

Mammals show a fascinating diversity of social systems, including solitary- and pair-living species, extended families and cooperative or communal breeding (Burda et al., 2000; Clutton-Brock, 1989). Understanding the evolution of this diversity of mammalian social systems received significant attention (Kleiman & Malcolm, 1981; Lukas & Clutton-Brock, 2013; Thierry et al., 2000). Comparative studies have made the arguments that the first placental mammal was solitary and that the more complex forms of social systems such as monogamy and cooperative breeding evolved later (Gebo, 2004; Lukas & Clutton-Brock, 2013). Here, we question the assumption that solitary living in mammals is primitive. Instead, we argue that solitary living in mammals is a specialized form of social organization which we need to study if we want to comprehensively understand mammalian social evolution and how to protect solitary living mammals.

What is solitary living?

We follow the concept of Kappeler and Schaik (2002) (updated by Kappeler, 2019) which identifies four components for each social system including the (1) social organization, (2) social structure, (3) mating system, and (4) the care system (see

Table 1 for definitions). It is now widely accepted that we have to clearly differentiate between these components, as, for example, not all pair-living species mate monogamously, display pair-bonds and biparental care (Fernandez-Duque et al., 2020; Huck et al., 2020; Kvarnemo, 2018). Previous studies defined solitary living based on a mixture of the mating system (only one breeding female) and care system (maternal care only) (Lukas & Clutton-Brock, 2013), which led to the problem that several species having social units consisting of several adults were categorized as solitary rather than group living (Schradin, 2017).

We define solitary living based on the social organization of social units (for definition see Table 1): both adult males and adult females sleep and forage alone for more than 50% of the time and mainly meet for courtship and mating. While for our definition the criteria of 50% applies (allowing all species on the continuum from 0 to 100% to be categorized), from our experience social units typically are either >75% of the time with the same conspecifics (then called group living) or >75% of the time alone (then called solitary living). Social units that forage alone but consistently (>50% of the time) share the same nesting site and territory with the same conspecific(s) are not regarded as solitary living, but as pair- or group-living solitary foragers. A social unit (a solitary individual, a pair or a group) can have only one form of social organization, while

Table 1 Glossary of important terms for the categorization of social systems in mammals used in our review (note that in other taxa, especially social insects, other terms and definitions might be used)

Term	Definition	Examples/comments
Terms from the classification by (Kappeler, 2019; Kappeler & Schaik, 2002)		
Care system	Describes who shows infant care.	Parental and allo-parental care; helpers at the nest.
Mating system	Describes who mates with whom and who reproduces.	Monogamy; singular or plural breeding; communal breeding.
Social organization	Composition and size of a social unit.	Solitary; pair living; group living.
Social structure	Social interactions including communication.	Social bonding; dominance hierarchy. Includes all social behaviours, amicable and aggressive ones.
Social system	The combination of the four components care system, mating system, social organization and social structure.	A biparental monogamous pair living species with pair bonds. A maternal, polygynous, solitary species where female kin tolerate each other but are aggressive towards non-kin.
Social unit	Individuals that live together and that share the same home range including sleeping sites.	A solitary male leopard. A pair of nocturnal prosimians that share the same home range and sleeping site. A group of baboons.
Additional terms		
Colony	Multiple social units (social organization) that live so close to each other that communication and visual contact between social units is possible (social structure). Interactions between social units are typically aggressive, within social units amicable.	Colonies of bats where (in some species) the social units forming a colony can consist of one breeding male and multiple females with offspring. In whistling rats (<i>Parotomys spec.</i>), social units are solitary females that defend their burrow and territory against other solitary females in the colony.
Social behaviour	Any behaviour shown in interactions between conspecifics. Includes amicable and aggressive behaviours (social structure) and behaviours of the care system.	Grooming, fighting, warming offspring.
Social	This term is not well defined. It is typically used to classify individuals/species with amicable interactions (social structure), but also those living in groups (social organization) or showing parental care (care system).	This term should be avoided and replaced by specific terms from the four components of social systems. It is not useful to rank species as 'very' social, 'highly' social, when no measure for comparison is provided.
Unsocial	This term is not well defined. It is typically used to classify individuals/species where nearly all interactions (social structure) between conspecifics are aggressive and individuals live solitarily (social organization).	This term should be avoided and replaced by specific terms from the four components of social systems.

