Social organisation of the narrow-striped mongoose (*Mungotictis decemlineata*) in Kirindy Forest C.N.F.E.R.E.F., Madagascar

Dissertation

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GENERAL INTRODUCTION

Social behaviour in animals influences the determinants of individual fitness, namely survival and reproduction. Natural selection of social behaviours has lead to a diversity of social systems including large variations of sociality among different species. Investigating animal social systems is particularly interesting for behavioural biologists because they integrate ecological, demographic and phylogenetic determinants and the interrelated evolutionary mechanisms. However, it can be challenging to distinguish between ultimate causes and consequences. This makes it often difficult to identify the direction of evolutionary transitions. In this respect, studies on phylogenetic closely related taxa which have evolved under distinct selection pressures over significant evolutionary time scales can help to determine the pace, determinants and mechanisms of social evolution. In the present thesis, I studied the social organisation and mating system of the narrow-striped mongoose (*Mungotictis decemlineata*), a representative of a poorly studied group of carnivores, the Malagasy Eupleridae. These endemic carnivores are the closest relatives of the mongooses (Herpestidae), and have evolved in isolation on the island of Madagascar for more than 20 millions of years. On this basis, the overall aim of this thesis is to shed light on the characteristics of the social organisation and mating system of the narrow-striped mongoose and to contribute to a better understanding of the determinants of social patterns in a comparative perspective to the Herpestidae and other Carnivora. For a thorough understanding, I will first present the distinct components characterising mammalian social systems under consideration of socio-ecological theory. In the following, I will describe important determinants which have been found to cause variation in social patterns with a focus on the social organisation and mating system. In this context, I will illustrate patterns of sociality within the Carnivora, and particularly within the mongooses. Based on this, I will define the approach and specific goals of this study.

Characteristics of social systems

Social organisation

The key aspects for the investigation of social systems include spacing, grouping and mating patterns, as well as the variability in patterns and quality of social relationships. In this respect, three discrete components of social systems were defined: social organisation, mating system and social structure (Kappeler & van Schaik 2002). These entities are interrelated, but can vary independently from each other because they are subject to different selection factors. The social organisation characterises the demographic structure, i.e. the number of individuals, their age and sex ratio, the cohesion of social units in space and time and their genetic structure. Solitary, pair-living and group-living species are generally distinguished within this concept. While in solitary species individuals are not permanently associated with conspecifics and do not synchronise their activity, in gregarious species, permanent associations of at least one male and one female (pair-living) or three or more adult individuals (group-living) exist (Kappeler 2009).

Solitariness represents the ancestral condition in mammals and the most common organisation, whereas only a small proportion lives in pairs (Lukas & Clutton-Brock 2013). Group-living species can be found in virtually all mammalian groups, but they show remarkable variation in group size and composition (Jarman 1974; Gittleman 1989a; van Schaik & Kappeler 1997; Ebensperger & Cofré 2001; Kerth *et al.* 2001; Mitani *et al.* 2012). To explain this variation in social organisation, multiple factors have been considered such as the distribution and characteristics of resources and predation risk, but also the influence of life-history traits (e.g. body size and sexual dimorphism), reproductive strategies and phylogenetic relationships (Clutton-Brock & Harvey 1977; Macdonald 1983; van Schaik 1983; Ruckstuhl 2007; Shultz *et al.* 2011; Clutton-Brock & Janson 2012; Kappeler *et al.* 2013).

The socio-ecological model is one particular framework which integrates predominantly ecological factors to explain species-specific distributions of females and males within populations as well as female social relationships (Crook 1970; Emlen & Oring 1977; Wrangham 1980; Terborgh & Janson 1986; Sterck *et al.* 1997). It predicts the distribution of females according to the distribution of resources and resulting feeding competition, and predation risk, whereas the distribution of males is predicted by the spatio-temporal distribution of receptive females. This difference is determined by different selection pressures operating on females and males due to differences in potential reproductive rates and investment in reproduction between the sexes (Trivers 1972; Clutton-Brock & Parker 1992). Particularly in group-living primates, the socio-ecological model has been used and modified to explain variation in group size and structure in relation to the distribution of and competition for food resources, and additionally the risk of predation and infanticide (Wrangham 1980; van Schaik 1996; Sterck *et al.* 1997). The same principles have also been applied in both solitary (mouse lemurs: Dammhahn & Kappeler 2009) and pair-living species (fork-marked lemurs: Schülke 2003). In contrast, the extent of its applicability in other taxa remains unclear (Aureli *et al.* 2008). An increased complexity arises from the largely unresolved question, how food distribution, abundance and predictability are interrelated in their relative impact on feeding competition (Clutton-Brock & Janson 2012). The lack of an accurate basis for assessing the intensity of feeding competition and its impact on group size hampers the empirical testability of the socio-ecological model. Therefore, Clutton-Brock & Janson (2012) propose the incorporation of other explaining factors such as phylogenetic information, and the integration of empirical evidence from other mammalian groups to a larger extent.

In other mammalian groups, related hypotheses have been brought up to explain variation in several aspects of social organisation. In carnivores, home range sizes are mainly set by metabolic needs and the type of diet (Gittleman & Harvey 1982). This link has been shown for several carnivore species and provides the fundament of the resource dispersion hypothesis (Macdonald 1983). This hypothesis predicts that territory size is determined by resource dispersion, while, within the territory, group size is constrained by heterogeneity and total richness of resources, irrespective of other direct individual benefits (Johnson *et al.* 2002).

In social ungulates, sexual segregation in organisation outside the breeding season has been related to sex differences in predation risk, forage selection and activity budget, emphasizing sexual body size dimorphism as a central evolutionary factor (Ruckstuhl & Neuhaus 2002). However, explicit testing in mammalian taxa other than ungulates, in particular in sexually non-dimorphic species has been notably rare (Ruckstuhl 2007).

In addition, social organisation is subject to large variations not only among, but also within mammalian species. Variations include the broad categories of solitariness, pair-living and group-living in space and time, and within and among populations (Schradin & Pillay 2005; Maher & Burger 2011; Garber *et al.* 2015). A closer investigation of intra-specific variation in social organisation can be highly useful to identify the proximate and ultimate mechanisms of sociality (Schradin 2013). Apart from proximate environmental factors such as food characteristics, the diverse set of environmental cues can determine developmental plasticity, social flexibility and demographic changes, leading to a remarkable variation in sociality within species (Piersma & Drent 2003; Ellers & Stuefer 2010; Siegeler *et al.* 2011). Furthermore, it has become apparent that genetic variation can induce variation in social organisation, for example as a result of alternative reproductive tactics in one or both sexes and local adaptations of different populations (Schradin 2013).

In general, the genetic basis of social organisation as well as the influence of genetic variation both within and among species is not well understood yet (Schradin 2013). Philopatry and dispersal are two major aspects shaping the demographic as well as the genetic structure of social units. They are strongly connected to the reproductive strategies of individuals, and mediated by the mechanisms of competition, kin discrimination and inbreeding avoidance (Perrin & Mazalov 1999; Perrin *et al.* 2001). For the majority of mammalian species, this results in a male-bias in dispersal (Greenwood 1980). The genetic structure underlying the social patterns thereby provides a strong link to the characteristics of the social and genetic mating system.

Mating system

The mating system describes the average number of sexual partners of males and females. It is distinguished from the reproductive system (=genetic mating system), which refers to the reproductive consequences of mating interactions (Kappeler & van Schaik 2002). Based on ecological and phylogenetic factors, a large diversity of mating systems has evolved. In mammals, monogamy and polyandry are rare; more than 90% of the species are polygynous or promiscuous, including large variations in the stability of mating bonds and sex-specific strategies (Emlen & Oring 1977; Clutton-Brock 1989).

Spacing patterns and mating system are in close relationship (Clutton-Brock & Harvey 1978). The ranging behaviour of females and the stability of female groups, both affecting the defensibility of females by males, represent the crucial determinants for the evolution of successful male mating strategies (Clutton-Brock 1989). *Mate guarding* and *roaming* can be distinguished as broad categories of male mating strategies, comprising several different varieties. Infanticide risk and paternal care have been assumed as the impacting factors for the evolution of monogamy (van Schaik & Kappeler 1997; van Schaik 2000). However, recent comparative analyses have indicated that competition and intolerance between females and resulting low female densities are the determinants for the evolution of social monogamy, while paternal care is rather a consequence than a cause of it (Lukas & Clutton-Brock 2013).

While in the majority of mammalian species, the variance of reproductive success is higher in males than in females, females compete stronger for breeding opportunities than males in some group-living species. This competition results in high levels of sex-specific reproductive skew, particularly evident in cooperative breeders (Faulkes & Abbott 1997; Clutton-Brock *et al.* 2006). Reproductive skew theory aims to reveal how reproductive partitioning in social groups of cooperative breeders arises in spite of intense reproductive competition (Vehrencamp 1983a, b; Reeve & Ratnieks 1993). Transactional skew models assume that one individual has full control over reproduction, but may have to relinquish a share of reproduction in order to prevent other individuals from leaving the group. By contrast, compromise models allow for incomplete control over reproduction within the group, but ignore group stability and outside options, such as emigrating to breed elsewhere (Reeve *et al.* 1998; Johnstone 2000; Johnstone & Cant 2009). Recently, it has been argued that the variety of models largely ignores the underlying genetics of skew, and that a quantitative genetic approach is essential in order to determine genetic and non-genetic characteristics of reproductive skew, to infer its heritability and thus the impact of natural selection (Nonacs & Hager 2011).

Enhanced researched on the genetic structure of social units in several species has revealed an influence of mate choice and alternative reproductive tactics, such as extra-group paternity on the distribution of reproductive success (Isvaran & Clutton-Brock 2007; Nichols *et al.* 2010; Sanderson *et al.* 2015). Furthermore, it has become apparent that reproductive competition can modify even the broad categories of social organisation within a species over time (Schradin *et al.* 2010). These results emphasise the close connection between social organisation and the mating system.

In contrast, the link of these two entities to the **social structure,** third component of the social system, is less pronounced. The social structure characterises the entirety of inter-individual relationships other than sexual interactions (Kappeler & van Schaik 2002). Specific subsets of behaviours add to the subsequent conclusions of the study regarding the characterisation of sex-specific competition and its consequences for the reproductive system, inter-sexual interactions, cooperation and communication, the identification of consistent features of dyadic relationships.

Social systems of the Carnivora

The Carnivora show a stunning diversity of ecological, morphological and behavioural adaptations, which makes them particularly suitable for studying the evolution of life-history strategies, social behaviour and ecology in a comparative approach (Bekoff *et al.* 1984).

Additionally, the Carnivora include some of the few mammalian species in which males and females differ in social organisation. This offers the opportunity of studying potential sex-specific factors such as infanticide risk, parental care or resource dispersion that favour different forms of sociality, but appear to be of variable importance in different lineages (Macdonald 1983; van Schaik 2000; Lukas & Clutton-Brock 2013).

The majority of the Carnivora species is solitary; only 10-15% of them are group-living (Bekoff *et al.* 1984). However, carnivores display considerable inter-specific variation in social organisation. In many species, individuals tolerate a significant range overlap with related conspecifics (Bekoff *et al.* 1984; Van Valkenburgh & Wayne 2010). Traditionally, two selective pressures have been considered to determine group-living in carnivores: first, the advantages of cooperative hunting and second, the need for defence against larger predators. These factors have been generally assumed to operate within the constraints upon group size and space use set by the patterns of resource dispersion (Macdonald 1983; Gittleman 1989a).

In particular, long-term data on the behaviour and ecology of Canidae, Felidae and Hyaenidae species have contributed to the understanding of carnivore social organisation, mating systems and social structure (e.g., African wild dogs: Frame *et al.* 1979; de Villiers *et al.* 2003; hyenas: Frank 1986a, b; Hofer & East 1993; Owens & Owens 1996; lions: Hanby *et al.* 1995). Canids are extraordinary among mammals because they are mostly monogamous, forming packs of an alpha pair and matured offspring (e.g. the grey wolf, *Canis lupus*: Mech 1970). Pair-bonding, provisioning of young by the alpha male, late sexual maturity and large litter sizes are typical characteristics of these systems. In contrast, in the only truly social felid, the lion (*Panthera leo*), the basic unit of groups consists of a mother and its maturing daughters (Kleiman & Eisenberg 1973; Kleiman 2011). The majority of felids comprises species of solitary, specialised hunters.

