RESEARCH ARTICLE

ethology | WILEY

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

Charlotte-Anaïs Olivier[1,2] | Adrian V. Jaeggi[3] | Loren D. Hayes[4] | Carsten Schradin[1,2]

[1]IPHC, UNISTRA, CNRS, Strasbourg, France

[2]School of Animal, Plant & Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa

[3]Institute of Evolutionary Medicine, University of Zurich, Zurich, Switzerland

[4]Department of Biology, Geology, and Environmental Science, University of Tennessee at Chattanooga, Tennessee, USA

Correspondence
Charlotte-Anaïs Olivier, IPHC, UNISTRA, CNRS, 23 rue du Loess, 67200 Strasbourg, France.
Email: charlotte-anais.olivier@iphc.cnrs.fr

Funding information
CNRS; University of Strasbourg; University of Tennessee at Chattanooga Center of Excellence in Applied Computational Science and Engineering

Abstract

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 However, one unpublished study indicated high levels of extra-pair paternity.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

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

1 | INTRODUCTION

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

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

Describing all four components of a social systems is a challenge, for a number of reasons. For example, it was previously assumed that "socially monogamous" species are pair-living (social organization), have pair bonds (social structure), and engage in biparental care (Kleiman, 1977; Mock & Fujioka, 1990). However, it is well known that several pair-living taxa do not fit this syndrome (Kleiman, 1977), such as dwarf antelopes (Bovidae) that do not exhibit biparental care (Komers, 1996), elephant-shrews (Macroscelididae) that do not have pair bonds (i.e., individuals showing a preference for a specific

opposite sex-individual, which can be tested experimentally: Carter et al., 1995a, 1995b; Garnier & Schradin, 2019) or exhibit biparental care (Rathbun & Rathbun, 2006). Most confusion, however, arises from the inconsistent use of the term "monogamy" (see above and Kappeler, 2019; Solomon & Ophir, 2020), which should be restricted to describe the mating system where reproduction occurs mainly within pairs (Kappeler, 2019; Kappeler & van Schaik, 2002; Mock & Fujioka, 1990). For understanding the evolution of pair living, the different components of social systems should be studied separately from each other (Fernandez-Duque et al., 2020; Huck et al., 2020; Kappeler, 2019).

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

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

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

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

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

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

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

2 | MATERIALS AND METHODS

2.1 | Literature searches

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

2.2 | Social organization

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

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

2.3 | Mating system

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

2.4 | Social structure

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

2.5 | Care system

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

2.6 | Dataset comparison

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

2.7 | Predictors for social organization

We included the following predictors in our Bayesian model described below: body mass, population density, number of studies per population, and habitat heterogeneity (see Tables S1–S3). Habitat

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

2.8 | Phylogenetic comparative analysis

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

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

the probability of differences between the probabilities of two social organizations.

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

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

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

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

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

3 | RESULTS

3.1 | Social organization

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

3.2 | Mating system

Our search generated only one paper that reported observations of mating in the field (Rathbun, 1979). A male _Rhynchocyon chrysopygus_ chased the female and then copulated with her during 2 s with five rapid copulations. Schubert et al. (2012) found in captive experiments that female _Macroscelides proboscideus_ showed as many sexual interactions with a neighboring male as with her pair partner, and that males actively aimed to mate with non-pair neighboring females. In an unpublished poster on a study using micro-satellites

to determine paternity in _Macroscelides proboscideus_, Peffley et al. (2009) found for the population studied by Schubert et al. (2009) that only two out of six mother-offspring families resulted from serially monogamous mating. From a sample of 19 offspring, the male of the pair was the sire of only seven. At least six offspring were sired by another male than the female's social mating partner.

