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ORIGINAL RESEARCH

Evolutionary correlates and consequences of sociality in feliform carnivorans

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group-living; habitat; activity period; body size and shape; diet; extinction risk; predation risk; speciation rate.

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Abstract

Living in social groups has a range of evolutionary and ecological implications for animals. On the one hand, increased local density of conspecifics could intensify competition or make the group as a whole more visible to predators. On the other hand, social groups provide opportunities for cooperation, can potentially increase access to mating opportunities, and enable group-based antipredator mechanisms, such as increased vigilance, group defence, and dilution effects. Here, we set out to investigate the evolutionary predictors and consequences of sociality in feliform carnivorans (cats, mongooses, civets, and relatives) using a phylogenetic comparative approach. We first tested for predictors of sociality and found that sociality was more likely in larger, diurnal species which live in more open habitats, with a less slender body shape and with a more insectivorous diet. This result is consistent with the expectation from previous studies that evolution of social groups entails greater competition and ecologies that facilitate group cohesion, and perhaps are also subject to greater predation pressure. Second, we used ancestral state estimation for sociality and historical biogeographic analyses of habitats to show that sociality evolved eight times in feliforms and typically was associated with ancestral presence in or shift towards more open habitat types. Third, we investigated the consequences of sociality in terms of speciation rates and extinction risks, and found that although social species did not differ in extinction risk compared with solitary species, they did tend to have slightly lower speciation rates. Taken together, our results provide evidence for a series of costs and constraints in the evolution of sociality in mammals (e.g. in terms of competition and higher predation risk) but that these appear to be offset by the benefits provided from group-living sufficiently to avoid the longer term population consequences of higher extinction risk.

Introduction

Sociality, whereby groups of animals have synchronised movement and activity (outside of reproductive activities), is a phylogenetically widespread attribute across vertebrate species and has evolved multiple times in fishes, reptiles, mammals, and birds (Halliwell et al., 2017; Taborsky & Wong, 2017; Ward & Webster, 2016). However, the extent of sociality varies greatly in these groups, and it is within birds and mammals where social behaviour is both more frequent and often more stable and complex (Clutton-Brock, 2021; Ward & Webster, 2016). For example, within mammals around 30% of species are social (Smith et al., 2017) and sociality has evolved a large (but as yet unknown) number of times independently in at least 12 taxonomic orders (Clutton-Brock, 2016; Zhu et al., 2023). However, the ecological factors underlying the evolution of sociality are not well understood, and neither are the macroevolutionary consequences. Herein, we first look at the ecological factors associated with the distribution of sociality amongst extant species of feliform (cat-like) carnivorans, focusing on variables associated with predation risk (body size, activity period, and habitat type), competition (body size, diet, and body shape), and ability to maintain group cohesion (habitat type and activity period). Next, we estimated evolutionary transitions in sociality and habitat over time to further investigate links between habitat types and sociality. Finally, we investigate whether sociality in turn might have shaped evolutionary patterns by influencing the rate of speciation and extinction risk in group-living species compared with solitary species.

Mammals and birds have a relatively high number of social species amongst vertebrate groups and have consequently been

a focus of studies to understand the ecological correlates of sociality across species. These studies have commonly found evidence that predation risk is an important factor in the evolution of sociality (Caro, 2005). This is presumably due to the many antipredator mechanisms that are available to group-living species, such as increased vigilance (via the many-eyes hypothesis), the dilution effect, confusion effect, and mobbing or other active group defences (Caro, 2005). Furthermore, group-living may provide additional predation-related benefits as shared vigilance may allow more time for feeding by each individual (Guindre-Parker & Rubenstein, 2020). Consequently, predator species richness is associated with sociality across birds (Bliard et al., 2024), and carnivoran mammals (Stankowich et al., 2014).

Two common proxies of predation risk are habitat openness and activity period (e.g. diurnal, nocturnal, crepuscular). These are often interrelated and their effects in terms of predation risk likely depend on the taxonomic group from which the species are most at risk of predation (Kohl et al., 2018; Palomo-Munoz et al., 2024; Stankowich et al., 2014). A study on predation risk amongst carnivoran mammals found that species tend to experience higher predation risk either from diurnal birds of prey or nocturnal mammals, but not both (Stankowich et al., 2014). As diurnal birds of prey usually detect prey visually from above, sometimes at great distances, more open habitats present greater predation pressure for prey (Ontiveros et al., 2005; Stankowich et al., 2014). For diurnal prey, the presence of multiple group members may therefore allow earlier and better predator detection (Boland, 2003), explaining why carnivoran species that are exposed to higher daytime avian predation risk are more likely to be social (Stankowich et al., 2014). Following a presumably similar line of thought, Gusset (2007) speculated that group-living in mongooses evolved as an antipredator response in diurnal species in open habitats. Similar benefits may explain why social weaver bird species (Ploceidae) and cooperatively breeding mammals are more likely to occur in open habitats (Lukas & Clutton-Brock, 2017; Song et al., 2022), and also why diurnality is linked with sociality in both primates and rodents (Müller & Soligo, 2005; Schultz et al., 2011). Conversely, for species that are primarily predated by nocturnal mammals, sociality may be less beneficial in detecting or deterring predators, and alternative defences such as noxious chemicals are more likely to evolve instead (Stankowich et al., 2014). This likely explains the negative relationship between sociality and nighttime predator risk in carnivoran species (Stankowich et al., 2014). In contrast, a study on birds found that sociality is associated with more closed habitats (Griesser et al., 2017), although it is unclear whether this relationship is related to predation risk as this was not examined directly. Some of the variation in results between studies might therefore be related to taxon-specific associations between habitat openness and predation risk. For instance, whether the main predators of a prey species are birds or mammals, or ambush versus active hunters, might influence whether cover is perceived as a safe refuge or a potential hiding place for a predator (Caro, 2005).