However, in spite of the seemingly uniform patterns within taxonomic groups, striking details have regularly mirrored the impressive variability in carnivore social behaviour and the selective forces driving reproductive strategies (e.g. cases of polygamy in grey wolves: Mech & Nelson 1989; avoidance of infanticide by promiscuity in felids such as lions: Wolff & Macdonald 2004). In this context, molecular genetic investigations have revealed interesting patterns in group structure, dispersal and breeding systems, providing implications for the role of kinship in social organisation, cooperative behaviour and reproductive strategies (e.g. African wild dogs: Girman *et al*. 1997; Ethiopian wolves: Randall *et al*. 2007; fosas: Lührs *et al*. 2013; lions: Packer *et al*. 1991).

Apart from canids and the lion, large groups can be found in the Hyaenidae (hyenas; e.g. *Crocuta crocuta* with clans of up to 75 individuals; Hofer & East 1993) and the Herpestidae (mongooses), as well as some other taxa such as the Eurasian badger *Meles meles* (Mustelidae; Revilla & Palomares 2002) and the white-noased coati *Nasua narica* (Procyonidae; Gompper *et al.* 1997).

The Herpestidae are one exemplary group of small-sized carnivores for which detailed behavioural, demographic and also genetic information has been collected, in particular on three group-living species of cooperative breeders (*Helogale parvula*: Rood 1983, 1986; Rasa 1987a; *Suricata suricatta*: Clutton-Brock *et al*. 1999a; Nielsen *et al*. 2012; *Mungos mungo*: Cant 2000; Sanderson *et al*. 2015). These eusocial mongoose societies have also been used for testing fundamental assumptions and predictions of socio-ecological theories on intra-sexual competition, reproductive skew and cooperative behaviour (Creel *et al.* 1993; Clutton-Brock *et al.* 2001b, 2006; Clutton-Brock 2002, 2009a; Cant *et al.* 2010). Group-living and cooperative breeding are mainly indicated to be determined by direct benefits for group members resulting from group augmentation in avoidance of predation risk, or by mutualism or reciprocity rather than kin selection (Rasa 1987b; Rasa 1989; Rood 1990; Clutton-Brock *et al.* 1999a, b, c; Clutton-Brock 2002, 2009c, b; Madden *et al.* 2012). But also several other mongoose species classified as ‘solitary’ revealed interesting gregarious tendencies and association patterns which allowed inferences on the determinants of philopatry and dispersal and their significance for the evolution of group-living (e.g. Waser & Waser 1985), the role of kinship for male coalition formation (e.g. Waser *et al.* 1994) and the influence of habitat and food characteristics on the evolution of gregariousness (Ben-Yaacov & Yom-Tov 1983; Palomares & Delibes 1993).

In contrast, the social systems of the closest related taxon, the Malagasy Eupleridae, remain poorly studied. Because this endemic group of carnivores has evolved in isolation on Madagascar for the past 24 million years (Yoder *et al.* 2003), we can consider them as a natural experiment in carnivore social evolution. The fosa (*Cryptoprocta ferox*) is the only euplerid species of which detailed information on social organisation and mating behaviour has been collected (Hawkins & Racey 2009; Lührs & Kappeler 2013, 2014). This species is distinct in its size and ecological role as a top predator in Malagasy forest ecosystems. Among the remaining species of Eupleridae, knowledge about the ecology and behaviour of the members of the clade Galidiinae (Malagasy ‘mongooses’; Yoder *et al.* 2003) is particularly rare and largely anecdotal. While some molecular studies investigated the phylogeography and taxonomy of euplerids (Veron *et al.* 2004; Bennett *et al.* 2009; Durbin *et al.* 2010; van Vuuren *et al.* 2012), virtually nothing is known about local genetic structures and relatedness patterns within populations.

Study species

The Malagasy narrow-striped mongoose (*Mungotictis decemlineata*, Grandidier 1867) is an endemic small carnivore with a snout-vent length of up to 30 cm, tail length of up to 25 cm and a body mass of between 400 and 700 g. It belongs to the Galidiinae within the monophyletic Eupleridae (Yoder et al. 2003).

M. decemlineata is currently known to occur in the dry deciduous forests in an isolated, fragmented area of less than 20,000 km² of western and south-western Madagascar. Two subspecies are recognized: *M. d. decemlineata* Grandidier, 1867 ("Northern Bokiboky" according to Duckworth et al. 2014) is found mainly in the Menabe region (including Kirindy Forest); *M. d. lineata*, Pocock, 1915 ("Southern Bokiboky") was rediscovered in the southern part of the range in 2004 (Goodman *et al.* 2005). The total population has been estimated at 8,400 to 12,000 individuals (Woolaver *et al.* 2006). The population trend is unknown, but can be assumed to decrease due to rapid deforestation in western Madagascar over the recent years (cf. Zinner *et al.* 2014).

A single phylogeographic study on *M. decemlineata* revealed low genetic variation among several populations within the species' distribution range, and only structuring ascribed to isolation by distance (van Vuuren *et al.* 2012).

Narrow-striped mongooses are diurnal, largely terrestrial, but also use arboreal spheres of their habitat. They are predators of a wide variety of prey, mainly of invertebrates, especially insect larvae, but also small vertebrates, such as reptiles, bird eggs and occasionally mouse lemurs (*Microcebus sp.*; Albignac 1976; Rasolofoniaina 2014; personal observations). As night shelters, the animals use ant burrows and holes in dead wood or trees, the latter particularly during the rainy season.

Pioneering studies by Albignac (1976) and Razafimanantsoa (2003) on this species indicated either a highly flexible or locally variable social system. Albignac (1976) described a system of "super groups", which occupied a range of 150 ha and did not overlap with other groups. Seasonally, they split up into pairs, maternal groups, multi-male groups and solitary individuals displaying variable inter-sexual relationships: outside the mating season (from April to July), the animals were territorial. Adult females and their offspring formed groups; some males roamed solitarily or in multi-male groups, while others lived in pairs with a female and their offspring. In August, males searched for females within the range of the "super group" and competed with other males for access to mating. From December to April, females gave birth and isolated themselves with their young and the offspring of the previous year (Albignac 1972b, 1976). The dominant female led the group, while the male followed it during the day, but denned separately. In contrast, in Kirindy Forest, Razafimanantsoa (2003) observed two groups composed of three to five individuals (thereof one or two adult females, subadult or juvenile females and males, and pups, and temporarily an adult male). Groups occupied home ranges of 12.8 and 17.8 ha, respectively, which overlapped by 1.5 ha. Territoriality by marking but no agonistic encounters between groups have been indicated (Razafimanantsoa 2003). Group movements were led by an adult female. Some adult males tolerated each other and interacted socially. From August on, several males visited the groups for mating, and were tolerated by the male of the group (Razafimanantsoa 2003). However, the number of mates of males and females remained undetermined.

(Razafimanantsoa 2003) reported synchronous pregnancies of females within groups. However, the pup of the “non-leading” female was abandoned; only the pup of the group-leading female was reared, involving grooming, playing and guarding behaviour also by other group members. Litters in captivity comprised one or rarely two pups, of which only one was reared successfully (A. Ochs, Berlin Zoo, personal communication). Relatively slow development of young compared to African mongooses was indicated (Albignac 1976). A life span of more than 11 years has been reported (H. Klös, Berlin Zoo, personal communication).

Based on the inconsistent evidence on a relatively small number of individuals, the social organisation, including the average composition of social units, in particular the number of adults of each sex remained unclear. Due to the lack of detailed spatial and genetic data on the local scale, it was not possible to determine the social and genetic mating system, sex-specific reproductive strategies and the genetic structure of social units before. The characteristics of dispersal and other life-history traits and interesting social patterns such as the stability of multi-male units were still unresolved. Thus, inferences of their determinants, e.g. regarding intra-specific competition, and a systematic comparison with the Herpestidae as well as general conclusions for carnivore social evolution were hampered.

Due to the obscure composition and demography, in particular age structure and number of adult individuals of social units reported from *M. decemlineata* before, I refer in the following to the neutral terms “unit” (in females) and “association” (in males) in order to account for potential deviations from “group-living” (which would imply three or more adult individuals which are permanently associated *sensu* Kappeler 2009). Thereby, I also distinguish them from the term “coalition”, which has been frequently used in carnivore terminology (e.g. Packer & Pusey 1982; Caro & Collins 1987; Gompper *et al.* 1997) and implies a behavioural strategy, for example outcompeting conspecifics in the access to mating partners.

Aims of the study

The general aim of this thesis is to provide a comprehensive, precise picture of the social organisation of the Malagasy narrow-striped mongoose including detailed information on the demography, the local genetic structure and relatedness within social units based on a 3-years study of the population in Kirindy Forest CNFEREF (*Centre National de Formation d'Etude et de Recherche en Environment et Foresterie*), which can be considered as one of the largest remaining natural populations of this species (e.g. Woolaver *et al.* 2006). Thereby, my intention is to contribute to an empirical basis for the comparison of Eupleridae and Herpestidae in order to allow conclusions about the evolutionary transitions between different levels of carnivore sociality as well as about the mechanisms driving social evolution in general.

As a basis for the comparative approach of this study, **Chapter 1** presents a comprehensive review on the literature of the social systems and life-history characteristics of the sister-taxa Herpestidae and Eupleridae, including the available information for all recognised species. The last review on the ecology and social evolution in the mongooses was published by Rood (1986). Since that time, the body of literature has grown substantially and particularly on group-living mongooses. I summarise the current state of knowledge on the social organisation, mating systems and social structure of mongooses and Malagasy carnivores, and evaluate the contributions of these studies to a better understanding of mammalian social evolution in general. Specifically, I investigate here the links between (i) female social organisation, social structure and life-history, and male social organisation and female distribution and the associated male reproductive strategies in solitary and group-living species, (ii) the linkages between the components of social systems and cooperative behaviour, (iii) the mechanisms connecting the components of social systems, (iv) the predictive power of the socio-ecological model and reproductive skew theory for the found patterns.

In **Chapter 2**, I describe the sex-specific social organisation of *M. decemlineata* based on spatial and demographic data and behavioural observations collected during multiple-year radio-tracking of known individuals. In order to account for possible influences of social and ecological determinants, I investigate the effects of social unit size and season on home range size. I analyse a variety of life-history characteristics of *M. decemlineata* and compare particularly reproductive traits to group-living and solitary mongooses. Distinct social patterns of *M. decemlineata* finally provide the substantial basis for discussing the determinants of sociality and implications for intra-sexual competition in this forest-dwelling Malagasy carnivore.

The genetic structure of populations and relatedness within social units as well as the distribution of reproductive success among individuals cannot be predicted straightforward from behavioural and demographic observations alone, especially when facing difficult observation conditions in wild populations (Nonacs & Hager 2011; Di Fiore 2012; Nidiffer & Cortés-Ortiz 2015). Thus, in **Chapter 3**, I investigate the local genetic structure, sex-specific and within-group relatedness and the level of reproductive skew in the population of *M. decemlineata* based on mitochondrial DNA and microsatellite markers. From the mtDNA haplotype structure and relatedness patterns, conclusions will be made about sex-specific philopatry and dispersal, and the significance of kinship for the determined social association patterns (**Chapter 2**). Furthermore, I infer important patterns of the mating system based on parentage and sibship analyses. The genetic information substantially supports my observations of social units (**Chapter 2**) and allows conclusions on reproductive competition and interesting hypotheses about reproductive strategies and female control of paternity.