Our categorization is based on Kappeler (2019) and Kappeler and Schaik (2002). We include additional terms that are commonly used when writing about social systems, but that are not well defined and which might therefore lead to confusion, stating how we use these terms in the current review or why we try to avoid them.

species consisting of many social units can have several forms of social organization, leading to intra-specific variation in social organization.

A species is said to be mainly solitary when most males and females follow this definition. This excludes dispersers, as most mammal species have a solitary dispersal phase, often biased but not restricted towards males (Lawson Handley & Perrin, 2007). Including dispersers in the classification of a species' social organization would inflate the number of species being partially solitary living to nearly 100% and make most species show intra-specific variation in social organization. While such a classification would be useless, understanding costs and benefits of solitary living will help us to better understand the life history of the many mammalian species that have a solitary disperser stage.

Many species show intra-specific variation in social organization (Schradin, Hayes, et al., 2018) and this includes species

where most individuals live solitarily, although some individuals form pairs or even groups (Makuya et al., 2022; Valomy et al., 2015). Therefore, one can differentiate between species that are obligately solitary living (all individuals are solitary), mainly solitary living (most individuals are solitary living) and facultatively solitary living (most individuals live in pairs or groups and less than 50% solitary). Considering such variation is important in comparative studies about social evolution and can challenge previous studies that ignored variation (Dalerum, 2007; Griesser & Suzuki, 2016; Olivier et al., 2024; Qiu et al., 2022).

Solitary living in mammals

It is often believed that most mammals are solitary living. For example, Lukas and Clutton-Brock (2013) classified 1741 out of 2545 (68%) of mammalian species as solitary living. This

included several hundreds of mammal species that have not been studied in the wild but that were assumed to be solitary living due to their nocturnal and cryptic lifestyle (Agnani et al., 2018; Schradin, 2017). Table 2 summarizes reviewed empirical data from field studies on mammals from a broad range of taxa. It becomes evident that solitary living is rather rare in mammals, being the obligate or main form of social organization in 22% (131 of 592) of the studied species (Table 2).

Phylogenetic heritage of solitary living? Evidence from palaeontology

Cynodonts living 250 million years ago gave rise to mammaliaforms, the ancestors of true mammals. Fossil evidence of parental care in cynodonts was reported already more than 60 years ago (Brink, 1956) and is available for two cynodont genera (Jasinoski & Abdala, 2017). Cynodonts were burrowing animals (Groenewald et al., 2001) and associations of both juveniles with adults as well as of several adults found in fossilized burrows are indicative of group living (Jasinoski & Abdala, 2017). The absence of sexual size dimorphism in the cynodont *Thrinaxodon* and the small number of adults found together (Jasinoski & Abdala, 2017) indicate that this species might have been pair living.

Some cynodonts were already pair or group living, and the same has been found for some early mammals. For example *Filikomys primaevus*, which lived 75 million years ago and belonged to the then dominant mammalian order of Multituberculata, was group living (Weaver et al., 2020). Fossils found at

a dinosaur nesting site in the United States indicate that this burrowing species lived in groups of multiple generations that shared one burrow system and nesting site. The stem-metatherian *Pucadelphys andinus* that lived in Bolivia 63 million years ago is a relative of extant marsupials (Ladeveze et al., 2011). Fossils of multiple adults of both sexes were found together with sub-adults and juveniles, indicating a group-living social organization (Ladeveze et al., 2011). The only major mammalian taxa for which no fossil evidence of group living exists are monotremes. Monotremes are regarded as the most primitive living mammals and typically regarded to be solitary (Nowak & Wilson, 1999). However, there have been numerous reports of den sharing in platypus (Makuya et al., 2022). In sum, fossil evidence indicates that ancestors of mammals and some early mammals were social, questioning a solitary ancestry for mammals.