Habitat openness and diurnality have also been linked to sociality via their proposed effects on group cohesion, allowing visual cues to be used to locate group members and to coordinate movement (Herbert-Read, 2016; Liao et al., 2024). Acoustic communication within groups may also be facilitated by more open habitats as plant leaves absorb sound energy (Martens & Michelsen, 1981; Watanabe & Yamada, 1996). This effect has been demonstrated in three species of social mongoose, whereby playback experiments found that calls degrade faster in more highly vegetated habitats (Arasco et al., 2022). Easier communication in open, diurnal habitats may also promote the evolution of cooperation within social groups, either in terms of hunting (Packer & Ruttan, 1988) or breeding (Koenig & Dickinson, 2016), which may bring additional benefits of increased survival and reproductive success (Guindre-Parker & Rubenstein, 2020; Silk, 2007). Nevertheless, the relationships between sociality, habitat openness, and diurnality remain unclear and could be related to either the implications of diurnal activity and open habitats for predation risk (as suggested by Gusset, 2007) and/or the ability to maintain group cohesion with fewer visual or acoustic barriers.

Whilst sociality may bring benefits relating to predator defence and cooperation, it also comes with increased local competition for resources and mating opportunities (Lukas & Clutton-Brock, 2014; Sterck et al., 1997). Since conspecifics typically occupy the same or highly similar niche, competition is likely to be intensified in mammals living at the higher local densities of a social group compared with independent solitary lifestyles (Adler et al., 2018; Forrester et al., 2006). Similarly, potential rivals for mates may be present within the group and therefore in closer proximity than if each group member had to independently search for a mate (Clutton-Brock & Huchard, 2013).

As a result, we expect traits that influence competition to be important in the evolution of sociality. Perhaps unexpectedly, given that larger animals require more energetic resources, both larger birds and rodents are more likely to be social (Bliard et al., 2024; Griesser et al., 2017; Müller & Soligo, 2005), possibly due to foraging benefits derived from social groups that enable growth to larger sizes. However, such a relationship was not found for carnivorans (Stankowich et al., 2014), which could be explained by the costs of increased competition from larger group members. Moreover, large body size can convey antipredator benefits – as prey get larger they may become harder for predators to subjugate or consume (Griffiths, 1980; Urban, 2008) – which may impose a balance between more intense competition in larger species (disfavouring sociality) and antipredator benefits of large body size (favouring sociality if groups are easier for predators to find than single individuals). Hence, whilst sociality may be more likely in larger species, this relationship may vary based on the relative importance of competition versus foraging or antipredator benefits in the taxon in question.

Body shape is an understudied attribute that may also be important in the evolution of sociality by influencing the costs of increased local competition, beyond those originating from body size. In carnivoran mammals in particular, body shape is a major component of morphological diversity, with substantial variation in shape from elongate weasels and linsang to stout bears and hyaenas (Law, 2020). Notably, this variation does

not seem tightly linked to ecological attributes, such as habitat use, hunting behaviour, or diet (Law, 2021), suggesting it is broadly independent from key aspects of resource acquisition. However, because of the higher surface area to volume ratios of elongate animals, they suffer higher energetic costs resulting from increased heat exchange with the environment (Brown & Lasiewski, 1972). Hence, if metabolism is higher for more elongate animals of a similar size, social species may be expected to be relatively more rotund as a way of increasing energetic efficiency and therefore reducing competition with other group members.

Diet has also been suggested as a factor in the evolution of sociality through its influence in competition. Foods that are locally abundant and clumped may reduce competition by allowing multiple group members to feed simultaneously and reducing the ability of a single individual to monopolise access to the resource. For example, high local abundances of seeds (due to their clumped distribution) may explain why social species of weaver birds tend to be more granivorous than insectivorous, with omnivores (eating both foods) showing an intermediate frequency of sociality (Song et al., 2022). Furthermore, frugivory is associated with sociality in rodents which is likely to again reflect the predictability, high energy content, and high abundance (at particular times) of fruit that reduces competition between group members (Müller & Soligo, 2005). Several previous authors have suggested that the density of small vertebrate prey in ecosystems might often be too low to sustain social groups of mongooses (Gilchrist et al., 2009; Gusset, 2007; Rood, 1975). Instead, a shift to a predominantly insectivorous diet could facilitate the evolution of sociality via reduced local competition for food, as invertebrates are a much more abundant prey than other food types used by feliforms. This idea has not been tested directly, although Stankowich et al. (2014) found that sociality in carnivorans is associated with less mammal prey in the diet and interpreted this as higher insectivory on the assumption that mammals versus insects is a main diet axis in this group.

Sociality may also impose long-term consequences for lineages and populations over time, in terms of speciation rates and extinction risks. For instance, sociality has been associated with reduced effective population sizes due to spatial structuring of populations and reproductive skew within groups, although this is likely dependent on social structures within and between groups (Marzluff & Dial, 1991). Effective population size can potentially influence the rate of evolution, but in directions that may vary across systems (Lanfear et al., 2014). However, current evidence for a relationship between sociality and speciation rates is limited. For instance, Marzluff and Dial (1991) found evidence that primate groups with higher species richness tended to be more social (bigger group sizes), but not in 12 other animal groups including various clades of hymenopteran insects, birds, and mammals. Muñoz-Durán (2002) found no evidence of sociality being associated with speciation rates, whilst Magnuson-Ford and Otto (2012) showed a statistically non-significant tendency for faster speciation in social species.

On the one hand, social species may be at lower risk of extinction than solitary species as the benefits of group-living may contribute to population stability, for instance where group-based defence lowers extrinsic mortality to predators or when cooperative breeders buffer reproduction against poor conditions (Covas et al., 2008). However, on the other hand, social species may require a minimal group size below which Allee effects reduce fitness further and so risk falling into an extinction vortex as populations decline (Courchamp et al., 1999). Empirical studies have found that highly social species have higher extinction risk (Muñoz-Durán, 2002), but that larger group size can either confer a lower extinction risk (Creighton & Nunn, 2023; Davidson et al., 2014), or have no detectable effect (Purvis et al., 2000), emphasising the remaining uncertainty as to how sociality relates to extinction risk.

Feliform carnivorans represent a good model system to investigate the causes and consequences of sociality as they represent a diverse assemblage in terms of sociality and the potentially associated traits described above. They consist of 133 species across seven families (Eupleridae, Felidae, Herpestidae, Hyaenidae, Nandiniidae, Prionodontidae, and Viverridae) and are generally well studied compared with many other animal groups, allowing greater confidence in data collation and good availability of phylogenetic information to enable comparative analyses.