Finally, I discuss the social organisation, genetic structure and reproductive characteristics in comparison to other mongoose, carnivore and mammalian taxa and in the context of socio-ecological theory. Under consideration of Madagascar’s evolutionary history, I aim to derive conclusions related to the social evolution in the herpestids and euplerids, and provide and outlook on potentially interesting future research questions in *M. decemlineata* and other related taxa.

CHAPTER 1

Social systems and life-history characteristics of mongooses

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Abstract

The diversity of extant carnivores provides valuable opportunities for comparative research to illuminate general patterns of mammalian social evolution. Recent field studies on mongooses (Herpestidae), in particular, have generated detailed behavioural and demographic data allowing tests of assumptions and predictions of theories of social evolution. The first studies of the social systems of their closest relatives, the Malagasy Eupleridae, also have been initiated. The literature on mongooses was last reviewed over 25 years ago. In this review, we summarise the current state of knowledge on the social organisation, mating systems and social structure (especially competition and cooperation) of the two mongoose families. Our second aim is to evaluate the contributions of these studies to a better understanding of mammalian social evolution in general. Based on published reports or anecdotal information, we can classify 16 of the 34 species of Herpestidae as solitary and nine as group-living; there are insufficient data available for the remainder. There is a strong phylogenetic signal of sociality with permanent complex groups being limited to the genera *Crossarchus*, *Helogale, Liberiictis, Mungos,* and *Suricata*. Our review also indicates that studies of solitary and social mongooses have been conducted within different theoretical frameworks: whereas solitary species and transitions to gregariousness have been mainly investigated in relation to ecological determinants, the study of social patterns of highly social mongooses has instead been based on reproductive skew theory. In some group-living species, group size and composition were found to determine reproductive competition and cooperative breeding through group augmentation. Infanticide risk and inbreeding avoidance connect social organisation and social structure with reproductive tactics and life histories, but their specific impact on mongoose sociality is still difficult to evaluate. However, the level of reproductive skew in social mongooses is not only determined by the costs and benefits of suppressing each other's breeding attempts, but also influenced by resource abundance. Thus, dispersal, as a consequence of eviction, is also linked to the costs of co-breeding in the context of food competition. By linking these facts, we show that the socio-ecological model and reproductive skew theory share some determinants of social patterns. We also conclude that due to their long bio-geographical isolation and divergent selection pressures, future studies of the social systems of the Eupleridae will be of great value for the elucidation of general patterns in carnivore social evolution.

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Introduction

The Carnivora are characterised by outstanding diversity of form and function among all mammalian groups, and have become eminent subjects of evolutionary, ecological and behavioural research. Their importance as an exemplary group for studying the evolution of life-history strategies and social behaviour from a comparative perspective has been emphasized (Bekoff *et al.* 1984). Although many species of carnivores are difficult to study under field conditions, several pioneering studies have generated impressive long-term data sets on their behaviour and ecology (e.g. lions: Hanby *et al.* 1995; Spong 2002; hyenas: Owens & Owens 1984, 1996; Frank 1986a, b; Hofer & East 1993; wild dogs: Frame *et al.* 1979; de Villiers *et al.* 2003). Field studies of group–living mongooses (Herpestidae), in particular, have also generated detailed behavioural and demographic data for comparative studies and tests of fundamental assumptions and predictions of general theories of social evolution (Creel *et al.* 1993; Clutton-Brock *et al.* 2001a, b; De Luca & Ginsberg 2001; Clutton-Brock 2002, 2009b, c; Gilchrist *et al.* 2004; Cant *et al.* 2010). By contrast, there is still a considerable lack of data on the characteristics of social systems and life-history traits of forest-dwelling mongooses and those not forming large groups (Tables 1 and 2). Even less is known about the closest relatives of the Herpestidae, the Malagasy mongooses (Eupleridae), but some recent data on their phylogeny, population genetics and sociality (Yoder *et al.* 2003; van Vuuren *et al.* 2012; Lührs *et al.* 2013) indicate that a comprehensive review of the variation in mongoose sociality and its determinants could provide a valuable basis for identifying the evolutionary transitions and mechanisms driving carnivore social evolution as well as convergences between the two independent mongoose radiations on and outside Madagascar. Because this growing body of literature has not been reviewed in more than 25 years (Rood 1986), we summarise new results of molecular phylogenetic studies, genetic investigations of reproductive systems as well as behavioural and demographic field studies of members of both mongoose families. Our second aim is to link the main results and conclusions of these studies to theoretical developments in the study of mammalian social evolution.

The Herpestidae have been recognised as a separate family by several phylogenetic studies (Gregory & Hellman 1939; Fredga 1972; Wozencraft 1989; Veron *et al.* 2004). Formerly, they were subdivided into the Herpestinae, Mungotinae and Galidiinae (i.e. the Malagasy genera *Galidia*, *Galidictis*, *Mungotictis* and *Salanoia*; Wozencraft 1989). By contrast, molecular studies revealed a single origin of the Malagasy carnivores (Eupleridae; Yoder *et al.* 2003; Eizirik *et al.* 2010; Nyakatura & Bininda-Emonds 2012). The divergence of the

Herpestidae and Eupleridae is estimated to have taken place in the Late Oligocene/Early Miocene (18-22 million years ago). In the Early Miocene, the Herpestidae further diverged into two clades: the 'true social mongooses' (*Crossarchus, Helogale, Liberiictis, Mungos, and Suricata,* with *Suricata* being the sister-taxon of the clade containing the other 'social' mongooses), and the solitary mongooses (*Ichneumia, Cynictis, Paracynictis, Rhynchogale, Bdeogale, Herpestes, Galerella,* and *Atilax;* Veron *et al.* 2004; Patou *et al.* 2009). Solitariness and forest-dwelling have been suggested as the ancestral states of the mongoose clade (Veron *et al.* 2004). Such a strong phylogenetic signal in mongoose social evolution also provides an opportunity to study the interplay between current and past adaptations, mediated by the functional relationship between taxon-wide morphological and life-history traits and behaviour (see e.g. McKitrick 1993; Kappeler 1996; Chapman & Rothman 2009; Kappeler & Kraus 2010, for other examples). The phylogeny of the Herpestidae and the single origin of sociality in this group are well supported by morphological, chromosomal and molecular data (Gregory & Hellman 1939; Wurster & Benirschke 1968; Fredga 1972; Veron *et al.* 2004; Patou *et al.* 2009). However, "solitary" and "social" have not always been clearly defined and distinguished (e.g. Leyhausen 1964; Kappeler & van Schaik 2002), and there is interesting variation among social systems and the underlying mechanisms within these main clades (see e.g. Ben-Yaacov & Yom-Tov 1983; Waser & Waser 1985; Palomares & Delibes 1993; Hays & Conant 2003). We therefore first briefly clarify the relevant terminology. We also use our classification of broad categories of mongoose social organisation in a phylogenetic reconstruction based on the most recent and comprehensive phylogeny of the Carnivora (Nyakatura & Bininda-Emonds 2012; Fig. 1).

The key aspects for the characterisation of social systems include spacing, grouping and mating patterns, as well as variability in patterns and quality of social relationships (Kappeler & van Schaik 2002). Based on this concept, we characterise the social organisation, mating system and social structure of the Herpestidae and Eupleridae. The social organisation characterises the demographic structure and the temporal and spatial cohesion of social units, and distinguishes among solitary, pair-living and group-living species. The mating system describes one subset of social interactions, i.e. the average number of sexual partners of males and females. It is distinguished from the reproductive system (=genetic mating system), which refers to the reproductive consequences of mating interactions. Social structure is characterised by the diversity of social interactions other than sexual interactions among conspecifics (Kappeler & van Schaik 2002). However, in many mongooses, a classification with regard to these three components can be only provisional or is not yet possible due to a lack of data, especially in forest-dwelling species. Our systematic review clearly identifies these gaps in our knowledge as important topics for future research. We also summarise life-history traits and examine their relation to social organisation. We consider reproductive strategies when discussing variation in mating systems. Other behavioural strategies characterising social structure are considered with regard to female competition, associations among males and cooperative behaviour. As the three elements of a social system represent conceptually discrete but interrelated entities, we also discuss possible causal, evolutionary and correlational links between them (see alsoKappeler & van Schaik 2002).

We consider two major theoretical frameworks when relating fitness-relevant behaviour to the defining characters of a social system: the socio-ecological model (Crook 1970; Wrangham 1980; Sterck *et al.* 1997; Kappeler 1999; Clutton-Brock & Janson 2012) and reproductive skew theory (Vehrencamp 1983a, b; Nonacs & Hager 2011). Whereas the former is primarily concerned with explaining variation in social organisation and female social relationships, the latter proposes competing transactional (concession and restraint models) and compromise (‘tug-of-war’) models to explain patterns of partitioning of reproduction among dominant and subordinate individuals (Reeve & Keller 1997; Reeve *et al.* 1998; Johnstone 2000; Buston *et al.* 2007). Transactional models assume that one individual has full control over reproduction, but may have to relinquish a share of reproduction in order to prevent other individuals leaving or evicting it from the group. By contrast, compromise models ignore outside options, such as emigrating to breed elsewhere, but allow for incomplete control over reproduction within the group (Keller & Reeve 1994; Johnstone & Cant 2009). A recent review of the primate evidence suggested that these models (originally developed for eusocial insects) may not meet realistic assumptions about (male) mammalian sociality (Port & Kappeler 2010), so that a similar consideration of the mongooses may provide interesting perspectives on this problem.

We therefore address the following specific questions: (1) how is female social organisation linked to female social structure and life-history traits, and how is male social organisation linked to the distribution of females and which reproductive strategies of males are associated with this, in solitary and group-living species? (2) What are the (sex-specific) determinants and linkages of the components of the social system to cooperative behaviour? (3) Which linking mechanisms among the components of social systems do the studies on solitary and social mongooses reveal? (4) What can we finally deduce from the existing studies about the predictive power of the two different theoretical frameworks for the patterns found in solitary and group-living mongooses? Can we define determining factors which these models have in common?

Social organisationand life-history patterns of mongooses

Of the 34 recognised species of Herpestidae (Wozencraft 2005; Patou *et al.* 2009), the available literature allows reliable classification of the social organisation of only 19 species (11 solitary: *Atilax paludinosus*, *Bdeogale jacksoni*, *Galerella flavescens*, *Galerella pulverulenta*, *Galerella sanguinea*, *Herpestes auropunctatus*, *Herpestes ichneumon*, *Herpestes javanicus*, *Herpestes brachyurus*, *Ichneumia albicauda*, *Paracynictis selousi*; eight group-living: *Crossarchus alexandri*, *Crossarchus obscurus*, *Cynictis penicillata*, *Helogale hirtula*, *Helogale parvula*, *Mungos gambianus*, *Mungos mungo*, *Suricata suricatta*; Table 1). The social organisation of the remaining species can currently be only inferred from anecdotal evidence. Accordingly, five species are presumably solitary (*Bdeogale crassicauda*, *Bdeogale nigripes*, *Herpestes edwardsii*, *Herpestes naso*, *Rhynchogale melleri*) and *Liberiictis kuhni* is presumably group-living. Our literature search did not yield any information on the social systems and very few data on life-history traits of the nine remaining species (*Crossarchus ansorgei*, *Crossarchus platycephalus*, *Dologale dybowskii*, *Galerella ochracea*, *Herpestes fuscus*, *Herpestes semitorquatus*, *Herpestes smithii*, *Herpestes urva*, *Herpestes vitticollis*). From a phylogenetic point of view, members of the genus *Herpestes* are more likely to exhibit a solitary lifestyle, but this genus has been shown to be polyphyletic (Nyakatura & Bininda-Emonds 2012).

The average size and composition of social units with regard to age, sex and relatedness of their members is summarised for the Herpestidae and Eupleridae below (see also Table 1). The phylogenetic reconstruction of mongoose social organisation indicated that a solitary social organisation was ancestral for the Herpestidae and Eupleridae (Fig. 1), in accordance with Veron *et al.* (2004).