Evidence from recent comparative studies

Multiple comparative studies on different mammalian taxa aimed at estimating the social organization of the common ancestor. In Xenarthra, most species were described to be solitary living, but too few studies were available for a comparative analysis (Makuya et al., 2022). In Eulipotyphla it was suggested that the ancestor might have been pair living (Valomy et al., 2015). Comparative studies using modern Bayesian statistics and databases based on field studies found pair living to be the most likely ancestral form of social organization in marsupials (Qiu et al., 2022), artiodactyla (Jaeggi et al., 2020),

Table 2 Solitary living in different mammalian taxa based on data from field studies

Taxa	Number of species (IUCN)	Number of species with field data	Species obligate solitary living	Species mainly solitary living	Species facultatively solitary living	Reference
Marsupials	345	65	20 (31%)	6 (9%)	8 (12%)	Qiu et al. (2022)
Xenarthra (sloths, armadillos and anteaters)	30	9	7 (78%)	1 (11%)	1 (11%)	Makuya et al. (2022)
Macroscelidea (elephant shrews)	19	8	1 (13%)	0	5 (63%)	Olivier, Jaeggi et al. (2022)
Eulipotyphla (insectivores)	445	16	7 (44%)	0	5 (31%)	Valomy et al. (2015)
Artiodactyla (even-toed ungulates)	226	100	5 (5%)	0 ^a	55 ^a (55%)	Jaeggi et al. (2020)
Carnivora (carnivores)	271	171	71 (42%)	0 ^a	<46 (27%)	Dalerum (2007)
Strepsirrhini (prosimians)	132	43	3 (7%)	5 (12%)	7 (16%)	Agnani et al. (2018)
Haplorhini (apes and monkeys)	450	180	0 (0%)	5 (3%)	0 (0%)	Olivier et al. (2024)

Included are all taxa for which detailed reviews are available (see 'Reference'), but unpublished data indicate that similar patterns are found in all other mammalian orders (Olivier, 2023). Given are total number of species and in brackets the percentage of solitary species relative to all species studied. Obligate: all observed social units were solitary living; mainly: >50% of observed units were solitary living; facultative: <50% of observed units were solitary living.

^aThe published database does not allow to differentiate between mainly and facultatively solitary species.

primates (Olivier et al., 2024) and even all mammals (Olivier, 2023).

Solitary living as a special adaptation

Both evidence from palaeontology as well as from comparative studies indicates that solitary living is not ancestral in mammals. If solitary living is not ancestral, then it must have evolved as a specific adaptation, and this probably occurred repeatedly in several lineages as indicated by the comparative studies on different mammalian taxa.

Solitary mammals are the product of millions of years of evolution. Today, they live in very diverse habitats, and many are exposed to environmental variation and harshness (Makuya et al., 2023; Schradin et al., 2023), factors associated with the evolution of a few complex mammalian societies (Lukas & Clutton-Brock, 2017). For example, in the harsh Kalahari, only 2 out of 90 mammal species listed by Anderson (1998) are cooperative breeders (meerkats and Damaraland mole rats), while 30 species are solitary living. Solitary living should be considered as a specialized adaptation to specific environments, in the same way as has been done for cooperative breeding. The problem is that so far solitary living has not been studied as an evolved trait.

There is some evidence that solitary living evolved as an adaptation to specific environments. Extant monotremes are highly specialized invertebrate feeders, and their solitary social organization might be an adaptation to this non-sharable and sparsely distributed food resource (Nowak & Wilson, 1999). Aardvarks (Taylor & Skinner, 2003), ant bears and armadillos are other specialized insect feeders that are solitary (Makuya et al., 2022). Being insectivorous means feeding competition does not allow large groups and might thus favour pair or solitary living, which is common in Eulipotyphla (Valomy et al., 2015). For some insectivorous species, being pair- or group-living solitary foragers can be a solution for, for example, insectivorous bats (Kerth, 2022). Large predators such as many bears and most large cats are solitary, maybe as an adaptation to the distribution and size of their prey (Nowak & Wilson, 1999). Thus, wide distribution of food sources might favour solitary living. Solitary living also occurs in folivorous sloths (Makuya et al., 2022) which are well camouflaged as a protection against predation, an advantage that would disappear if groups of sloths would occupy the same tree.