We here address three aims related to the evolution of sociality using a phylogenetic comparative approach in feliform carnivorans. First, we tested for predictors of sociality, expecting to find that social feliforms are likely to be large, rotund, diurnal species living in open habitats and feeding more on invertebrates than solitary species. Second, we used ancestral state estimation for sociality and historical biogeographic analyses of habitats to infer origins of sociality in this clade and investigate whether these origins tend to occur in habitat types that are more open. Third, we investigated the long-term consequences of sociality in terms of speciation rates and extinction risks.

Materials and methods

Data collection

We first obtained 1000 node-dated phylogenetic trees, based on sequenced species only, for the clade Feliformia from VertLife (https://vertlife.org; Upham et al., 2019). We calculated a maximum clade credibility tree in phangorn 2.12.1 (Schliep, 2011) and used this for all subsequent analyses, which were conducted in R 4.4.2 (R Core Team, 2024) unless otherwise stated. The resulting tree contained 106 species (80% of feliforms). Basic handling of phylogenies in R was done using ape 5.8 (Paradis & Schliep, 2019).

We collected data on sociality (binary: whether living in social groups is a typical occurrence for each species or not), body mass (kg), body length (cm), and activity period (diurnal, crepuscular, cathemeral, or nocturnal) using information from the PanTHERIA database (Jones et al., 2009) and Wilson and Mittermeier (2009). We relied on descriptions (particularly text-based species accounts in Wilson & Mittermeier, 2009) stating whether or not each species lived in groups other than male–female breeding pairs to record sociality, and where such information was missing in these sources we excluded the

species from our study entirely. We calculated a 'rotundness index' as a measure of body shape that aims to capture the gradient from slender and elongate species on one hand to more bulky species on the other. For this purpose, we divided the cube root of body mass by the body length, with the cube root taken to alleviate scaling issues resulting from mass being related to volume (i.e. proportional to length cubed for similar shaped animals). We recorded which major habitats each species occurs in based on the first level (broad) classification of the IUCN Habitats Classification Scheme version 3.1 (IUCN, 2024a), as this provides a standardised coding of habitats across species. Note that we combined all marine categories as 'coastal' since these are rare and all involve coastal activity in feliform carnivorans, and we also excluded artificial habitats from our data. We additionally coded habitat type of each species as predominantly living in either open habitats (e.g. savanna, grassland, wetland, rocky areas, desert, and coast) or closed habitats (forest and shrubland) based on the aforementioned categories from the IUCN Red List (IUCN, 2024b), with confirmation from more nuanced narrative descriptions in Wilson and Mittermeier (2009). The proportion of invertebrates in the diet was extracted from the EltonTraits database for each species (Wilman et al., 2014).

To assess the long-term population consequences of sociality we collated data on species-specific speciation rates and extinction risks. For speciation rates we used the DR metric (Jetz et al., 2012) as obtained from VertLife (https://vertlife.org; Upham et al., 2019) and for extinction risk we used two binary variables collated from the IUCN Red List (IUCN, 2024b). Specifically, we first recorded whether each species was threatened or not based on IUCN status, with Least Concern and Near Threatened considered non-threatened and higher Red List categories considered threatened. We also recorded whether or not each species was reported to have declining populations based on the IUCN population trend category (with 'Decreasing' considered to represent declining populations and 'Increasing' or 'Stable' not).

Phylogenetic imbalance ratios

Before fitting any models to our data, we first assessed the suitability of our categorical traits for modelling in a phylogenetic comparative context by calculating the phylogenetic imbalance ratio (PIR; Gardner & Organ, 2021) in windex 2.0.8 (Arbuckle & Minter, 2015). PIR values range between 0 and 1, with lower values indicating greater suitability of the data for model fitting. Although advising against strict thresholds, Gardner and Organ (2021) suggested that PIR <0.1 is likely to indicate that the traits contain sufficient information to enable reasonable parameter estimation from phylogenetic comparative models.

We calculated PIR for each of our categorical traits: sociality, both extinction risk measures (threatened and population declines), activity pattern, and habitat type. We also calculated PIR for pairwise combinations of traits which are included in regression-style models with one predicting another (e.g. sociality and habitat type). In almost all cases these calculations support our ability to fit models to our data as PIR <0.1 (Table S1). The exceptions with PIR >0.1 are activity pattern paired with sociality (PIR = 0.141) and activity pattern paired with whether a species is threatened (PIR = 0.104). Hence, results pertaining to activity period as a predictor of sociality or threatened status should be interpreted more cautiously. However, both PIR values are not far above the guideline of 0.1 and this result is likely due to low numbers of cathemeral and crepuscular species in the dataset, so parameters related to nocturnal and diurnal habits should be estimated reasonably well. We also note that our main comparison of interest is diurnal vs nocturnal species, but we have also included cathemeral and crepuscular species in the dataset as these activity patterns do occur in 12 of our 106 species. Moreover, these 'intermediate' activity periods may be expected to show intermediate relationships with sociality, though clear predictions are more challenging as they may behave more similarly to diurnal or nocturnal species depending on sensory considerations such as sensitivity to low light levels in each species.

Testing predictors of sociality

We used phylogenetic logistic regression via maximum penalised likelihood in phylolm 2.6.5 (Ho & Ane, 2014) to test our hypothesised predictors of sociality. We fit the model with sociality as the response variable and activity pattern, habitat type (open vs. closed), log-transformed body mass, rotundness index, and proportion of invertebrates in the diet as explanatory variables.

Ancestral state estimation of sociality

We estimated ancestral states for sociality using Bayesian stochastic mapping (Bollback, 2006; Huelsenbeck et al., 2003) as implemented in phytools 2.3.0 (Revell, 2024). We used 1000 simulations under an All Rates Different model with a root node prior estimated from the stationary distribution of the estimated transition matrix to obtain estimates of the presence or absence of sociality at all nodes in the phylogeny.

Historical biogeography of habitats

To facilitate assessment of how habitat type may influence sociality, we estimated ancestral habitats occupied through the history of the clade using a historical biogeography approach applied to our individual habitat categories. We conducted these analyses in two stages using BioGeoBEARS 1.1.3 (Matzke, 2013). In the first stage, we constructed and fit a set of six models to our habitat data: DEC, DIVALIKE, and BAYAREALIKE each with and without an additional jump dispersal parameter (+J). In the second stage, we compared these six models using AICc, supplemented with likelihood ratio tests comparing each model with and without the +J parameter, and estimated ancestral habitats using the best fitting model.