(1) Herpestidae: solitary species

Solitary mammals are defined by a lack of synchronised activity and movements among individuals, who usually forage alone (e.g.Charles-Dominique 1978; Bearder 1987). According to Sandell (1989), the absence of selection pressures favouring cooperation is the main determinant of solitariness in carnivores, mediated by small-sized and abundant food resources as well as the absence of male parental care. The available data on solitary mongooses are mainly on activity and space use.

In *H. brachyurus*, exclusive home ranges were observed in females, and male ranges overlapped with those of several females (Jennings *et al.* 2010). In some other species (e.g. *G. sanguinea*: Waser *et al.* 1994; *H. naso*: Ray 1997), a substantial overlap in male home ranges, but little overlap amongst females has been observed. This pattern basically resembles that found in some other solitary carnivores (e.g. *Lynx rufus*: Berg 1981, in Sandell 1989; *Panthera tigris*: Sunquist 1981; *Mustela erminea*: Erlinge & Sandell 1986; *Acynonix jubatus*: Caro & Collins 1987; *Mustela vison*: Yamaguchi *et al.* 2004). By contrast, other studies (*I. albicauda*: Waser & Waser 1985; *H. javanicus*: Hays & Conant 2003) reported a large overlap among female ranges, indicating increased sociality in high-density populations. These studies suggested that ecological advantages of philopatry and various anti-predator benefits are the driving mechanisms in the evolutionary transition to stable social groups. A particular habitat structure and food characteristics were postulated to stabilise a solitary lifestyle and to prevent the formation of stable groups: *H. ichneumon* exhibit pronounced variability in social organisation, ranging from solitary individuals to pairs and groups (consisting of one adult male and up to three adult females), which show cooperative tendencies, particularly in areas with abundant and clumped food resources (Ben-Yaacov & Yom-Tov 1983; Palomares & Delibes 1993) questioned the classification of *H. ichneumon* as a solitary carnivore.

(2) Herpestidae: group-living species

Traditionally two selective pressures have been considered to favour group-living in carnivores: the advantages of cooperative hunting and the need for defence against other predators. It has been stated that these selective pressures operate within the constraints upon group size and space use set by the patterns of resource dispersion (Macdonald 1983; Gittleman 1989b). There is still disagreement about whether cooperative hunting should be considered a cause of sociality (Creel & Creel 1995) or a consequence thereof (Packer & Ruttan 1988; Moehlman 1989). By contrast, several studies of mongooses, which are subject to high predation risk in open landscapes, have stressed the significance of group-living and group size for defence against larger predators (Waser 1981; Gittleman 1989b). These advantages result mainly from shared vigilance (Moran 1984; Manser 1999) and cooperative predator mobbing (Rasa 1977; Rood 1983b; Clutton-Brock *et al.* 1999a; Graw & Manser 2007; Clutton-Brock 2009c). Relatively small body sizes in group-living species (see Table 2) are in accordance with the hypothesis that high predation risk represents a determinant of group-living of small-bodied mongooses in open habitats (Gorman 1979; Rood 1986; Palomares & Delibes 1993).

The yellow mongoose (*C. penicillata*) and the common cusimanse (*C. obscurus*) have been described living in mixed-sex aggregations of up to 20 individuals. Because *C. penicillata* has been allied with the solitary mongooses (Patou *et al.* 2009), it may represent a transitional stage in sociality. In this species, groups contain single, paired or several related adults and show pronounced natal philopatry in high-density populations (Earlé 1981; Wenhold & Rasa 1994; Cavallini & Nel 1995; Le Roux *et al.* 2008). Few data are available for *C. obscurus* and its congeners *C. alexandri*, *C. ansorgei* and *C. platycephalus*. For *C. obscurus*, a complex and hierarchical group structure based on kin and characterised by a dominant breeding pair has been suggested (Goldman 1987). A re-classification of this species by Patou *et al.* (2009), who grouped it with meerkats, banded and dwarf mongooses, might gain support from more detailed field studies.

Much more is known about the meerkat (*S. suricatta*), banded mongoose (*M. mungo*) and dwarf mongoose (*H. parvula*). They form the largest mixed-sex groups among the Herpestidae, and they have been characterised as 'highly social' (Bateman *et al.* 2012; we adopt their terminology below without necessarily endorsing it) because their groups are based on kin, display a high degree of cooperation and communication, and because they exhibit an age-dependent matriarchal hierarchy dominated by an alpha pair (*H. parvula*: Rasa 1987a; *S. suricatta*: Clutton-Brock *et al.* 1998) or a cohort of adults (*M. mungo*: Cant *et al.* 2010). For example, Rood (1990) described a typical pack of *H. parvula* as comprising two adult males, 2–3 adult females and five or more yearlings and juveniles.

These three species show relatively greater litter sizes and reproductive rates compared to solitary species (Table 2). Packs behave territorially on relatively small home ranges that can overlap between packs (e.g. Rood 1990; Clutton-Brock *et al.* 1999a; Cant *et al.* 2001; Jordan *et al.* 2007). Dispersal patterns are poorly known for solitary mongooses, but they have been investigated in detail for males and females in the highly social species, including their evolutionary causes and behavioural consequences (Rood 1987; Doolan & Macdonald 1996; Cant *et al.* 2001; Stephens *et al.* 2005; Russell *et al.* 2007). Dispersal events can be far-ranging (>23 km in *M. mungo*) and occur in one of two distinct modes: after aggression and eviction by dominants or same-sex intruders, or voluntarily. It is indicated that dispersal is biased towards males. In meerkats, independent of their physical condition or reproductive potential, females never disperse voluntarily due to the high costs of dispersal, while the strongest young males disperse first in search of breeding opportunities (Russell *et al.* 2007). This pattern has consequences for social structure and male reproductive success. In particular, models developed by Stephens *et al.* (2005) imply that long-term fitness considerations can explain group-size regulation in meerkats, which supports the strong linkage of dispersal, eviction, reproductive strategies and the degree of reproductive skew (see Section V). Until recently, Allee effects were supposed to govern group dynamics in obligate cooperative breeders such as meerkats. However, recent models suggest that conventionally density-dependent demographic factors, e.g. emigration, determine those group dynamics (Bateman *et al.* 2012).

(3) Eupleridae

The Eupleridae are assumed to be mostly solitary forest-dwellers, but empirical data to support this exist only for *Cryptoprocta ferox* and the two species of *Eupleres* (*E. goudotii, E. major*; Albignac 1972b; Hawkins & Racey 2005, 2009; Dollar *et al.* 2007; Lührs *et al.* 2013). By contrast, limited evidence suggests that *Fossa fossana* lives in pairs (Nowak 1991). Recent studies revealed that 2–3 adult males may associate permanently and hunt cooperatively in *C. ferox* (Lührs & Dammhahn 2010; Lührs *et al.* 2013). Despite some pioneering field studies (e.g. Albignac 1976; Hawkins 1998; Razafimanantsoa 2003), the size and composition of social units has not been determined for the majority of the Eupleridae. Similarly, limited life-history data from the Eupleridae indicate small litter sizes (i.e. in most species only one young) and low reproductive rates. Relatively slow life histories are also indicated by relatively long gestation periods, late sexual maturity, and late dispersal (the latter especially in comparison to solitary Herpestidae; Table 2). Dewar & Richard (2007) related the slow life-history patterns of Malagasy mongooses and other mammals to their hypervariable environment, which is ultimately due to climatic unpredictability.

Mating systems and reproductive strategies of mongooses

Spacing patterns and mating system are closely related (Clutton-Brock & Harvey 1978). In mammals, the variation in male-female mating bonds and mating tactics depends on the presence of paternal care, the size, and, hence, the defensibility of female ranges by males, the size and stability of female groups, and the density and distribution of females in space (Clutton-Brock 1989). Accordingly, in solitary carnivores – as in general models of socio-ecology (Davies 1991) - food determines the distribution of females, and spacing in males is primarily determined by the distribution of females, at least during the mating season. Two basic mating tactics of male mongooses have been distinguished: monopolisation by mate guarding, and roaming and competing over access to females (Sandell 1989). By contrast, studies on highly social and cooperative mongooses have highlighted the mechanisms of social control of reproduction, which determine patterns of reproductive skew among group members (Cant 2000; Clutton-Brock *et al.* 2001b; Gilchrist 2006a, b; Cant *et al.* 2010), rather than the role of food resource distribution. This concept provides a framework for sexual selection operating through intra-sexual competition for reproductive opportunities (Clutton-Brock *et al.* 2006).

(1) Mating and reproductive systems of the Herpestidae

The exclusive home-range use of males in high-density populations of some solitary mongooses suggested the existence of a polygynous mating system (*I. albicauda*: Waser & Waser 1985; *H. ichneumon*: Palomares & Delibes 1993), in line with Sandell (1989). However, the majority of mongooses can be classified as promiscuous (see Table 1), and exhibit a number of reproductive strategies:

(*i*) male coalition formation leads to a monopolisation of several females by related males and results in shared paternities (*G. sanguinea*: Waser *et al.* 1994; also assumed in *H. javanicus*: Hays & Conant 2003). In the highly social species, males disperse together, immigrate into other groups and take over breeding positions (Rood 1990; Griffin *et al.* 2003; Clutton-Brock *et al.* 2006).

(*ii*) In the hierarchical groups of highly social species, a dominant breeding pair monopolises reproduction to a large extent by suppression (*H. parvula*: Rasa 1973; Creel *et al.* 1992), eviction and infanticide (*H. parvula*: Keane *et al.* 1994; *S. suricatta*: Clutton-Brock *et al.* 1998, 2001b, 2010; Kutsukake & Clutton-Brock 2006; Young *et al.* 2006) at the expense of subordinate, sexually mature individuals. This monopolisation results in a high level of reproductive skew in both sexes. In *S. suricatta,* the breeding tenure of dominant females is determined by body mass, testosterone level and aggressive behaviour, and lasts longer and reproductive benefits are higher than in males. Dominant males are more frequently replaced by immigrants than it is the case in females (Clutton-Brock *et al.* 2006).

(*iii*) Extra-group paternity by prospecting subordinate males is known in *S. suricatta* (Young *et al.* 2007).

(*iv*) Mate-choice and mate-guarding behaviour is exhibited by top males of a breeding cohort (older males guard the oldest, most fecund females in *M. mungo*: Nichols *et al.* 2010). Subordinates are evicted *en masse* by dominants during the late stage of the dominant female’s pregnancy (Cant *et al.* 2001, 2010).

(*v*) Oestrous and birth synchrony of females reduces the risk of infanticide by other females and competitive disadvantages among littermates (*M. mungo*: Cant 2000; Gilchrist 2006a, b; Hodge *et al.* 2011).

(*vi*) Older females enter oestrus slightly earlier than younger group mates and gestate larger litter sizes (*M. mungo*: Cant 2000).

The consequences of these strategies for reproductive systems have been investigated in detail in highly social species. Although the mating system of most mongooses can be classified as promiscuous, there are strong tendencies for the monopolisation of reproduction by a single pair in dwarf mongooses and meerkats (Rood 1986; Lukas & Clutton Brock 2012). By contrast, in banded mongooses, sex-specific reproductive strategies result in a relatively low skew of female and a high skew of male reproduction.

Reproductive skew is indicated to arise from incest avoidance and reproductive suppression of subordinates, and it differs between the sexes and among different sites (in *S. suricatta*: dominant females produce 88-100% of pups; dominant males sire 72-88%; Griffin *et al.* 2003). By contrast, Keane *et al.* (1996) noticed a lack of incest avoidance in dwarf mongooses, analysing pedigrees under the assumption that the dominant pair produced all pups in a pack. They found that subordinate males produced 24% and subordinate females 15% of pups, with multiple paternity existing in some cases (Keane *et al.* 1994). In meerkats, mixed paternities of dominant and subordinate immigrant males were common in litters of dominant females, whereas subordinate females usually bred only with outside males (i.e. males which enter the territory without becoming group members; Griffin *et al.* 2003). Thus, prospecting for extra-group paternity represents an important alternative reproductive tactic for subordinate males (Young *et al.* 2007).