Solitary species need not be asocial

Solitary living in mammals is assumed to develop due to offspring dispersing when reaching adulthood either because they themselves develop the urge to leave, or because the mother rejects them. Maternal aggression towards offspring reaching puberty has been observed in European hamsters (*Cricetus cricetus*; Eibl-Eibesfeldt, 1953) and in some, but not all, species of elephant shrews (Rathbun, 1979; Schubert et al., 2012). More studies are needed to know how common maternal aggression is in inducing dispersal, or whether its internal motivation of the offspring when/after reaching puberty driving them to disperse and become solitary living.

Solitary species do not have to be asocial, actively repelling each other. Instead, species with a solitary social organization often have a complex social structure in which individuals do interact in a non-random way. For example the puma (*Puma concolor*) displays a complex social structure characterized by hierarchical reciprocal tolerance of adult females centred around dominant adult males (Elbroch et al., 2017). Similarly, female leopards (*Panthera pardus*) share space according to kinship (Roex et al., 2022). Complex social structures influencing fitness also occur in nocturnal solitary prosimians (Agnani et al., 2018; Müller & Thalmann, 2000) as well as in solitary living but colony-forming rodents such as Columbian ground squirrels (*Urocitellus columbianus*, Viblanc et al., 2016) and Brants' whistling rat (*Parotomys brantsii*, Jackson, 1999). The spatial distributions of solitary species can affect social interactions and fitness (Siracusa et al., 2021). Solitary species can gain fitness benefits by living near familiar neighbours (Walmsley et al., 2023). In sum, social interactions often play an important role in solitary species.

Costs and benefits of solitary living

While for decades studying the benefits of group living has been a main focus of behavioural ecology, little is known about the benefits of solitary living. To understand why a species is group or solitary living, we must know the costs and benefits. Many studies found good evidence that group living provides benefits but we still lack good measures of the costs of group living (Clutton-Brock, 2021; Krause & Ruxton, 2002). Benefits of solitary living arise when costs of group living can be avoided (Table 3). Thus, benefits of solitary living are the costs of group living and missing benefits of group living represents costs of solitary living (Table 3). Whether a species benefits from solitary or from group living depends on the net cost-benefit calculation of all factors summarized in Table 3, and it is the environment that influences the outcome for each factor. For example, while for a species under its environmental condition one factor such as foraging might favour group living, high costs of group living due to increased predation risk might nevertheless lead to the evolution of solitary living. Here, we discuss how solitary living animals might compensate or avoid these costs. Understanding benefits of solitary living will not only allow us to understand why so many species have this form of social organization, but will also lead to a better understanding of the evolution of sociality.

Parasites and disease

Decreased risk of disease and parasite transmission has been discussed to be a main benefit of solitary living (Krause & Ruxton, 2002). Indeed, a positive correlation between parasite load and colony size has been reported in both birds (Brown & Brown, 1986) and mammals (Lopez et al., 2013), although empirical evidence is mixed, as sociality can also lead to decreased parasite load (Lutermann et al., 2013). Thus, removal of ecto-parasites would be a benefit for group living (Table 3). Meta-analyses focus on gregarious species living in groups of different sizes, having very little data from solitary

Table 3 Environmental factors influencing the costs and benefits of group versus solitary living