3.3 | Social structure

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

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

3.4 | Care system

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

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

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

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

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

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

3.5 | Dataset comparison

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

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

3.6 | Phylogenetic comparative analysis

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

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

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

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

TABLE 4 Care system identified in literature for Macroscelidea

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

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

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

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

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

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

In order to understand which kind of variable social organization was the most likely ancestral state, a second analysis was conducted using all different categories of variable social organization (model 2; Figure 2; Tables S9). The phylogenetic signal of this analysis was moderate (mean = 0.32, 95% CI = 0.0027–0.74). Solitary + pair-living + group-living was the most likely ancestral state (mean = 0.29, 95% CI = 0–1), followed by pair + group-living ((mean = 0.28, 95% CI = 0–1) and solitary + pair-living (mean = 0.19, 95% CI = 0–1). Those three social organizations were part of the category "variable"

in our first analysis (Figure 1) and were respectively 60%, 67%, and 45% more likely than pair-living (Figure 2; Tables S9). The probability that the ancestral social organization was solitary was relatively low (mean = 0.12, 95% CI = 0–0.99). Group-living (mean = 0.06, 95% CI = 0–0.52) and pair-living (mean = 0.05, 95% CI = 0–0.32) were the least likely ancestral social organization.

In model 3, we calculated what the ancestral state would be if we only took the main social organization into account, neglecting variability (Figure 3). The phylogenetic signal was again moderate (mean = 0.36, 95% CI = 0.00008–0.8). Pair-living was the most likely ancestral state (mean probability = 0.58, 95% CI = 0–1), but again with large uncertainty. Group-living (mean = 0.08, 95%
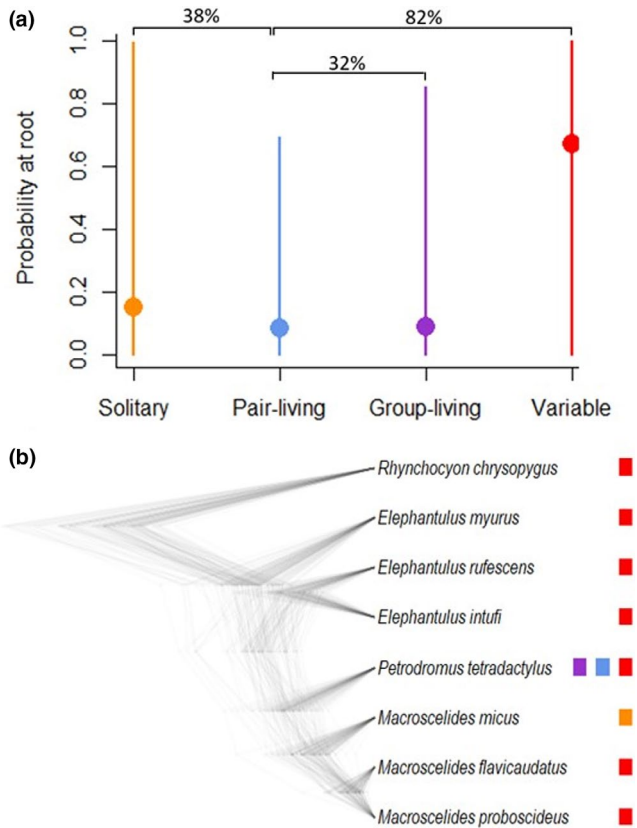
FIGURE 1 (a) The likelihood of each social organization (solitary, pair-living, group-living, and variable) being the ancestral state ("probability at root"). Percentages represent the probability that the difference between the estimated probabilities of different social organizations compared to pair-living was greater than 0 (e.g., variable is 82% more likely than pair-living). (b) Phylogeny of the eight Macroscelidea species with data on social organization from 12 populations. Colored boxes at the tip of phylogenetic tree correspond to social organization(s) observed within species (orange = solitary; blue = pair-living; violet = group-living; and red = variable), and if two populations of the same species had different social organization, then two boxes are shown