In these breeding systems, intra-group incest avoidance, breeding tenure and the resulting reproductive tactics have far-reaching consequences for dispersal and kinship patterns (see Section V). Keane *et al.* (1994) suggested that in *H. parvula*, dominants concede some reproduction to high-ranking subordinates in order to retain them as helpers. However, because subordinate females only mate with outside prospecting males, dominant individuals do not have full control over reproduction of subordinates. It has therefore been suggested that the mating systems of group-living mongooses correspond to ‘limited control’ or ‘tug-of-war’ models of reproductive skew better than to ‘transactional’ models (Cant *et al.* 2001, 2010; Clutton-Brock *et al.* 2001b; Clutton-Brock *et al.* 2008).

Considering the larger variation in female than male reproductive success in meerkats, it is interesting that dominants do not adjust offspring sex ratio towards daughters, who would theoretically achieve higher fitness benefits than sons (MacLeod & Clutton-Brock 2013). Apart from the long breeding tenure of dominant females, which suppress their daughters' reproduction, alternative strategies by the sons of the dominant are among the possible explanations for this demographic pattern.

(2) Mating and reproductive systems of the Eupleridae

Among the Eupleridae, only the mating behaviour of the fossa (*Cryptoprocta ferox*) has been investigated in some detail. Their promiscuous mating system is characterised by extended and profuse mating activity of solitary females on traditional mating trees, which has been functionally linked to mate finding in a species with large ranges and low population density (Hawkins & Racey 2009). However, other functions of hyper-polyandrous matings, such as infanticide avoidance and indirect genetic benefits, are indicated (M.-L. Lührs & P.M. Kappeler, unpublished data). Some males form permanent coalitions with other males, and members of these male associations are significantly heavier than solitary males and females (Lührs *et al.* 2013). Females dominate both types of males but mate preferably with heavy males during their period of likely receptivity and solicit matings from lighter males afterwards (M.-L. Lührs & P.M. Kappeler, unpublished data). Information on the mating systems of other euplerids is mostly based on indirect evidence. For example, Marquard *et al.* (2011) inferred spatial patterns of male and female *G. grandidieri* from capture data, and speculated about possible mating systems based on morphometric data. To our knowledge, however, neither observations of mating behaviour nor genetic studies of reproductive skew have been conducted in any other Malagasy carnivore to date.

Social structure: competition, associations and cooperative behaviour

(1) Social relationships in the Herpestidae

(*a*) *Territorial behaviour and inter-group competition*

Territorial behaviour is common among the Herpestidae. In the majority of solitary species, or those forming groups with low cohesion, there is little interaction among adult females, which share a home range with their offspring. Home-range sizes are mainly determined by food abundance (e.g. *I. albicauda*: Waser & Waser 1985; *C. penicillata*: Cavallini & Nel 1995; *H. brachyurus*: Jennings *et al.* 2010). In social species, territories are scent-marked and defended by several group members. The contributions of individuals to territorial scent-marking and the intensity of aggressive defence against intruders are higher in high-density populations, which also display a higher degree and thus within-species variation of sociality (*C. penicillata*: Le Roux *et al.* 2008). Encounters between groups often lead to physical conflict, including wounding and killing of individuals (*H. parvula*: Rasa 1987a; *M. mungo*: Rood 1975; Cant *et al.* 2001; *S. suricatta*: Young 2003). While in yellow mongooses, a 'dear enemy' effect of greater tolerance against neighbours than against unfamiliar intruders has been observed (Le Roux *et al.* 2008), in banded mongooses, a 'nasty neighbour' effect of higher aggression against neighbours than intruders has been noted (Müller & Manser 2007). Encounter location and group size have been suggested to govern risk-taking decisions and outcomes of inter-group contests (Furrer *et al.* 2011). In meerkats, males, which are at higher risk of losing their dominance status, show higher investment in territorial defence. Additionally, the individual contribution to territorial defence varies with the costs and benefits of other cooperative behaviour, e.g. with the investment in pup feeding (Mares *et al.* 2012). Social network analyses of inter-group relationships in meerkats indicated a stable social structure despite variation in group size and sex ratios over time; spatial factors are the most important predictors of roving patterns of individuals between groups (Drewe *et al.* 2009).

Intra-sexual overmarking behaviour has been investigated in detail in banded mongooses. Among males, it is supposed to be an honest indicator of quality and dominance in intra-sexual competition for mating success rather than in female mate choice (Jordan *et al.* 2011a, b). By contrast, high-score overmarking females tend to be preferred and mate-guarded by stronger males, while there is no evidence that overmarking plays a role in food competition (Jordan *et al.* 2011c). Territorial marking by latrines may also have an important role in mate defence in *S. suricatta* (Jordan *et al.* 2007).

(*b*) *Intra-group competition*

Intra-group social networks depend on group attributes, individual attributes and ecological factors, and become less dense with increasing group size, indicating a limitation of individuals in the number of interaction partners. Interestingly, groups with more established dominant females are more despotic in dominance interactions, but more egalitarian with regard to interactions like grooming and foraging competition (Madden *et al.* 2009a). Within the matriarchal groups of *S. suricatta*, dominant and heavier individuals exhibit higher frequencies of agonistic interactions and exert aggression towards a larger number of conspecifics than subordinates and lighter individuals do (Madden *et al.* 2011). Network analyses revealed a positive relationship between dominance interactions and kinship within the group, while grooming and foraging competition are not related to kinship (Madden *et al.* 2012).

As a result of intensive female competition for dominance and breeding opportunities in highly social mongooses, many females never breed successfully at any stage of their life (*H. parvula*: Creel & Waser 1997; *S. suricatta*: Clutton-Brock *et al.* 2006; Clutton-Brock 2009b; Sharp & Clutton-Brock 2011b). By contrast, in *M. mungo*, within-group direct female competition is rather low and mediated by their age-based hierarchy (Cant 2000). However, in banded mongooses, reproductive competition strongly influences the evolution of extreme reproductive synchrony: females synchronise births in order to maximise survival of their pups, which could be subject to infanticide if born too early, or lose in competition to older pups if the female gives birth too late (Hodge *et al.* 2011). There are also substantial costs for females when preventing competitors from breeding: dominant female's pups were in poorer condition when they had to invest in suppression of competitors than when they were undisturbed during gestation (Bell *et al.* 2012). The costs experienced by female banded mongooses in this context depend on resource availability: when resources (predicted by rainfall) are scarce, more dominant females respond to this cost by suppressing competitor's breeding by temporary or permanent eviction of subordinates (Nichols *et al.* 2012b). Extensive female competition for breeding opportunities in social mongooses can be expressed in high rates of infanticide, not only exerted by dominants, but also by subordinates, although subordinates suffer higher losses (*H. parvula*: Rasa 1994; Creel & Waser 1997; *M. mungo*: Gilchrist 2006a; *S. suricatta*: Young & Clutton-Brock 2006). This pattern coincides with suppression and eviction, particularly of older subordinates (*S. suricatta*: Kutsukake & Clutton-Brock 2006), and abortion of litters of subordinates (Gilchrist 2006b). Suppression and eviction are predicted by the frequency of aggressive behaviour of the dominant female. Overall, these patterns indicate close interrelationships between female competition and reproductive strategies.

(*c*) *Male associations*

The formation of male associations has been repeatedly observed in otherwise solitary mongooses. These associations vary in stability among species and are assumed to serve in reproductive coalitions or cooperative hunting (*G. flavescens*: Rathbun & Cowley 2008; *H. ichneumon*: Palomares & Delibes 1993). In *G. sanguinea*, associated males are closely related, indicating that these associations formed before dispersal from the natal territory, and reproductive skew among coalition members is low (Waser *et al.* 1994). In group-living species, males usually disperse in association with other males and immigrate into neighbouring groups or found new ones (Rood 1987; Clutton-Brock *et al.* 1998, 2004; Cant *et al.* 2001). Social network analyses in meerkats revealed high assortativity between males (Madden *et al.* 2011). Here, for example, subordinate males groomed dominants more, but dominant males groomed subordinate males for longer than they groomed subordinate females. This asymmetry between males increased with increasing group size, with dominants receiving grooming by subordinate males for longer in larger than in smaller groups (Kutsukake & Clutton-Brock 2010). In this context, it is important to point out that allogrooming and submission in meerkats seem to function as a facultative response to aggression rather than a pre-emptive strategy to inhibit the initiation of aggression by reinforcing social bonds, as has been assumed for other mammals (Madden & Clutton-Brock 2009).

(*d*) *Cooperation*

Some highly social mongooses represent the most outstanding examples of cooperative breeders among mammals, together with African mole-rats (Bathyergidae; Faulkes & Abbott 1997; Bennett & Faulkes 2000; Faulkes & Bennett 2007). In general, delayed dispersal, reproductive suppression and care for others' offspring are regarded as the definitional hallmarks of cooperative breeders (Bekoff *et al.* 1981; Koenig *et al.* 1992; Solomon & French 1997). Although data on dispersal ages are rare, delayed dispersal of females has been recorded in solitary mongooses (e.g. *I. albicauda*: Waser & Waser 1985; *G. sanguinea*: Waser *et al.* 1994). In eusocial mongooses typical cooperative activities comprise babysitting, pup feeding, social digging of sleeping burrows, guarding, and allolactation. In meerkats and dwarf mongooses, offspring are reared communally (*H. parvula*: Rood 1978, 1980, 1983b, 1990; Rasa 1987a; Creel & Creel 1991; *S. suricatta*: Clutton-Brock *et al.* 2000, 2001a, b; Brotherton *et al.* 2001). However, individual contributions can differ distinctively with regard to rank (dominants *versus* subordinates) and sex, and they depend critically on the helper:pup ratio (*S. suricatta*: Clutton-Brock *et al.* 2004; English *et al.* 2008, 2010; Madden *et al.* 2009d). They also underlie a trade-off with other cooperative activities, such as the costs for helpers due to their contributions to communal territorial defence (Mares *et al.* 2012).

Usually, females show a higher responsiveness to offspring begging than males (English *et al.* 2008). Recent results suggest a role for oxytocin as a single hormonal system providing the proximate causal basis for different forms of cooperative behaviour in meerkats (Madden & Clutton-Brock 2011).

Indirect sibling competition among littermates in meerkats is indicated by the observation that they separate their begging signals in space and time (Madden *et al.* 2009b, c), thereby influencing the rate of care-taking by associating with particular helpers (Hodge *et al.* 2007). By contrast, conspicuous pup-helper bonds ('escorts') exist in banded mongooses (Cant 1998; Gilchrist 2004), characterised by higher investment of breeders *versus* non-breeders in pup care (Gilchrist & Russell 2007), and leading to differences in growth rate and probability of survival of pups of the same litter (Hodge 2005). These findings indicate strong interrelationships between cooperative breeding and the level of reproductive skew.

In meerkats, natal philopatry and cooperative breeding behaviour cannot be explained by kin selection alone, as there is evidence that unrelated immigrants feed pups as frequently as close relatives (Clutton-Brock *et al.* 2001a). Instead, direct benefits for helpers by maintaining group size, or by mutualism or reciprocity (Clutton-Brock *et al.* 1999a, 2000, 2001a; Clutton-Brock 2002, 2009c; Madden *et al.* 2012; Santema & Clutton-Brock 2012) may have shaped the evolution of cooperative meerkat societies as well. Foraging success, growth, reproductive potential, breeding success, and survival of all group members increase with group size, especially when predators are abundant (*H. parvula*: Rasa 1989; Rood 1990; *S. suricatta*: Clutton-Brock *et al*. 2001b; Russell *et al*. 2003, 2007), underlining the close association between the number of helpers and individual fitness benefits.