Testing predictors of extinction risk

We used phylogenetic logistic regression as described above to test whether sociality predicts extinction risk. Specifically, we

fit two models each using one of our extinction risk metrics (threatened status or declining populations) as the response variable. We fit sociality as an explanatory variable alongside the following traits that may be related to both traits and hence were included to control for them whilst testing the effect of sociality: activity pattern, habitat type (open vs. closed), log-transformed body mass, and rotundness index.

Testing sociality as a predictor of speciation rate

We used two approaches to investigate whether sociality is associated with speciation rates in feliform carnivorans. In the first, we inferred tip diversification rates across our phylogeny using Bayesian Analysis of Macroevolutionary Mixtures 2.5.0 (BAMM; Rabosky, 2014). We gave our global sampling probability as 0.8 (as our phylogeny contains 80% of all described feliform species), set expected number of shifts as 1, and used priors on initial speciation and extinction rates as calculated in BAMMtools 2.1.12 (Rabosky et al., 2014). We set the prior probability of time-variable (vs. time-constant) diversification rates to be 0.5 and allowed rate shifts to occur on all branches. We ran four Markov Chain Monte Carlo (MCMC) chains for 10 million generations, sampling every 1000, and removed the first 10% of posterior samples as burnin before processing the output. We plotted the log-likelihood across the chain and calculated effective sample sizes for parameters to confirm the MCMC had ran sufficiently well (i.e. that log-likelihood estimates have plateaued and effective sample sizes are at least >200). We then tested for an association between sociality and the estimated tip diversification rates using STructured RAte Permutations on Phylogenies (STRAPP; Rabosky & Huang, 2015), also implemented in BAMMtools and using Mann–Whitney tests on 1000 permutations. Although we focus here on speciation rates as they are more robustly estimated (Rabosky, 2014), BAMM also estimates extinction and net diversification rates and so we also ran STRAPP on these latter two rates to test for associations with sociality.

As a second and alternative approach we used phylogenetic regression in phylolm 2.6.5 (Ho & Ane, 2014) to test whether sociality predicts speciation rate as estimated with the DR metric for each species. We fit DR as the response variable and sociality as our main explanatory variable; we also included activity pattern, habitat type (open vs closed), log-transformed body mass, and rotundness index as additional explanatory variables to control for any confounding effects these may have on any relationship between sociality and speciation rate.

Results

Predictors of sociality

Sociality was more likely to occur in larger species (when controlling for phylogeny) that are diurnal and live in more open habitats (Table 1). Specifically, 53% of social species were found in more open habitats compared with 22% of solitary species, and 65% of social species were diurnal compared with 20% of solitary species. We also found that social species were more rotund (less elongate body shape) and had a much more insectivorous diet than solitary species (Table 1, Fig. 1).

Table 1 Summary of phylogenetic logistic regression predicting sociality (vs solitary habits), the reference levels for categorical predictors being nocturnal for activity pattern and closed habitats for habitat type

	β	SE	z	P
Intercept	−5.590	1.887	−2.962	0.003
Activity pattern (cathemeral)	1.484	0.667	2.226	0.026
Activity pattern (crepuscular)	0.368	0.607	0.606	0.545
Activity pattern (diurnal)	1.412	0.542	2.605	0.009
Habitat type (open)	1.226	0.479	2.561	0.010
log(body mass)	1.549	0.603	2.568	0.010
Rotundness index	51.942	23.447	2.215	0.027
Proportion of invertebrates in diet	3.584	1.235	2.902	0.004

β, regression coefficient; SE, standard error.

Ancestral state estimation of sociality

Our ancestral state estimation for sociality provided strong support for a solitary ancestor ($P_{\text{solitary}} = 0.80$) and several origins of sociality (with a mean of ~8 gains and ~4 losses of sociality across the stochastic maps). Most origins of sociality were at the base of recent and small clades or along branches leading to single tips, but a major exception is the clade of mostly social mongooses (Fig. 2). The traditional division of mongooses (Herpestidae) into a mostly social clade and a mostly solitary clade of similar diversity is supported here by high probabilities of the respective state at the root of each clade (Fig. 2). However, the ancestral state of mongooses as a whole is poorly resolved ($P_{\text{solitary}} = 0.63$ vs. $P_{\text{social}} = 0.37$) so it remains unclear whether sociality evolved at the root of the social mongoose clade or at the root of mongooses and then was subsequently lost in the solitary mongoose clade. The estimated transition rates underlying this estimation suggest that sociality is lost at a rate three times faster than it is gained ($q_{\text{solitary}\to\text{social}} = 0.017$, $q_{\text{social}\to\text{solitary}} = 0.052$), indicating that sociality is often a relatively unstable trait over evolutionary time, perhaps explaining the 'tippy' distribution (appearing near the tips of the tree) with the exception of social mongooses (Fig. 2).

Historical biogeography of habitats

The best fitting model for historical biogeography was BAYAREALIKE, which absorbed almost all the Akaike weight in the model set ($w = 0.744$ without jump dispersal and $w = 0.256$ with jump dispersal). The weaker evidence for the +J version was also confirmed by a likelihood ratio test of the BAYAREALIKE models with and without J, which provided no support for the extra parameter improving the model ($\chi^2 = 0.015$, d.f. = 1, $P \approx 1$). Hence, we estimate ancestral habitats under the BAYAREALIKE model. This model does not allow 'vicariance' or 'range-switching' processes, but rather