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

4 | DISCUSSION

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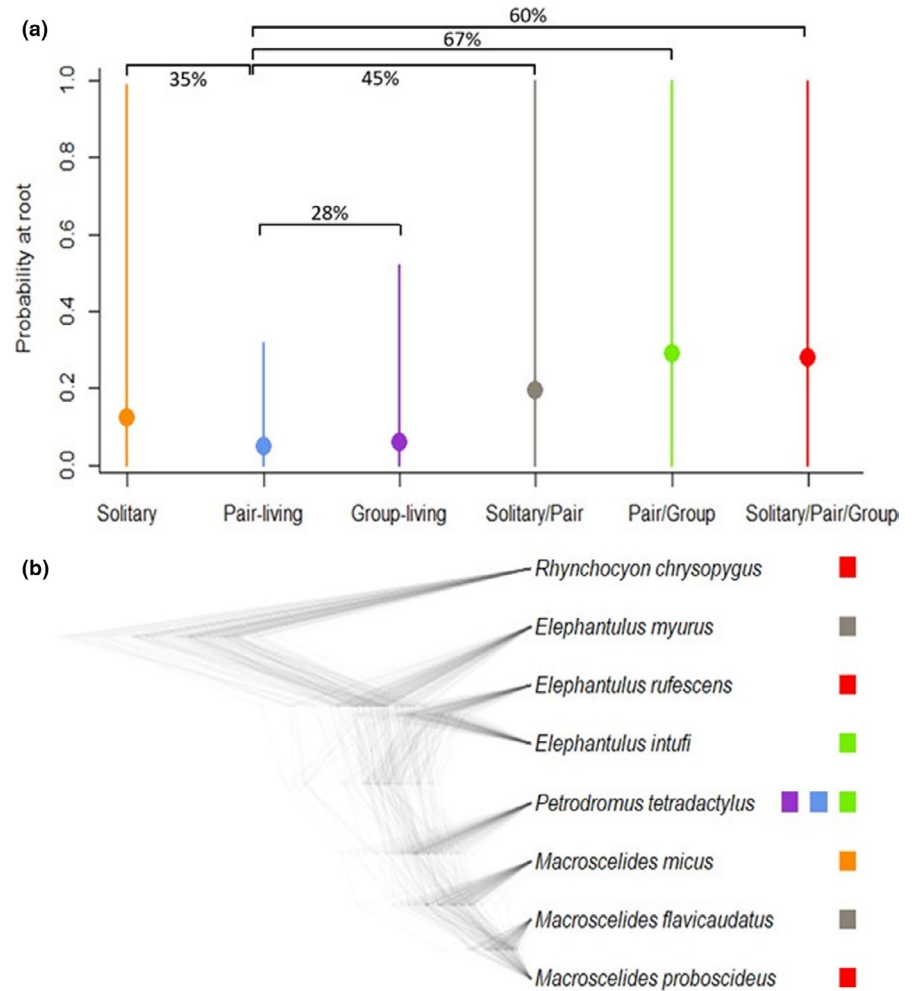
4.1 | Social system