Coordination of cooperative activities appears to rely heavily on vocal communication (e.g. alarm calls: Manser 2001; Manser *et al.* 2001; moving and recruitment calls, decision-making: Bousquet *et al.* 2011; Zöttl *et al.* 2013; vigilance behaviour: Townsend *et al.* 2011b; individual recognition: Müller & Manser 2008; Townsend *et al.* 2011a; close calls and vocal cues: Jansen *et al.* 2012). There are differences in behavioural plasticity related to the social organisation of the species, as exemplified by the smaller, less context-dependent repertoire containing an urgency-based alarm call system of facultatively social yellow mongooses (Le Roux 2007; Le Roux *et al.* 2009b) and the functionally referential alarm calls in obligatorily social meerkats and dwarf mongooses (Beynon & Rasa 1989; Manser 2001; Manser *et al.* 2002; Furrer & Manser 2009). Within species, vocal communication has been shown to be flexible depending on variation in the social environment of individuals, and the adaptive function of vocal phenomena has been related to a larger evolutionary context among animal societies (Townsend & Manser 2011; Townsend *et al.* 2012). For example, in meerkats, roaming males are less likely to produce alarm and recruitment calls than males in coalitions or groups (Townsend *et al.* 2012). Analyses of sentinel behaviour in meerkats supported more general models of anti-predator behaviour (Bednekoff 1997), highlighting sentinel behaviour as the individual's optimal strategy, and refuting a higher predation risk for sentinels and the significance of kin selection (Clutton-Brock *et al.* 1999c; Manser 1999). Interspecific comparisons revealed how vigilance behaviour varies with the level of social organisation. While meerkats rely on communal vigilance, in yellow mongooses, the presence of conspecifics during foraging results in higher individual vigilance and reduces foraging time, contradicting the typical group-size effect on individual vigilance (Le Roux *et al.* 2009a).

(2) Social relationships in the Eupleridae

In contrast to these outstanding contributions of mongoose sociality to mammalian behavioural ecology and sociobiology, knowledge about the social structure of the societies of the Malagasy carnivores is still very limited. Stable male associations in fossa involve about a third of all males, often, but not necessarily, including kin (Lührs *et al.* 2013). They facilitate cooperative hunting of the largest prey categories (arboreal primates) and yield advantages in male-male competition over access to receptive females (Lührs & Dammhahn 2010; M.-L. Lührs & P.M. Kappeler, unpublished data). Male associations therefore represent a striking convergent feature of their social structure with herpestids. Social relationships in the other Malagasy carnivores remain largely undescribed (Albignac 1976). Territorial scent-marking behaviour has been mentioned in *Galidia elegans* (Goodman 2003b), and a matriarchal hierarchy within family groups and hints of cooperation in the rearing of offspring have been indicated in *Mungotictis decemlineata* (Razafimanantsoa 2003). However, existing data presently do not allow the classification of euplerid social structure apart from *C. ferox*.

Interrelationships among the components of mongoose social systems

A social system of a species is characterised by its social organisation, mating system and social structure. We consider these three components as discrete but interrelated entities. However, these interrelationships are often not exclusively of causal, evolutionary or correlational nature, and can vary independently (Kappeler & van Schaik 2002). Thus, we will focus on the most pronounced patterns for solitary and group-living mongooses, and discuss them with regard to predictions of the socio-ecological model (SEM) and reproductive skew theory.

(1) Solitary species

Among solitary mongooses, there is a link between the distribution of females and the reproductive tactics of males that has also been found in other carnivores. Furthermore, the spatial distribution of females in combination with the absence of paternal care behaviour (*H. ichneumon*: Palomares & Delibes 1993) makes a polygynous mating system possible. However, without additional behavioural data, it is difficult to explain patterns of spatial organisation, e.g. whether male home ranges overlap due to extensive roaming and excursions (e.g. in American mink *Neonvison vison*: Yamaguchi *et al*. 2004), or due to male associations (e.g. in cheetahs *A. jubatus*: Caro & Collins 1987). Similarly, male associations can be driven by ecological or reproductive factors, and more contextual data are required for an explanation.

(2) Group-living species

(*a*) *Determinants of male association patterns in group-living mongooses*

Among the group-living mongooses, male coalition formation, in particular among kin, as a strategy to increase breeding opportunities during immigration into a new group has been reported for dwarf mongooses (Waser *et al.* 1994), similar to patterns found in lions *Panthera leo* (Packer *et al.* 1991) and white-nosed coatis *Nasua narica* (Gompper *et al.* 1997). The benefits for dominant individuals arising from group augmentation may explain the interrelationships between this and other reproductive tactics, on the one hand, and kin relationships, group composition and structure, on the other hand (Kokko *et al.* 2001; Griffin *et al.* 2003).

(*b*) *Determinants of female distribution and dispersal patterns*

Among mammals, group-living mongooses are supposed to fall between the extremes of variation in female dispersal and philopatry (Clutton-Brock & Lukas 2012). It has been shown that dispersal is costly due to chronic stress during extraterritorial movements, perhaps selecting for delayed dispersal and sociality (Young & Monfort 2009). Dispersal of mammalian females can be stimulated by changes in resource abundance (Nunes 2007), but food distribution does not explain dispersal patterns in highly social mongooses. Instead, social factors, including intra-sexual competition, the associated behavioural tactics and the resulting pattern of reproductive skew, have been emphasised.

Female suppression and eviction of subordinates in highly social mongooses is mediated by the proximate mechanisms of higher body mass, higher testosterone levels, aggressive behaviour and secondary growth in successfully breeding females (Clutton-Brock *et al.* 2006; Young *et al.* 2006). In meerkats, the frequency of eviction varies with the costs and benefits to dominants of suppressing subordinate breeding, and depends on the dominants' reproductive status, the size of their group (i.e. more frequent eviction in larger groups), and the relatedness of subordinates (i.e. less likely eviction of closely related subordinates; Clutton-Brock *et al.* 2010). Under the conditions of food scarcity, females suffer greater costs of co-breeding. The net benefits (i.e. heavier own pups with higher competitive ability and survival probability) dominants receive from evicting subordinates are supposed to be higher in larger groups, as the costs of increased reproductive competition exceed the benefit of retaining more helpers in the group (Nichols *et al.* 2012b). If evicted mongooses are accompanied by same-sexed individuals they have a higher chance of invading another pack (*H. parvula*: Rood 1986, 1987), or successfully establishing a new pack (*M. mungo*: Cant *et al.* 2001), resembling dispersal patterns of cohorts of young lionesses (Pusey & Packer 1987a; Packer *et al.* 2001). However, these females do not form coalitions as is the case in some primates (e.g. Chapais 1992; Silk *et al.* 2004). In mongooses, participants of intra-group aggression usually agitate against lower-ranking individuals (*H. parvula*: Rasa 1987a). Reproductive suppression and monopolisation by the dominant, and possibly the type of feeding on small dispersed food items which are not defendable seem to prevent coalition formation. Overall, emigration after eviction indicates that dispersal patterns and philopatry in group-living mongooses are rather a consequence than a cause of social organisation and structure.

(*c*) *Determinants of reproductive skew*

Reproductive skew is determined by incest avoidance, reproductive suppression and eviction of subordinates, and infanticide (Keane *et al.* 1996; Clutton-Brock *et al.* 1998; Griffin *et al.* 2003; Young *et al.* 2008; Clutton-Brock 2009a; Hodge *et al.* 2011). In turn, the significance and variation of these factors among sexes and sites are determined by variation in social organisation. For example, in male meerkats, tenure length and reproductive rate of dominants are strongly affected by group size, presumably due to higher survival rates in large groups and higher capacity to fend off extra-group males, and by group composition, i.e. the number of intra-group competitors and adult females (Spong *et al.* 2008). Breeding success of subordinate males can be predicted by access to an unrelated opposite-sex breeder *via* immigration, whereas female subordinates display a highly variable degree of relatedness to opposite-sex breeders. Subordinate philopatric males usually do not breed within the group, and are commonly the sons of the dominant female (Griffin *et al.* 2003). However, extra-group paternity by prospecting subordinated male meerkats (Young *et al.* 2007) indicates that intra-sexual competition has led to the evolution of alternative reproductive tactics. These, in turn, have consequences for population demography and individual life histories, as they significantly reduce the age at first reproduction in subordinate males, allow subordinates to breed without dispersing, and influence genetic group structure.

Some recent evidence suggests that odour-based mechanisms underlie kin discrimination in mongooses (Leclaire *et al.* 2013b). However, there is evidence for relatively high levels of inbreeding in meerkats, and inbreeding avoidance seems to function effectively only within groups (Nielsen *et al.* 2012). Apparently, subordinate females are not able to discriminate between roving kin and non-kin males from other groups, indicating that due to the combined costs of dispersal and the benefits of breeding (even with related individuals) there is no strong selection on kin discrimination.

(*d*) *The influence of group size and composition and linking mechanisms*

Group size and composition exert another major influence on behavioural outcomes, as reproductive conflict between dominant and non-offspring males is moderated in groups with small numbers of subordinates (Kutsukake & Clutton-Brock 2008). Thus, dominants display a flexible behavioural strategy enabling them to adjust the intensity of reproductive conflict in response to their social environment. Biological market theory has been suggested to explain the variable outcomes resulting from the magnitude of benefits and costs that dominants experience as a function of variation in the number of subordinates (Noë & Hammerstein 1994; Kutsukake & Clutton-Brock 2008).

Infanticide connects social organisation and social structure with reproductive tactics. Larger litter sizes and higher *per capita* survivorship in the case of birth synchrony imply that some offspring of subordinate mongooses survive (*H. parvula*: Keane *et al*. 1994; *M. mungo*: Cant 2000). Considering the more egalitarian pattern of female reproduction in banded mongooses, dominant females may benefit from subordinate reproduction by reducing their predation and infanticide risk (‘beneficial sharing’; Cant & Johnstone 1999; Cant 2000; Gilchrist 2006a, b). Similarly, extreme birth synchrony might be the result of selection against costs for offspring in competition with older littermates for the acquisition of ‘helper escorts’ (Gilchrist 2006a, b; Hodge *et al.* 2011). Also, abortion by subordinates and infanticide by dominants has been shown to be more frequent in large meerkat groups, where the fitness benefits of recruitment are smaller, but do not depend on the degree of relatedness between dominants and subordinates (Clutton-Brock *et al.* 2010).

(*e*) *Determinants of cooperative behaviour*

The role of philopatry for cooperative breeding and the variation between facultative and obligate cooperation has been discussed in social mongooses (English *et al.* 2008; Le Roux *et al.* 2008). Females, in particular, gain direct (by increasing group size) and indirect (by recruitment of helpers when inheriting the breeding position) benefits if they remain in their natal group and invest in young (English *et al.* 2008). However, the question remains whether group selection, kin selection or direct benefits for individuals represent the major evolutionary cause for cooperative breeding. Because groups of social mongooses consist of relatives, the distinction between group and kin selection is difficult, and eventually not necessary. Moreover, the combination of intense competition, reproductive suppression and eviction do not fit the predictions of group-selection models (Clutton-Brock 2009b). A better explanation may be that effects on the fitness of other group members are unselected by-products of the adaptive strategies of individuals, and that direct benefits arising from group augmentation can sufficiently explain cooperative behaviour in social mongooses (Clutton-Brock *et al.* 1999a, b, c; Kokko *et al.* 2001; Clutton-Brock 2002; West *et al.* 2007; Clutton-Brock 2009b, c; Madden *et al.* 2012). However, it has become apparent that the relationship between group size and individual fitness benefits in cooperative breeders is not that easy to formulate, since recent models on meerkat group dynamics have suggested that recruitment increases do not keep pace with increasing group size, leading to reduced *per capita* recruitment in larger groups (Bateman *et al.* 2012).

Recently, food availability has been emphasised as another determinant of the investment in communal pup care. In banded mongooses, juvenile helpers and non-breeding females invest less when food is scarce, while adult males and breeding females do not alter their investment under those conditions. Thus, direct benefits from helping and long-term fitness costs (due to weight loss under food scarcity) result in the observed patterns of pup care (Nichols *et al.* 2012a).

Regarding female competition, it appears that inclusive fitness benefits of helping relatives, combined with the cost of challenging dominants seem to explain the long breeding tenure of dominant females and the stability of the group hierarchy in meerkats. The costs of displacing a closely related breeder and the low probability of success, and eviction in the case of failure may override the direct fitness benefits of producing own offspring (Sharp & Clutton-Brock 2011b).