Factor	Benefits of group living	Costs of solitary living	Costs of group living	Benefits of solitary living
Parasites	Removal of ectoparasites by grooming.	Reduced ectoparasites removal rate.	Increased infection risk.	Decreased infection risk.
Disease	None (possibly taking care of sick in humans and a few other species).	None.	Increased infection risk.	Decreased infection risk.
Predation risk	Reduced predation due to (1) dilution effect, (2) confusion effect, (3) overall increased vigilance but decreased individual vigilance, (4) group defence against predators.	Overall increased risk to be predated if detected by predator.	Increased risk of being detected by predator as groups are more conspicuous than single individuals.	Reduced risk to be detected.
Foraging and competition for food	Finding good food sites. Catching prey. Shared foraging grounds.	Increased individual vigilance. No information transfer regarding good food sites. Decreased success in catching prey. Smaller foraging grounds. Smaller territory.	Competition for food, reduced food availability.	Monopolized access to food.
Territoriality	Large territory due to group defence.	Increased investment to find mates.	Larger territory needed to have sufficient resources.	Smaller territories that are less costly to defend.
Reproduction	Easy access to potential mates.	Infants alone for longer, higher individual costs of infant care.	Direct competition for access to mates. Reproductive suppression. High reproductive skew. Costs of showing allo-parental care.	All individuals can reproduce. No mate monopolization. Low reproductive skew. All parental investment goes into own offspring.
Infant care	Help by allo-parents.	High costs of thermoregulation.	Increased risk of infection with disease and parasites due to body contact between individuals.	Males invest time and energy into mate searching instead of paternal care.
Thermoregulation	Reduced costs of physiological thermoregulation due to huddling.			

Left: Commonly stated benefits of group living and how this induces costs of solitary living by missing these benefits. Right: Costs of group living inducing benefits of solitary living, when being avoided. Whether a species evolves group or solitary living depends on the net outcome of all the factors combined. Dark grey columns: Commonly stated benefits of group living and how this induces costs of solitary living by missing these benefits. Light grey columns: Costs of group living inducing benefits of solitary living, when being avoided.

species, finding that parasite intensity and prevalence but not parasite species richness increase with group size (Patterson & Ruckstuhl, 2013). Surprisingly few studies have measured parasite load in solitary species. In rodents, no effect of sociality on endoparasite richness was found, but solitary rodents have a higher ectoparasite richness (Bordes et al., 2007). The weak evidence of increased risk of disease with increased sociality could be due to evolved mechanisms to reduce infection risk/parasite load. This includes allo-grooming to remove parasites, sickness behaviour (sick individuals being inactive and thus reducing spread of disease; Hart & Hart, 2019), and possibly a stronger immune system to cope with increased disease load (Bordes et al., 2007). In sum, while it is a plausible hypothesis that solitary species have a lower disease transmission rate, empirical data supporting this hypothesis are so far missing, maybe because so few solitary species have been studied. Another problem is that research has focussed on ectoparasites, which can be removed by conspecifics in social species, while few data are available regarding the spread of infectious disease caused by bacteria and viruses.

Predation risk

While living in groups can be of great benefit to avoid predation due to the dilution and confusion effect as well as group defence (Krause & Ruxton, 2002), this is mainly the case for large mammals. For small mammals (and most mammals are small) such as rodents, insectivores and small carnivores, it is less clear whether moving around in a group would bring benefits of predator avoidance, or rather attract predators (Krause & Ruxton, 2002). Little research has been done on this topic in mammals, but from birds it is known that larger flocks can attract more predator attacks (Cresswell, 1994) and that nests in colonies suffer higher predation rate than solitary nests (Andersson & Wiklund, 1978). Small mammals that are central place foragers can benefit from high densities when warning each other with warning calls, whether they are truly social (marmots; Blumstein et al., 2006) or whether colonies consist of many solitary individuals (whistling rats; LeRoux et al., 2002; see Table 1 for a definition of colony). Similarly, solitary Formosan squirrels *Callosciurus erythraeus* have alarm calls to inform the neighbourhood and they mob together against predators (Tamura, 1989; Tamura et al., 1989). Thus, solitary small mammals can benefit from conspecifics by forming colonies, while solitary small mammals not living in colonies reduce predation risk by being less conspicuous than a group.