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

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

4.2 | Dataset comparison

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

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

4.3 | Phylogenetic comparative analysis

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

Most Macroscelidea had a variable type of social organization which was also the most likely ancestral form of social organization. More precisely, it was solitary + pair-living + group-living followed by pair + group-living that were the most likely ancestral forms of social organization. The uncertainty surrounding these inferences was large. Of note is that the previous assumption, of a pair-living ancestral social organization was the least supported. Importantly, when considering the variation reported from the field, pair-living always received very little support as the ancestral form. In contrast, when we considered only the main social organization (and ignored variation), pair-living became the most likely ancestral form of social organization, but with a lower mean probability than the variable ancestral state in the first analysis. What we can hypothesize is that the ancestor of all Macroscelidea was able to be pair-living, but with
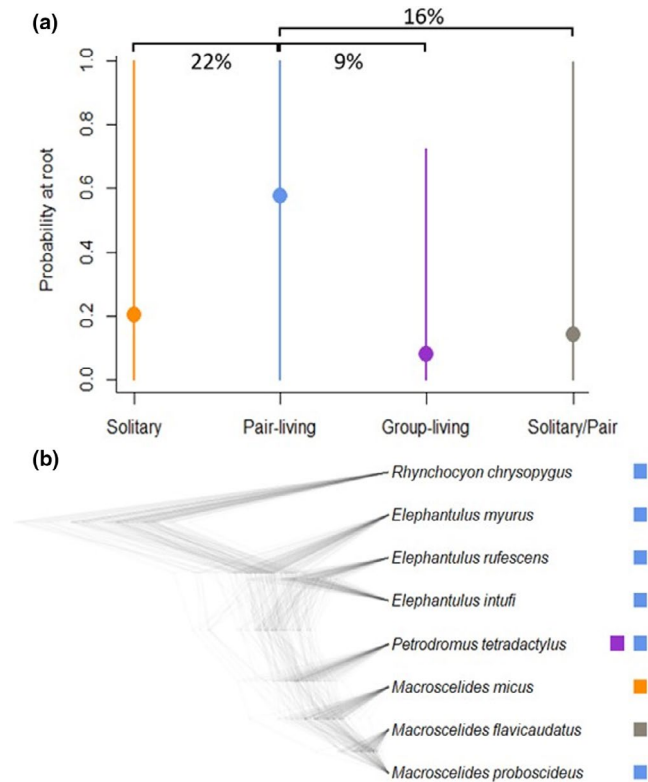
elephant-shrews to be pair-living and Lukas and Clutton-Brock (2013) reported 93% of species as pair-living. There are several explanations for these differences. We relied only on information from field studies, whereas Lukas and Clutton-Brock (2013) also included data from captivity and assumed that species without data have the same form of social organization as closely related species. Thus, their database comprised of 15 species while we only found field data for eight species. The references in their database include one paper making the general statement that Macroscelidea are monogamous (Rathbun & Rathbun, 2006), one paper reporting data from captivity (Lawes & Perrin, 1995), one paper that cannot resolve the social organization of the studied species (*Petrodromus tetradactylus*; Jennings & Rathbun, 2001), as well as one paper that does not provide data on social organization (Koontz & Roeper, 1983). Interestingly, the only species which they do not regard to be monogamous but solitary, *Petrodromus tetradactylus*, was reported by us to be group or pair-living. Our results compare well with the expert opinions published in the book Walker's Mammals of the World (Nowak & Wilson, 1999). Like us, they report data for only eight species, 12.5% of which were believed to be solitary, 25% to be pair-living, and 62.5% to be variable. Based on these differences, we argue that our database based on primary field studies is the most robust of these datasets.

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

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

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

social organization, more field studies would be needed, especially on the 11 species for which we could not find any data.

4.4 | Social monogamy versus sengi syndrome

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

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

It was recognized early on that Macroscelidea did not fit the typical description of social monogamy (Kleiman, 1977; Rathbun & Rathbun, 2006). Instead, Rathbun & Rathbun, 2006 discussed a "sengi syndrome" for small mammals with the sengi typic morphology: compact body, large head and long and narrow snout. Species falling under this syndrome have a relatively long life expectancy, produce few precocial young and have an insectivorous diet, which can explain a conserved social organization of pair-living even though the different species inhabit diverse habitats. The sengi syndrome has been discussed in relation to their phylogenetic ancestry (Rathbun & Rathbun, 2006). We found that phylogeny has a moderate effect on social organization, suggesting that social organization is somewhat

constrained by phylogenetic history, but can also adapt to local ecology. Indeed, the phylogenetic signal in all of our three models had a much higher mean probability compared to other studies (e.g., 0.05 in Jaeggi et al., 2020 on Artiodactyla social organization). Thus, our study is not in contrast to the suggested sengi syndrome but indicates that instead of fixed pair-living, a flexible social organization including solitary and pair-living is likely part of this syndrome.

5 | CONCLUSIONS

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

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

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

ORCID
Charlotte-Anaïs Olivier https://orcid.org/0000-0003-3382-6354
Adrian V. Jaeggi https://orcid.org/0000-0003-1695-0388
Loren D. Hayes https://orcid.org/0000-0003-0713-416X
Carsten Schradin https://orcid.org/0000-0002-2706-2960

REFERENCES
Agnani, P., Kauffmann, C., Hayes, L. D., & Schradin, C. (2018). Intraspecific variation in social organization of Strepsirrhines. *American Journal of Primatology*, *80*(5), e22758. https://doi.org/10.1002/ajp.22758

Baker, A. J., Lengel, K., McCafferty, K., & Hellmuth, H. (2005). Black-and-rufous sengi (*Rhynchocyon petersi*) at the Philadelphia Zoo. *Afrotherian Conservation*, *3*, 6–7.