Interestingly, the comparison among social mongooses reveals how reproductive skew influences contributions to rearing offspring by breeders and non-breeders. While in the high-skew system of meerkats breeders contribute less to cooperative pup care than the same-sexed and similarly aged non-breeders (Clutton-Brock *et al.* 2004), in the (female-) low-skew system of banded mongooses, breeders contribute more than non-breeders, except for yearling males. In this species, males generally contribute more than females. Thus, in low-skew societies, non-breeders are less constrained, have to invest less and can save resources for their own future breeding attempts (Gilchrist & Russell 2007; Nichols *et al.* 2012b). Furthermore, while in meerkats the number of helpers is positively correlated with group size and an increase in the helper:pup ratio (Clutton-Brock *et al.* 2001b; Clutton-Brock *et al.* 2004), this is not the case in banded mongooses. Gilchrist (2006a) therefore argues that not group size *per se*, but the availability of care determines group reproductive success.

Finally, considering other kinds of cooperation and inter-specific differences, the correlation between group size and individual fitness benefits need not always exist. For example, an increase in foraging group size has led to higher individual vigilance in the more solitarily foraging yellow mongoose, whereas in meerkats it has been assumed that communal vigilance reduces individual costs (Le Roux *et al.* 2009a). These authors suggest that foraging group size in herpestids is constrained by species-distinct vigilance patterns, which would imply that behavioural strategies determine social organisation. However, social organisation may also determine behavioural tactics and social structure in this as well as other cases of social communication (Le Roux *et al.* 2008; Furrer & Manser 2009; Le Roux *et al.* 2009b), demonstrating that it is difficult to deduce the polarity of the interactions among the components of a social system.

Overall, the present studies clearly indicate that group-living results in intensive reproductive competition among females, which varies according to the cost-benefit ratio for dominants under the influence of group size and composition (including relatedness). The diverse social relationships among group members find their expression in varying social mechanisms (e.g. risk of infanticide, suppression, and eviction), that, in turn, determine the evolution of reproductive strategies and connected life histories (e.g. birth synchrony), mating success and reproductive skew, and, ultimately, fitness outcomes. Reproductive skew is indicated to influence individual investments in cooperative behaviour, and thus connects individual behavioural strategies and reproductive tactics with characteristics of social structure.

In turn, cooperative care behaviour influences pup survival and thus group reproductive success, providing the link to the observed demographic patterns.

Theoretical implications of mongoose sociality

(1) Reproductive skew theory

Reproductive skew models predict a negative relationship between relatedness and the degree of reproductive skew. Variation in kin structure among highly social mongooses permits preliminary tests of the consistency of this prediction. As banded mongooses often remain in their natal group beyond the age of reproductive maturity, and thus are often related, subordinate reproduction may represent an indirect fitness component for dominants, and a direct one for subordinates (Gilchrist 2006a). However, Gilchrist (2006a) observed a decrease in mean reproductive success with an increase in the number of breeding females. Although differential infanticide by dominant breeders represents one theoretically possible way of dealing with this conflict (Clutton-Brock *et al.* 1998; Clutton-Brock *et al.* 2001b) dominant females appear to reduce the reproductive costs of subordinate breeding by evicting breeding subordinates *en masse*, in agreement with the assumptions of transactional models, in particular of ‘restraint’ models. However, there is a lack of evidence that subordinates restrain reproduction to avoid being evicted pre-emptively, suggesting that the reproductive patterns are not the result of threats of eviction. This is supported by the fact that pregnant subordinates are allowed to re-enter the group after abortion, and that even non-pregnant subordinates are evicted (Cant *et al.* 2010). Furthermore, there is no evidence in mongooses suggesting that dominants concede breeding opportunities to subordinates in exchange for assistance in future breeding attempts, refuting the assumptions of ‘concession’ models (Cant *et al.* 2001; Clutton-Brock *et al.* 2001b, 2008).

‘Limited control’ models predict the reproductive, kin and dispersal patterns found among highly social mongooses. In meerkats, subordinates are most likely to breed when the dominant female’s ability to exert control is reduced, i.e. at the beginning of her tenure. Additionally, subordinate breeding is most frequent among subordinates of the same generation as the dominant, i.e. heavier and older individuals, which are more difficult to control. It has been shown that the breeding frequency of subordinates is neither related to group size nor to the probability of dispersal. The latter, in turn, does not depend on the degree of relatedness among dominants and subordinates (Clutton-Brock *et al.* 2001b).

(2) Socio-ecological model

Predictions of the SEM have not yet been explicitly tested in mongooses. We noticed a contrast between studies of solitary mongooses, most of which took (some) ecological determinants into account, and the large number of studies on three highly social mongoose species that focused on testing the assumptions and predictions of reproductive skew theory instead. Testing of the SEM is hampered by the notorious difficulties connected with studying far-ranging solitary carnivores, as well as the lack of comparative socio-ecological data on the Eupleridae.

The extent to which aspects of the SEM developed from primate studies can be applied across taxa is unknown (Aureli *et al.* 2008). However, one can argue that the same ecological principles should apply to other mammals as well (Pazol & Cords 2005; Clutton-Brock & Janson 2012). Some mongoose studies have addressed questions on the effects of resource distribution on spatial organisation, territory size, inter-individual encounters and group formation, in particular among females, as well as seasonal variation of roaming patterns of males in response to female distribution (Palomares & Delibes 1993; Cavallini & Nel 1995; Gilchrist & Otali 2002). In *H. ichneumon*, a species with pronounced social variability, spatial organisation of females has been related to patches of food resources. Their core home ranges did not overlap, and they hardly interacted with each other. Males occupied territories covering several female ranges, and some males formed pairs or family groups together with females out of the mating season (Palomares & Delibes 1993). In the group-living banded mongoose, clumped food resources led to more concentrated home ranges as well, but resulted in higher encounter rates between groups sharing the same food patches (Gilchrist & Otali 2002).

In analysing female dispersal patterns, an important distinction has to be made between singular and plural breeders (Lukas & Clutton-Brock 2011; Clutton-Brock & Lukas 2012). Among social mongooses, species differ markedly in their sex-specific levels of reproductive skew. While monopolisation of female reproduction is strong in meerkats and dwarf mongooses (Rasa 1987a; Rood 1987; Clutton-Brock *et al.* 2006), female reproductive skew of banded mongooses is much lower (Cant 2000; Cant *et al.* 2010). In dwarf mongooses, adolescent females are more likely to disperse if their father is still reproductively monopolising the group (Rood 1987). However, in social mongooses, females rarely leave their natal group voluntarily (Clutton-Brock *et al.* 1998). By contrast, primatologists have related female dispersal to the distribution of resources and feeding competition, but also discussed the risk of infanticide, habitat saturation and inbreeding avoidance in this context (Pusey 1980; Wrangham 1980; Pusey

& Packer 1987b; Stewart & Harcourt 1987; Van Schaik 1989; Sterck *et al.* 1997; Koenig 2002; Isbell 2004).

The patterns described for social mongooses fit the general assumptions and predictions of the SEM according to Sterck *et al.* (1997) to some extent, but not entirely: as in 'resident-nepotistic' primate species, within-group contest is high, dominance asymmetry strong and dispersal rare. However, we can presently not evaluate the underlying assumptions about food distribution (which are assumed to be 'clumped' in that case) and the level of within- and between-group contest, although there is evidence of highly aggressive encounters between groups (*H. parvula*: Rasa 1987*a*; *M. mungo*: Rood 1975; Cant *et al*. 2001; *S. suricatta*: Young 2003). Furthermore, scent-marking patterns do not indicate intra-sexual competition for food, but rather support the idea of competition for breeding opportunities (Jordan *et al.* 2011a; Jordan *et al.* 2011c).

It is difficult to perform formal tests of many assumptions and predictions of the SEM due to its verbal nature and the lack of accurate measurements of ecological parameters (e.g. food distribution; Clutton-Brock & Janson 2012). Formal tests of the SEM were further hampered by the fact that studies relating ecological factors to the social patterns of group-living mongooses used indirect indicators, such as variation in rainfall as a predictor for variation in food availability (Clutton-Brock *et al.* 1999a; Nichols *et al.* 2012a, b). Although social mongooses may be selective in their choice of feeding sites (Clutton-Brock *et al.* 1999a), they mainly feed independently on small invertebrates, which are assumed to be evenly distributed in their open-landscape habitats (Rood 1975, 1986). Thus, the feeding ecology of social mongooses does not support the assumptions of the SEM regarding 'resident-nepotistic' groups, and does not explain why females stay in their natal group.

The evaluation of the relationship between SEM and reproductive skew theory is further hampered by the fact that, among mammals, the impact of resource availability on the level of reproductive skew within social groups has received little attention (Russell 2004; Hodge 2009). However, the ecological constraints hypothesis (Emlen 1982) has been widely accepted in explaining the influence of the availability of resources on costs and benefits of dispersal of subordinated individuals (Hatchwell & Komdeur 2000). Furthermore, recent studies revealed how variation in food availability leads to variation in suppression and eviction patterns in social mongooses, mediated by the costs of co-breeding for dominants (Nichols *et al.* 2012b).

Female gregariousness is primarily seen as an adaptation to reduce predation risk (Rasa 1987b; Rasa 1989; Rood 1990; Clutton-Brock *et al.* 1999a; Clutton-Brock 2009c). Rood (1986) emphasised pair bonding as an essential trait in the evolution of group-living. It might have evolved *via* pair formation between males and dispersed females. According to this notion, predation pressure favoured pairs whose offspring remained with the family. Kin selection and higher survival due to group augmentation could have possibly outweighed the costs of reproductive suppression for young adults (Rood 1986). However, the risk of extra-group infanticide has to be considered in this scenario as well (Cant & Johnstone 1999).

We conclude that key variables of the SEM (e.g. predation risk, food abundance and distribution, infanticide risk) can also explain some of the essential traits of mongoose social organisation, and there are functional and conceptual links with patterns of reproductive skew that deserve more detailed future study.

Since Rood's (1986) review, we have noticed strong support for a phylogenetic division of solitary and social taxa within the mongooses. Recent evidence from primates and other mammals indicates, however, that phylogenetic proximity and life-history parameters are better predictors of social traits and strategies than broad categories of ecological parameters (e.g. food distribution; Clutton-Brock & Janson 2012). The life-history traits of the Malagasy mongooses suggest a strong link with the prevailing unpredictable environmental conditions (Dewar & Richard 2007). Thus, it is important to improve the resolution and breadth of phylogenetic, life-history and ecological data to disentangle their inter-relationships more clearly.

Along the same lines, it is worth emphasizing the importance of long-term field studies and their unique contributions to the study of reproductive and behavioural strategies (Clutton-Brock & Sheldon 2010). Long-term studies of social mongooses, in particular, have contributed to a proper classification of species as singular or plural breeders, and detailed life-history data have allowed tests of the determinants and mechanisms involved in the evolution of cooperative breeding. By contrast, there is still little known about the social behaviour and mechanisms of species such as *C. penicillata* or *M. decemlineata*, which Rood (1986) mentioned as important candidates in the study of evolutionary transitions from solitary to group living. Furthermore, detailed comparative studies of Malagasy mongooses are needed because their adaptations to a forest-dwelling lifestyle in environments characterised by strong climatic unpredictability and presumably relaxed predation risk will complement our current understanding of the evolution of mongoose sociality. The rapid loss of natural ecosystems on Madagascar adds a sense of urgency to this plea.

Conclusions

(1) Our survey of the social system and life history of 34 species of Herpestidae and the 10 species of Eupleridae revealed a large discrepancy between solitary and group-living species, on the one hand, and between the Herpestidae and the Eupleridae, on the other hand, with regard to the number of detailed studies and the amount of available empirical data. The average size and composition of the social units with regard to age, sex and relatedness is still unknown in the majority of mongooses. While spatial patterns and social relationships in solitary species have been mainly related to ecological factors (e.g. food resources, predation risk), social factors, in particular reproductive competition, have been considered extensively in explaining patterns in the most intensively studied group-living species. Intra-specific variation in sociality of some herpestids in response to food distribution, habitat and population density has implications for the mechanisms driving social evolution in mongooses. For some important social patterns such as male associations, there is still no universal explanation.