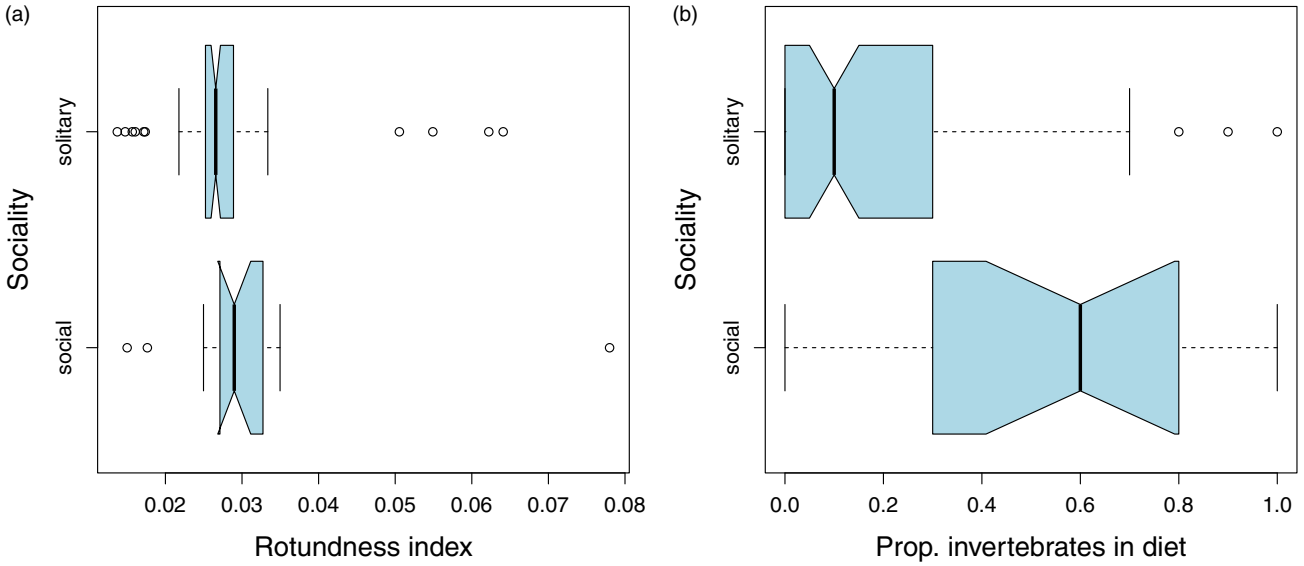

Figure 1 Association of sociality and rotundness index (a) and the proportion of invertebrates in the diet (b). Social species are more rotund and more insectivorous than solitary species. Outliers are indicated by open circles and notches are provided to aid interpretation and represent confidence intervals around the median (proportional to interquartile range and inversely proportional to sample size).

suggests that habitat evolution in this group follows a pattern of colonising new habitats whilst still existing in the original one and sometimes 'abandoning' a habitat entirely (on an evolutionary timescale).

Our ancestral habitat estimates suggest that feliforms originated and spent the early part of their evolutionary history in both forest and shrubland habitats, with several later restrictions to forest habitats only and expansions into more open habitats such as savannah and grasslands (Fig. 2). Consistent with our results from phylogenetic logistic regression (Table 1), sociality tended to evolve either in lineages already occupying at least some open habitats or (often) concordant with a shift towards more open habitat preferences compared with immediate ancestors (Fig. 2).

Evolutionary consequences of sociality

Sociality was not associated with either of our two measures of extinction risk, threatened status or experiencing population declines (Table 2). Indeed, of all the variables included in these models, only habitat type was found to have any influence in this group, whereby species in open habitats are less likely to be experiencing population declines (Fig. 3).

Our STRAPP analyses did not detect any association between sociality and speciation rate ($P = 0.942$), nor with estimated extinction ($P = 0.868$) or net diversification rate ($P = 0.942$). However, this may be lacking sensitivity in our dataset as BAMM detected very little variation in diversification rates across the phylogeny in general, with a single possible but only moderately supported increase in speciation rates in genets (genus *Genetta*).

In contrast, our phylogenetic regressions of speciation using the DR metric found that sociality was associated with slower speciation rates (Table 3, Fig. 4). We note that diurnality was associated with increased speciation rates with an effect size of similar magnitude (but opposite sign) to sociality (Table 3). Since sociality is also associated with diurnal activity patterns (Table 1), the ability of regression-style analyses to account for such confounding variables may explain why an effect was detected in this analysis but not by STRAPP, which only considers a single trait and so cannot account for such counteracting influences.

Discussion

Our results collectively demonstrate that the evolution of sociality in feliform carnivorans is associated with diverse ecological attributes that reflect the costs and constraints of group-living, for instance greater local competition, requirements for group cohesion, and defence from diurnal predation pressure. In particular, social feliforms tended to be larger, diurnal species that live in more open habitats, with a less slender body shape and a more insectivorous diet. Nevertheless, sociality evolved eight times in feliform carnivorans and we found no impact of sociality on extinction rates, so the benefits of group-living and/or sociality are often able to sufficiently offset the costs to avoid longer term population consequences. We do, however, find that social species tend to have slower speciation rates. This imposes a macroevolutionary 'cost', as species selection acts against sociality, and alongside the other costs and constraints this contributes to explaining the relative rarity of social species across vertebrates.

Increased local intraspecific competition in group-living species is perhaps the cost which our results support most clearly. Although some of our predictors of sociality could be interpreted in multiple ways, for example, diurnality may facilitate