Foraging and competition for food

Solitary individuals cannot benefit from following knowledgeable conspecifics to good food sources, although it has often been observed that solitary predators, such as cougars (Elbroch et al., 2017) and Tasmanian devils (Andersen et al., 2020), meet at carcasses, leading to severe competition.

Conspecifics compete with each other for food, inducing costs, especially when food is scarce and patchily distributed.

A group will deplete a resource faster than a single individual. Thus, the amount and distribution of food sources will determine to what extent it is costly to forage in groups.

Territorial solitary individuals can benefit from monopolizing access to food sources. It has been argued that species feeding on dispersed insects as well as those preying on large widely distributed prey (leopards, tigers, bears) are solitary to avoid competition. While plausible, an empirical test of these hypotheses is missing. Many insectivorous Eulipotyphla are more sociable than previously believed (Valomy et al., 2015), and most canids as well as lions do live in groups (Dalerum, 2007). Comparative studies testing whether food distribution affects social organization are needed. One empirical study was done by Dammhahn and Kappeler (2009) where they looked at two solitary foraging mouse lemur species that differed in the spatial ranging and sleeping associations of females. *Microcebus berthae* relied on small, dispersed food patches causing within-group scramble competition that could explain low associations between females. In contrast, *M. murinus* made use of patchily distributed large food resources allowing females to overlap their home ranges and to form sleeping groups.

Territoriality

Territoriality is a way to monopolize access to resources, which can include food, mates, and shelter. The quantity of food available per square meter is one determinant of territory size, and higher food abundance leads to smaller territories (Schoepf et al., 2015; Schradin, Schmohl, et al., 2010). As more individuals need more resources, groups need to defend larger territories and also might have to travel larger distances. One benefit of solitary living is thus that smaller territories need to be defended and that smaller distances need to be travelled to obtain sufficient food, which would reduce energetic costs and could reduce predation risk when this means the individual can spend more time under cover. A solitary carnivore, the leopard, was found to display relaxed territoriality under high population density, which reduced the risk of injury due to territorial disputes (Roex et al., 2022).

Reproduction

It is sometimes argued that one benefit of group living is easy access to mates. However, whether finding a mate is difficult rather depends on population density than on sociality. A solitary female that has several male neighbours might easily find a mate without being constrained in choosing which male to mate with compared to a female living in a group with a clear male hierarchy.

One major benefit of solitary living is the absence of direct reproductive competition within groups that can lead to reproductive suppression (behavioural or physiological) in both sexes, and infanticide by females (Clutton-Brock et al., 2006; Faulkes & Bennett, 2001; Schradin et al., 2012). Female infanticide also occurs in solitary species, but it is much more common in group-living species (Lukas & Huchard, 2019). While dominant individuals might benefit from living in groups