Cantoni, D., & Vogel, P. (1989). Social organization and mating system of free-ranging, greater white-toothed shrews, *Crocidura russula*. *Animal Behaviour*, *38*(2), 205–214. https://doi.org/10.1016/S0003-3472(89)80083-1

Carter, C., Courtney Devries, A., & Getz, L. L. (1995a). Physiological substrates of mammalian monogamy: The prairie vole model. *Neuroscience & Biobehavioral Reviews*, *19*(2), 303–314. https://doi.org/10.1016/0149-7634(94)00070-H

Carter, C., Courtney Devries, A., & Getz, L. L. (1995b). *Prairie voles social behavior attachment monogamy oxytocin vasopressin adrenal steroids*.

Clutton-Brock, T. H. (1989). Review lecture: Mammalian mating systems. *Proceedings of the Royal Society B: Biological Sciences*, *236*(1285), 339–372. https://doi.org/10.1098/rspb.1989.0027

Clutton-Brock, T. H. (2021). Social evolution in mammals. *Science*, *373*(eabc9699). https://doi.org/10.1126/science.abc9699

Cohas, A., & Allainé, D. (2009). Social structure influences extra-pair paternity in socially monogamous mammals. *Biology Letters*, *5*(3), 313–316. https://doi.org/10.1098/rsbl.2008.0760

Dalerum, F. (2007). Phylogenetic reconstruction of carnivore social organizations. *Journal of Zoology*, *273*(1), 90–97. https://doi.org/10.1111/j.1469-7998.2007.00303.x

de Villemereuil, P. (2014). *General quantitative genetic methods for comparative biology*. https://doi.org/10.1007/978-3-662-43550-2_11

Dobson, F. S., Way, B. M., & Baudoin, C. (2010). Spatial dynamics and the evolution of social monogamy in mammals. *Behavioral Ecology*, *21*(4), 747–752. https://doi.org/10.1093/beheco/arq048

Emlen, S. T., & Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science*, *197*(4300), 215–223.

Fernandez-Duque, E., Huck, M., Van Belle, S., & Di Fiore, A. (2020). The evolution of pair-living, sexual monogamy, and cooperative infant care: Insights from research on wild owl monkeys, titis, sakis, and tamarins. *American Journal of Physical Anthropology*, *171*(S70), 118–173. https://doi.org/10.1002/ajpa.24017

Fitzgibbon, C. D. (1995). Comparative ecology of two elephant-shrew species in a Kenyan coastal forest. *Mammal Review*, *25*(1–2), 19–30. https://doi.org/10.1111/j.1365-2907.1995.tb00434.x

Fitzgibbon, C. D. F. (1997). The adaptive significance of monogamy in the golden-reumped elephant-shrew. *Journal of Zoology*, *242*(1), 167–177. https://doi.org/10.1111/j.1469-7998.1997.tb02937.x

Garber, P. A., Porter, L. M., Spross, J., & Di Fiore, A. (2016). Tamarins: Insights into monogamous and non-monogamous single female social and breeding systems. *American Journal of Primatology*, *78*(3), 298–314. https://doi.org/10.1002/ajp.22370

Garnier, L., & Schradin, C. (2019). Pair bonding in monogamously and polygynously kept African striped mice, Rhabdomys pumilio. *Animal Behaviour*, *150*, 69–76. https://doi.org/10.1016/j.anbehav.2019.02.001

Geist, V. (1974). On the relationship of social evolution and ecology in ungulates. *American Zoologist*, *14*, 205–220. https://doi.org/10.1093/icb/14.1.205

Gowaty, P. A., & Buschhaus, N. (1998). Ultimate causation of aggressive and forced copulation in birds: Female resistance, the CODE hypothesis, and social monogamy. *American Zoologist*, *38*(1), 207–225. https://doi.org/10.1093/icb/38.1.207

Heritage, S. (2018). Order MACROSCELIDEA. In D. E. Wilson, & R. A. Mittermeier (Eds.), *Handbook mammals of the World, 8. Insectivors, sloths and colugos*. Lynx Edicions.

Hoffmann, S., Bennett, N. C., Jansen van Vuuren, B., & Lutermann, H. (2019). Space use and the evolution of social monogamy in eastern rock sengis. *Ethology*, *126*(4), 393–402.