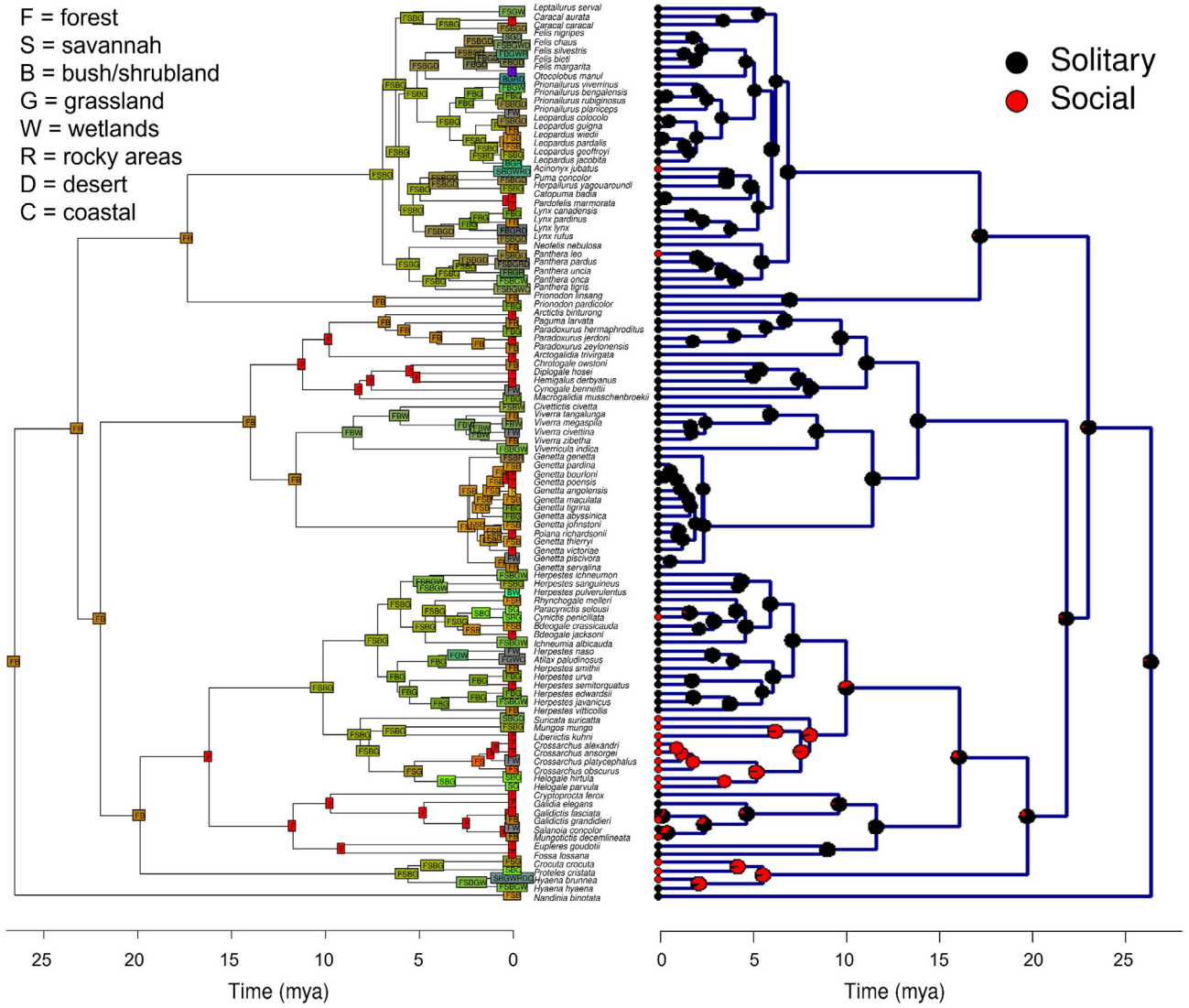

Figure 2 Ancestral state estimation of habitats (left) and sociality (right) across Feliformia.

group cohesion but could also increase predation risk (Caro, 2005), both body shape and insectivorous diets are exclusively related to competition in the context of our study. Consistent with Stankowich et al. (2014) but more directly testing the hypothesis proposed by previous authors (Gilchrist et al., 2009; Gusset, 2007; Rood, 1975), social species feed more on abundant invertebrate prey that are difficult to monopolise, which likely reduces the impact of competition for limited resources. This may also partly explain why insectivorous carnivores have relatively small home range sizes in comparison to vertebrate-eating carnivores (Gittleman & Harvey, 1982). Similarly, an effect of body shape was predicted on the basis of the higher energetic costs of more slender species (Brown & Lasiewski, 1972). Hence, our finding that social species tend to be more rotund further supports the idea that reducing such metabolic costs (and so requiring less energy per individual) has been important in the evolution of sociality in feliform carnivorans. This is likely to be a general relationship across taxa, as the hypothesised mechanism is not specific to feliforms, and so body shape may be important in the evolution of sociality in other species (Newman et al., 2011). The importance of competition may explain the generally unstable nature of sociality as revealed by our ancestral state estimations, since any reduction in the benefits received from sociality may allow the costs of competition to dominate and sociality to be lost over time.

Body size may also relate to competition, but the expected direction is unclear and perhaps dependent on other aspects of physiology or ecology that vary by taxon (e.g. interactions between habitat productivity, diet, and metabolic rate). For instance, larger animals will typically use more energy overall, but smaller animals have higher mass-specific metabolic rates

Table 2 Summary of two phylogenetic logistic regressions predicting extinction risk, one using whether the species is threatened and the other using whether the species is experiencing population declines as response variables

	β	SE	z	P
Threatened Red List status				
Intercept	−0.395	0.942	−0.419	0.675
Sociality (social)	0.274	0.651	0.421	0.674
Activity pattern (cathemeral)	0.449	0.788	0.569	0.569
Activity pattern (crepuscular)	−0.030	0.714	−0.043	0.966
Activity pattern (diurnal)	−0.160	0.540	−0.296	0.767
Habitat type (open)	−0.883	0.451	−1.955	0.051
log(body mass)	0.860	0.474	1.816	0.069
Rotundness index	11.280	24.844	0.454	0.650
Declining populations				
Intercept	0.421	0.858	0.491	0.623
Sociality (social)	−0.773	0.710	−1.087	0.277
Activity pattern (cathemeral)	−0.475	0.917	−0.518	0.604
Activity pattern (crepuscular)	1.015	1.053	0.964	0.335
Activity pattern (diurnal)	0.106	0.627	0.168	0.866
Habitat type (open)	−1.693	0.535	−3.165	0.002
log(body mass)	0.905	0.531	1.705	0.088
Rotundness index	0.710	29.463	0.024	0.981

The reference levels for categorical predictors are solitary for sociality, nocturnal for activity pattern, and closed habitats for habitat type. β, regression coefficient; SE, standard error.

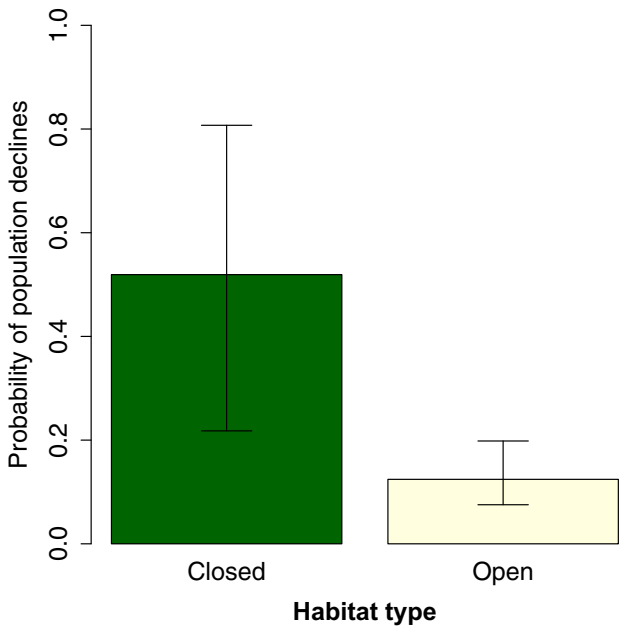

Figure 3 Relationship between habitat type and the probability of population declines, as estimated by our phylogenetic logistic regression. Species in more open habitats are less likely to be experiencing population declines. Error bars are standard errors and both those and the probabilities are plotted based on model estimates.