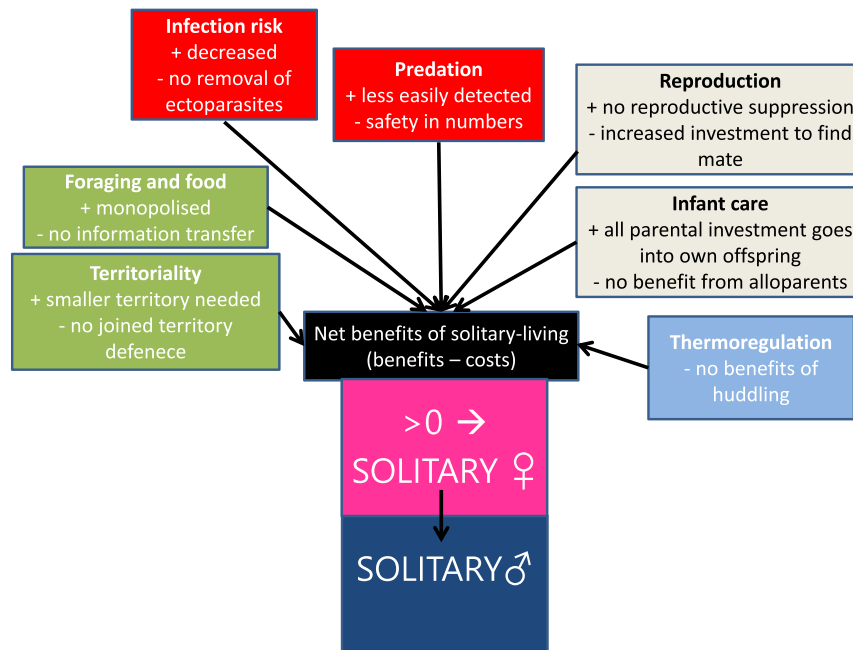


Figure 1 Socio-ecological model of solitary living. Seven main factors that influence the social organization of a species. + indicates which condition favours solitary living, – which favours group living. Combined, these factors influence whether solitary or group living leads to a net benefit for females. In mammals, social organization is mainly determined by how females distribute themselves, while males follow female social organization, being solitary living when females are solitary, joining groups when females form groups.

where they can monopolize reproduction while they and their offspring benefit from helpers, for subordinate individuals of lower competitive ability, solitary living can be beneficial. But even large competitive females might prefer solitary breeding over communal breeding to avoid infanticide, if they are the first females to give birth during the season (Hill et al., 2015; Schradin, König, et al., 2010).

Infant care

Allo-parental care where offspring especially of dominant individuals benefit is common in group-living species (Kokko et al., 2002; Riedman, 1982). Allo-parental care can lead to indirect fitness benefits if directed towards close kin (Riedman, 1982; Schradin, Vuarin, et al., 2018). Allo-parental care evolves when constraints such as habitat saturation and reproductive suppression by dominants make independent reproduction costly (Emlen, 1982a, 1982b). Solitary living is a tactic to avoid such constraints (Schradin, König, et al., 2010). Solitary breeding females benefit from being able to invest all care into their own offspring, while solitary males can invest their time into further mate searching for direct reproductive success instead of investing into allo-parental care.

Thermoregulation

Thermoregulation via huddling can lead to significant energy savings, especially in small mammals (Canals et al., 1997; Schradin & Ancel, 2019). For solitary mammals, many of

which are small, missing thermoregulatory benefits of huddling represents a major cost of solitary living. In some species, this can be compensated by spending the inactive period in well-insulated burrows (Kinlaw, 1999), while other species use sun-basking to reduce thermoregulatory costs (Geiser et al., 2002; Zduniak et al., 2019). So far it is unknown whether solitary species invest more in these mechanisms than group-living species that can use the same mechanisms to save energy.

Benefits of solitary living: simplicity of life?

Solitary living could be summarized as a strategy to avoid costs of group living: avoiding social transmission of disease and parasites, less conspicuous to predators, no competition for resources within the smaller territory, no social stress and dominance hierarchy causing reproductive suppression, and all parental investment goes into own offspring. However, it also induces the costs of missing all the benefits of group living, and no study so far tried to measure the net benefit of solitary living. Figure 1 summarizes a conceptual framework for such studies.

Conclusions

Solitary living in mammals cannot be regarded as a primitive default stage that needs no scientific explanation. Instead, we have to study why some species are solitary living in the same way as we investigated for decades why some species are

group living. For this, costs and benefits and associated ecological drivers of solitary living must be studied. Without a comprehensive understanding of solitary living our understanding of mammalian social evolution is significantly constrained and conservation efforts for solitary mammals will often be inadequate (Olivier, Schradin, et al., 2022). We hope our review will motivate research groups worldwide to study the socio-ecology and broad diversity of solitary living mammals.

Acknowledgements

The comments of two anonymous referees significantly improved this manuscript. This study was supported by a joint Wits-CNRS PhD program.

Conflict of interest

The authors declare that no competing interests exist.

Author contributions

Both authors contributed to reviewing the literature and writing the manuscript.

Inclusion statement

Our study brings together authors from two different countries including the global South. All authors were engaged with the research to ensure that the diverse sets of perspectives they represent was considered.

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