Huck, M., Di Fiore, A., & Fernandez-Duque, E. (2020). Of apples and oranges? The evolution of "Monogamy" in non-human primates. *Frontiers in Ecology and Evolution*, *7*, 472. https://doi.org/10.3389/fevo.2019.00472

Huck, M., Löttker, P., & Heymann, E. W. (2004). Proximate mechanisms of reproductive monopolization in male moustached tamarins (*Saguinus mystax*). *American Journal of Primatology*, *64*(1), 39–56. https://doi.org/10.1002/ajp.20060

Jaeggi, A. V., Miles, M. I., Festa-Bianchet, M., Schradin, C., & Hayes, L. D. (2020). Variable social organization is ubiquitous in Artiodactyla and probably evolved from pair-living ancestors. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1926), 20200035. https://doi.org/10.1098/rspb.2020.0035

Jennings, M. R., & Rathbun, G. B. (2001). *Petrodromus tetradactylus*. *Mammalian Species*, *2001*(682), 1–6. https://doi.org/10.1644/15451410(2001)682<0001:PT>2.0.CO;2

Kappeler, P. M. (2019). A framework for studying social complexity. *Behavioral Ecology and Sociobiology*, *73*(1), 13. https://doi.org/10.1007/s00265-018-2601-8

Kappeler, P. M., & Pozzi, L. (2019). Evolutionary transitions toward pair living in nonhuman primates as stepping stones toward more complex societies. *Science Advances*, *5*(12), eaay1276. https://doi.org/10.1126/sciadv.aay1276

Kappeler, P. M., & van Schaik, C. P. (2002). Evolution of primate social systems. *International Journal of Primatology*, *34*.

Kingdon, J., Happold, D., Butynski, T., Hoffmann, M., Happold, M., & Kalina, J. (2013). *Mammals of Africa* (Vol. *1*). A&C Black (and earlier editions).

Kleiman, D. G. (1977). Monogamy in mammals. *The Quarterly Review of Biology*, *52*(1), 39–69. https://doi.org/10.1086/409721

Kleiman, D. G. (1981). Correlations among life history characteristics of mammalian species exhibiting two extreme forms of monogamy. *Natural Selection and Social Behavior*, 332–344.

Komers, P. E. (1996). Obligate monogamy without paternal care in Kirk's dikdik. *Animal Behaviour*, *51*(1), 131–140. https://doi.org/10.1006/anbe.1996.0011

Koontz, F. W., & Roeper, N. J. (1983). *Elephantulus rufescens*. *Mammalian Species*, *204*, 1. https://doi.org/10.2307/3503972

Kvarnemo, C. (2018). Why do some animals mate with one partner rather than many? A review of causes and consequences of monogamy: Causes and consequences of monogamy. *Biological Reviews*, *93*(4), 1795–1812. https://doi.org/10.1111/brv.12421

Lawes, M. J., & Perrin, M. R. (1995). Risk-sensitive foraging behaviour of the round-eared elephant-shrew (*Macroscelides proboscideus*). *Behavioral Ecology and Sociobiology*, *37*(1), 31–37. https://doi.org/10.1007/BF00173896

Linn, I., Perrin, M. R., & Hiscocks, K. (2007). Use of space by the four-toed elephant-shrew *Petrodromus tetradactylus* (Macroscelidae) in Kwazulu-Natal (South Africa). *Mammalia*, *71*(1/2). https://doi.org/10.1515/MAMM.2007.012

Loue, S. (2007). *Sexual partnering, sexual practices, and health*. Springer Science & Business Media.

Lukas, D., & Clutton-Brock, T. H. (2013). The evolution of social monogamy in mammals. *Science*, *341*(6145), 526–530. https://doi.org/10.1126/science.1238677

McElreath, R. (2019). *Statistical rethinking*, 2nd ed. CRC Press.

Mock, D. W., & Fujioka, M. (1990). Monogamy and long-term pair bonding in vertebrates. *Trends in Ecology & Evolution*, *5*(2), 39–43. https://doi.org/10.1016/0169-5347(90)90045-F

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*(2), 133–142.

Nowak, R. M., & Wilson, E. (1999). *Walker's mammals of the World*, 6th ed. John Hopkins University Press.