Table 3 Summary of phylogenetic regression predicting species-specific recent speciation rates (DR), the reference levels for categorical predictors being solitary for sociality, nocturnal for activity pattern, and closed habitats for habitat type

	β	SE	t	P
Intercept	0.259	0.020	13.281	$<2.2 \times 10^{-16}$
Sociality (social)	−0.014	0.005	−2.917	0.004
Activity pattern (cathemeral)	0.015	0.007	2.266	0.026
Activity pattern (crepuscular)	0.019	0.005	3.627	4.629×10^{-4}
Activity pattern (diurnal)	0.017	0.005	3.154	0.002
Habitat type (open)	0.004	0.004	1.003	0.318
log(body mass)	0.002	0.006	0.363	0.717
Rotundness index	−0.257	0.168	−1.524	0.131

β, regression coefficient; SE, standard error.

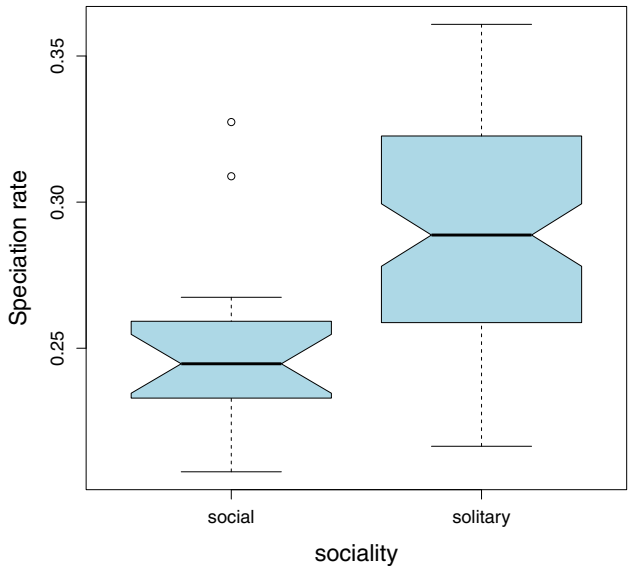

Figure 4 Association of sociality and recent speciation rates as estimated with the DR metric. Social species tend to have slower speciation rates than solitary species. Outliers are indicated by open circles and notches are provided to aid interpretation and represent confidence intervals around the median (proportional to interquartile range and inversely proportional to sample size).

and so use relatively more energy for their size (Speakman, 2005). In contrast to Stankowich et al. (2014) who found no relationship between body size and sociality in carnivorans, and Gusset's (2007) speculations that small species would be more social, we found that social species tended to be larger. It is unclear whether this difference results from the inclusion of caniform carnivorans or other variables in the models, different coding of sociality, or other reasons. It is certainly possible that any one clade (such as feliforms) may show different patterns and have different correlates than a broader or

different clade, but we have no reason to assume that the general ecological factors that might facilitate the evolution of sociality, as examined here, would be greatly different in wider groups such as carnivorans or mammals overall. Nevertheless, our results are consistent with studies in other taxa such as birds and rodents and so suggests that social species being larger than solitary species may be a general pattern (Bliard et al., 2024; Griesser et al., 2017; Müller & Soligo, 2005). The implication here is that requirements for more energy in bigger animals are offset in social species either by cooperative hunting or shifts in other attributes that reduce competition (e.g. diet or metabolic rate). In accordance with this, cursorial hunters (those using endurance to exhaust prey), particularly those focused on large prey, are more likely to cooperate with conspecifics in a range of situations including hunting (Smith et al., 2012). This may explain why group size appears to be determined by the benefits of cooperative hunting, combined with intraspecific competition and the need to defend offspring and territory from conspecifics, at least in large carnivorous mammals such as African lions *Panthera leo* (Packer et al., 1990), and African wild dogs, *Lycaon pictus* (Creel, 1997). There may also be a trade-off between reducing energy requirements and risk of predation, since larger individuals may be better able to defend against predators (Caro, 2005). However, body size may also have an effect on an individual's attractiveness as prey to predators, which is presumably the rationale for Gusset's (2007) suggestion that social species should be smaller for enhancing antipredator benefits. These factors could be especially important in social species if they are more detectable to predators via visual or auditory conspicuousness of groups.

Our finding that social species tend to be diurnal and live in more open habitats could be related to either facilitation of group cohesion or predation risk, so these explanations are difficult to tease apart and are not mutually exclusive. Reduced visual and acoustic barriers in more open habitats should certainly help group members to coordinate their activities, as should daylight if visual cues play any role in this. This may be why diurnal habitats facilitate sociality in other taxa (Müller & Soligo, 2005; Schultz et al., 2011), but since sociality is associated with higher diurnal predation risk in carnivorans there may also be an important defensive component to group-living (Stankowich et al., 2014). Indeed, it may be that sociality evolves under a combination of the existence of meaningful benefits such as antipredator defence *and* the ability to maintain group cohesion.

Previous studies have shown a variable relationship between habitat openness and sociality, with sociality either being associated with more closed habitats (in birds: Griesser et al., 2017), more open habitats (Ploceidae weavers: Song et al., 2022; cooperative mammals: Lukas & Clutton-Brock, 2017), or with no association (carnivorans: Stankowich et al., 2014). Our results add to this assemblage of studies using a combined approach of regression-based associations and historical considerations of the evolutionary history of both habitats and sociality. We find that more open habitats tend to facilitate the evolution of sociality in feliform carnivorans as suggested by Gusset (2007) for mongooses, which therefore appears to be the most common pattern in mammals. The opposing pattern in birds may therefore reflect different risks associated with cover in taxonomic groups with differing predation risks and avoidance strategies (Caro, 2005). The potential dependency on taxon and presumably ecological relevance of cover to predator–prey interactions suggests that predation risk is a bigger influence in the evolution of sociality than group cohesion. This is because group cohesion should not vary strongly between birds and mammals, as both can use visual cues and mammals often use contact calls similarly to bird calls for maintaining group cohesion (Clutton-Brock, 2016; Gilchrist et al., 2009; Jennings & Veron, 2019).

Sociality had no detectable influence on extinction risk in our dataset, in line with Purvis et al.'s (2000) work on primates and carnivorans but in contrast to further work which has found either higher or lower extinction risk in social mammals (Creighton & Nunn, 2023; Davidson et al., 2014; Muñoz-Durán, 2002). Due to conflicting results even when focused on the same clades, there is remaining uncertainty over the influence of sociality on long-term population persistence that could result from the balance of different processes in different species. For instance, where benefits to sociality are strongly dependent on group size such that costs exceed benefits in small groups, Allee effects may drive some species into an extinction vortex as populations decline (Courchamp et al., 1999). In other species, or perhaps above a group size that would result in Allee effects, cooperation within groups or other benefits of sociality may buffer social groups against harsh conditions, reducing susceptibility to population declines and extinction (Covas et al., 2008). The life histories and social systems of different species may alter the balance of these processes, and so phylogenetic comparative studies looking across a clade may find associations in either direction or none at all depending on the details of the taxa included.

A notable result in our study was that species living in more open habitats are less likely to be experiencing population declines. Because open habitats are also associated with sociality, it seems that social feliform species are indeed more likely to have reduced extinction risk but only as a consequence of living in open habitats and not once this is accounted for. Hence, an alternative explanation for the conflicting results in the literature concerning the relationship between sociality and extinction risk (Creighton & Nunn, 2023; Davidson et al., 2014; Muñoz-Durán, 2002; Purvis et al., 2000) is that different conclusions may be drawn if important confounding variables are missing from the statistical models.

Sociality appears to be associated with a reduction in speciation rates, a result that conflicts with previous work suggesting either no association with speciation rates (Magnuson-Ford & Otto, 2012; Muñoz-Durán, 2002) or suggesting faster speciation in social primates, but not other mammals, based on species richness across genera or families (Marzluff & Dial, 1991). Importantly, both studies that considered speciation rates only considered one trait (e.g. sociality) at a time, similar to our analysis with BAMM which also found no association between sociality and speciation rates. However, our regression-based analysis, which enabled us to simultaneously consider covariates, revealed slower speciation in social species

and also faster speciation in diurnal species. This last result is particularly important because Magnuson-Ford and Otto (2012) also found some evidence for diurnal species having faster speciation rates. Because we also found diurnality was associated with sociality, this raises the possibility that single-variable analyses may fail to tease apart the effects of sociality on speciation rates from those of correlated traits.

The slower speciation rates in social species that we find in this study may be a consequence of the population genetic implications of sociality, for instance in relation to effective population size. Whether effective population size increases, decreases, or has no effect on the rate of evolution depends on the mutation rates and fitness effects of mutations in the population (Lanfear et al., 2014), and empirical studies of speciation rate have therefore found conflicting relationships with effective population size (Huang et al., 2018; Parreira & Chikhi, 2015). Although many theoretical expectations predict faster speciation in social species, more realistic models of social group structures make the opposite prediction that sociality should minimise the loss of genetic diversity within populations that may ultimately lead to speciation (such that different populations retain more similarity over longer periods) (Parreira & Chikhi, 2015). Our results provide support for this and similar models that suggest sociality may affect population genetics in a way that hinders speciation. Furthermore, if social groups buffer against harsh environments (Covas et al., 2008), they may also reduce speciation by reducing mortality in poor conditions and hence partially shielding populations from selection. Therefore, our finding of slower speciation in social species may be a general pattern, but one that needs careful consideration of other associated traits to detect.

Although our results provide a range of insights into the correlates and consequences of sociality, there remains substantial scope for future work. For instance, several of the patterns we document for feliform carnivorans are consistent with some but not all previous research on other study systems. In particular, the association of open vs closed habitats with sociality appears to be highly system dependent, with a tendency for bird studies to find more sociality in closed habitats and vice versa for mammals. Understanding the reasons for this variation (suggested above to be related to predator communities and hunting strategies) would be productive for fully grasping how habitat influences the evolution of sociality. In particular, the tendency of social mammals to use visual and auditory cues to maintain contact and proximity to group members may have different ecological implications to the use of chemical cues and place-based association (e.g. returning to nests rather than staying close to conspecifics) by many social insects. Similarly, associations between sociality and both speciation rates and extinction risk have been highly variable between studies, and hence it would be fruitful for further work to investigate the underlying causes of this variation. In this vein our emphasis that controlling for correlated variables (rather than considering sociality in isolation) may be an important approach, since sociality may have a complex relationship with speciation and extinction via confounding or mediating variables.

Conclusion

We provide evidence for a set of costs and constraints on the evolution of sociality in mammals using a phylogenetic comparative approach applied to feliform carnivorans. Sociality imposes increased local competition as a result of group-living, and we find that it is therefore associated with body shapes and diets that reduce competition. Social species also tend to be larger, which increases absolute energetic demands but likely enables benefits such as better defence or cooperative hunting. Ecologies that are consistent with facilitating group cohesion such as diurnal activity and living in more open habitats are also associated with sociality, but these may also be related to increased predation risk, which may further enhance the benefits of group-living. Sociality has evolved multiple times in feliforms and is not linked to higher extinction risk, suggesting that the benefits often outweigh the costs, but it is also relatively ephemeral over evolutionary time and is associated with slower speciation rates, which might explain its rarity across the vertebrate tree of life. Taken together, sociality evolves when a (perhaps finely balanced) 'golden trio' of factors occur: (1) the environment enables groups to maintain cohesion, (2) costs of competition can be mitigated, and (3) sufficient benefits accrue to outweigh the costs.

Author contributions

K.A. conceived the ideas; K.A. and H.J.N. supervised the project; I.S. and K.A. collected the data; I.S. and K.A. analysed the data; I.S. wrote the first draft of the manuscript; all authors revised the first draft and agreed on the final submission.

Data availability statement

The data and R code used for this study, plus additional output files for BAMM and BioGeoBEARS analyses are deposited in FigShare and are freely accessible here: https://doi.org/10.6084/m9.figshare.27651678.v2.

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Supporting Information

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

Table S1. Phylogenetic imbalance ratios for all categorical variables (and pairwise combinations) used in our models.