Oxenham, K. H., & Perrin, M. R. (2009). The spatial organization of the four-toed elephant-shrew (*Petrodromus tetradactylus*) in Tembe Elephant Park, KwaZulu-Natal, South Africa. *African Zoology*, *44*(2), 171–180. https://doi.org/10.3377/004.044.0205

Peffley, S., Griffin, M., Redus, L., Scott, E., Schubert, M., & Ribble, D. (2009). *Investigation on monogamous lifestyles of the Round-eared sengi from South Africa. Poster presentation, Poster available upon request from last author C. Schradin*.

Rathbun, G. B. (1979). The social structure and ecology of elephant-shrews. *Zeitschrift Fur Tierpsychologie*, *20*, 1–75.

Rathbun, G. B., & Dumbacher, J. P. (2015). Home range and use of diurnal shelters by the Etendeka round-eared sengi, a newly discovered Namibian endemic desert mammal. *PeerJ*, *3*, e1302. https://doi.org/10.7717/peerj.1302

Rathbun, G. B., & Rathbun, C. D. (2006). Social structure of the bush-veld sengi (*Elephantulus intufi*) in Namibia and the evolution of monogamy in the Macroscelidea. *Journal of Zoology*, *269*(3), 391–399. https://doi.org/10.1111/j.1469-7998.2006.00087.x

Ribble, D. O., & Perrin, M. R. (2005). *Social organization of the Eastern Rock Elephant-shrew (Elephantulus myurus): The evidence for mate guarding*. 9.

Ricci, J.-C., & Vogel, P. (1984). Nouvelle méthode d'étude en nature des relations spatiales et sociales chez *Crocidura russula* (Mammalia, Soricidae). *Mammalia*, *48*(2). https://doi.org/10.1515/mamm.1984.48.2.281

Rovero, F., Rathbun, G. B., Perkin, A., Jones, T., Ribble, D. O., Leonard, C., & Doggart, N. (2008). A new species of giant sengi or elephant-shrew (genus Rhynchocyon) highlights the exceptional biodiversity of the Udzungwa Mountains of Tanzania. *Journal of Zoology*, *274*(2), 126–133. https://doi.org/10.1111/j.1469-7998.2007.00363.x

Sauer, E. G. F. (1973). Zum sozialverhalten der kurzohrigen elefanten-spitzmaus, *Macroscelides proboscideus*. *Z. Saugetierkd*, *38*, 65–97.

Schradin, C., Hayes, L. D., Pillay, N., & Bertelsmeier, C. (2018). The evolution of intraspecific variation in social organization. *Ethology*, *124*(8), 527–536. https://doi.org/10.1111/eth.12752

Schubert, M., Pillay, N., Ribble, D. O., & Schradin, C. (2009). The Round-eared sengi and the evolution of social monogamy: Factors that constrain males to live with a single female. *Ethology*, *115*(10), 972–985. https://doi.org/10.1111/j.1439-0310.2009.01684.x

Schubert, M., Rödel, H. G., Pillay, N., & von Holst, D. (2012). Promiscuous tendencies in the round-eared sengi: A male's perspective. *Journal of Ethology*, *30*(1), 43–51. https://doi.org/10.1007/s10164-011-0288-7

Schülke, O., & Kappeler, P. M. (2003). So near and yet so far: Territorial pairs but low cohesion between pair-partners in a nocturnal lemur, Phaner furcifer. *Animal Behaviour*, *65*, 331–343.

Solomon, N. G., & Ophir, A. G. (2020). Editorial: What's love got to do with it: The evolution of monogamy. *Frontiers in Ecology and Evolution*, *8*, 110. https://doi.org/10.3389/fevo.2020.00110

Tecot, S. R., Singletary, B., & Eadie, E. (2016). Why "monogamy" isn't good enough. *American Journal of Primatology*, *78*(3), 340–354. https://doi.org/10.1002/ajp.22412

Valomy, M., Hayes, L. D., & Schradin, C. (2015). Social organization in Eulipotyphla: Evidence for a social shrew. *Biology Letters*, *11*(11), 20150825. https://doi.org/10.1098/rsbl.2015.0825

SUPPORTING INFORMATION

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