(2) Broad categories of social organisation (solitary or group-living) are reasonably good predictors of reproductive and other behavioural tactics as well as patterns of social relationships in mongooses. First, group size and composition, age structure and relatedness determine the significance and variation of incest avoidance, reproductive suppression and eviction, and reproductive success. In particular, group size is a determinant of reproductive skew. Second, group size and composition determine the number of inter-individual relationships (network density) and social interactions. Third, group size is a strong determinant of the characteristics of cooperative breeding systems (e.g. helper:pup ratio, individual investment).

(3) Mechanisms such as infanticide risk connect social organisation and structure with reproductive tactics and life histories (e.g. oestrous synchronisation). Extreme reproductive competition and variance in breeding success and fitness costs in group-living species have consequences for the evolution of life histories (e.g. oestrous and birth frequencies), so that cooperative breeding systems function within the constraints of life-history trade-offs. Not kin selection alone, but predominantly the direct individual fitness benefits of group-living and group augmentation are indicated to determine philopatry and cooperative behaviour. The costs of intra-sexual competition influence dispersal patterns of males and females, ultimately in the form of eviction.

(4) The patterns of competition have been primarily related to ‘limited control’ models of reproductive skew theory. By contrast, resource abundance has been little investigated, but it also influences reproductive skew and explains the dominant’s response of suppressing and

evicting subordinates, providing a link between variation in resource abundance and female dispersal. Thus, the basic factors of both the socio-ecological model and reproductive skew theory are not as different from each other as often assumed. The socio-ecological model broadly predicts the ecological determinants of social organisation and roaming patterns among solitary mongooses.

(5) Considering the phylogenetic relationship of the Herpestidae and Eupleridae, the lack of studies of the Eupleridae hampers their comparison with regard to the pace and determinants of carnivore social evolution. More detailed studies of the social systems of the Eupleridae against the background of the distinct selection pressures on Madagascar are therefore needed.

Table 1 Social systems of mongoose-like species (Herpestidae and Eupleridae)

Species	Social organisation	NI	Mating system	Reproductive skew	Social structure	Other characteristics	References
Herpestidae							
Atilax paludinosus	Solitary		?	?	territorial	Nocturnal/crepuscular	Ray (1997)
Bdeogale crassicauda	Solitary(?)		?	?	?	Nocturnal(?)	Kingdon (1997)
Bdeogale jacksoni	Solitary		?	?	?	Nocturnal, crepuscular	Kingdon (1997)
Bdeogale nigripes	Solitary(?)		?	?	?	Nocturnal	Kingdon (1997)
Bdeogale omnivore **							
Crossarchus alexandri	Groups	~20	?	?	?	Diurnal, partly nocturnal	Kingdon (1997)
Crossarchus ansorgei	?	?	?	?	?	?	
Crossarchus obscurus	Groups of 2-3 family units	10-20	Dominant individuals breeding	relatively high(?)	territorial; hierarchy; foraging alone or in group	Diurnal	Goldman (1987); Kingdon (1997)
Crossarchus platycephalus	?	?	?	?	?	?	
Cynictis penicillata	mixed-sex groups; alpha pair; large range overlap in ♂♂, but not in ♀♀	~7-20	Dominant breeding pair	?	territorial; loose sociality	Diurnal	Earlé (1981); Cavallini & Nel (1995)
Dologale dybowskii	?	?	?	?	?	Diurnal	Dorst (1970)
Galerella flavescens	Solitary; ♂♂ ranges largely overlap		?	?	No paternal care(?); intraspecific fights determine hierarchy on food patch; hunting dyads of ♂♂	Diurnal	Rathbun *et al.* (2005); Rathbun & Cowley (2008)
Galerella ochracea	?	?	?	?	?	?	-
Galerella pulverulenta	solitary, ♂♂ large range overlap		?	?	loose ♂♂ associations, possible territoriality in ♀♀	Diurnal	Cavallini & Nel (1995)

Table 1 continued

Species	Social organisation	NI	Mating system	Reproductive skew	Social structure	Other characteristics	References
Helogale hirtula	Mixed-sex groups (?)	?	?	?	?	Diurnal	Kingdon (1997)
Helogale parvula	mixed-sex groups, lifelong-bonded alpha pair	9; 2-32	Promiscuous; dom. breeding pair monopolises reproduction	High (in both sexes)	matriarchal; ♀♀ higher ranked, age-dependent hierarchy; intergroup territoriality; communal cooperative breeding, spontaneous lactation; subordinate suppression by rank-dep. dominance effect (♀:endocrine, ♂: aggress.); high paternal care	Diurnal; oestrus synchrony; dispersal weakly male biased	Rood (1980, 1987, 1990); Rasa (1987a); Creel & Creel (1991); Creel *et al.* (1991, 1992, 1993)
*Herpestes auropunctatus****	Solitary		Promiscuous; ♂♂associations overlap with many ♀♀ home ranges	?	Male associations during breed. season; high aggression among ♂♂	Diurnal	Gorman (1979); Nellis (1989); Roberts (1997); Hays & Conant (2003)
Herpestes brachyurus	Solitary; exclusive ♀♀ home ranges; ♂ overlap with several ♀♀		polygyneous(?)	?	territorial	Diurnal	Jennings *et al.* (2010)
Herpestes edwardsii	Solitary (?)		?	?	In captivity: age-dependent hierarchy when mating	Diurnal	Roberts (1997); Santiapillai *et al.* (2000); Veron *et al.* (2004)
Herpestes fuscus	?	?	?	?	?		
Herpestes ichneumon	solitary, also pairs and family groups; ♀♀ranges overlap	1.7; 1-5	Polygynous; no. of ♀♀ per ♂ correlates with ♂ weight		Territorial; mainly associations of ♀, (♂) and young; coop. hunting; little ♀♀ interaction; pup care in associations when high food abundance	Diurnal, crepuscular; studies indicate intra-specific variation of social system in relation to food resources	Ben-Yaacov & Yom-Tov (1983); Palomares & Delibes (1992, 1993); Santiapillai *et al.* (2000)

Table 1 continued

Species	Social organisation	NI	Mating system	Reproductive skew	Social structure	Other characteristics	References
*Herpestes javanicus****	Solitary; large ♀♀ home range overlap		Promiscuous; ♂♂associations overlap with many ♀♀ home ranges	?	Male associations during breed. season; aggression among ♂♂	Diurnal	Gorman (1979); Nellis (1989); Roberts (1997); Hays & Conant (2003)
Herpestes naso	solitary(?); large home range overlap in ♂♂ in stream habitats	?	?	?	?	Diurnal	Ray (1997)
Herpestes semitorquatus	?	?	?	?	?	Only on Borneo; rare	
Herpestes smithii	?	?	?	?	?	?	
Herpestes urva	?	?	?	?	?	Diurnal	Wang (1999)
Herpestes vitticollis	?	?	?	?	?	Diurnal	Pillay (2009)
Ichneumia albicauda	Solitary; little range overlap betw. ♂♂, ♀♀ partly in common ranges, but do not interact		Polygynous(?); ♂ ranges overlap with several ♀ranges	?	Natal philopatry, delayed dispersal; gregariousness, matrilinear(♀+offspring in the same home range)	Nocturnal	Taylor (1972); Waser & Waser (1985); Admasu *et al.* (2004)
Liberiictis kuhni	Group living(?)	3-5	?	?	?	Diurnal	Goldman & Taylor (1990); Nowak (1991)
Mungos gambianus	Mixed-sex groups	6.7; 1->40	Promiscuous	?	Intergroup aggression	Diurnal	Kingdon (1997); Sillero-Zubiri & Bassignani (2001)
Mungos mungo	Mixed-sex groups	24; 8-75	Promiscuous; 'core' breed. cohort: 1-5 ♀♀, 4-12♂♂; mate-guarding by top males	♀: low ♂: high	coop. breed. (pup-helper bond), eviction of subordinates; high oestrus and birth synchrony; intergroup territoriality	Diurnal	Cant (2000, 2003); Cant *et al.* (2001, 2010); Gilchrist (2004); Hodge (2005); Nichols *et al.* (2010)
Paracynictis selousi	Solitary; occasionally pairs		?	?	?	Nocturnal	Skinner & Chimimba (2005)
Rhynchogale melleri	Solitary(?)	?	?	?	?	Nocturnal	Kingdon (1997)

Table 1 continued

Species	Social organisation	NI	Mating system	Reproductive skew	Social structure	Other characteristics	References
Suricata suricatta	mixed-sex groups, alpha pair	3-50	promiscuous; dominant breeding pair monopolises reprod. (80%); males disperse and immigrate into other groups	high in both sexes	matriarchal; communal coop. breeding; eviction of subordinated ♀♀ at domin. late pregnancy, infanticide; intergroup territoriality (aggress.)	Diurnal	Clutton-Brock *et al.* (1998, 1999c, 2001c, 2006) , http://www.kalahari-meerkats.com
Eupleridae							
Cryptoprocta ferox	Solitary		Promiscuous; male coalition forming to defend access to ♀♀	?	♂♂ associations; cooperative hunting	Cathemeral	Albignac (1972b); Goodman *et al.* (2003); Hawkins & Racey (2005, 2009); Lührs & Dammhahn (2010)
Eupleres goudotii	Solitary(?)		?	?	?	Cathemeral	Albignac (1973); Nowak (1991); Goodman *et al.* (2003)
*Eupleres major*****	Solitary (?)		?	?	?	Cathemeral	See *Eupleres goudotii*
Fossa fossana	pairs(?)	?	?	?	?	Nocturnal	Nowak (1991); Goodman *et al.* (2003)
Galidia elegans	?	?	?	?	Territorial scent-marking	Diurnal, terrestrial and arboreal	Albignac (1972b); Goodman (2003b)
Galidictis fasciata	?	?	?	?	?	Nocturnal	Goodman (2003a)
Galidictis grandidieri	?; ♀: exclusive ranges;♂:overlap with several ♀♀	?	?	?	?	Nocturnal	Goodman (2003a); Marquard *et al.* (2011)
Mungotictis decemlineata	?	?	?	?	"Leader" female; communal rearing	Diurnal, terrestrial and arboreal	Razafimanantsoa (2003)
Salanoia concolor	?	?	?	?	?	Diurnal	Goodman *et al.* (2003)
Salanoia durrelli	?	?	?	?	?	?	

NI: Number of individuals in group-living species (mean; min-max); ?: not known; (?): conflicting statements in literature or concluded from anecdotal descriptions; *: Definition according to Gittleman (1986); **: species status uncertain (not regarded as a distinct species by Wozencraft (2005), but as a subspecies of B. crassicauda); ***: taxonomic conflict regarding previous taxonomy (H. auropunctatus and H. javanicus should be considered as two distinct species; Patou et al. (2009); H. auropunctatus not recognised as a distinct species by Nyakatura & Bininda-Emonds (2012); ****: after Goodman & Helgen (2010).

Table 2 Life history traits of mongoose-like species (Herpestidae and Eupleridae)

Species	BM [kg]	ASM [m]	LS	BirthM /EmM [g]	LY/ IB-I [d]	G [d]	W [d]	I [d]* /D [m]	L [y]	References
Herpestidae										
Atilax paludinosus	3.3	8.5	2.4	100 /?	2 /?	76	36	?	>20.8	Ernest (2003); De Magalhaes & Costa (2009)
Bdeogale crassicauda	1.6	?	1	?	?	?	?	?	?	Ernest (2003)
Bdeogale jacksoni	2.5	?	1(?)	?	?	?	?	?	?	Smith *et al.* (2003)
Bdeogale nigripes	2.5	?	1	?	?	?	?	?	>15.8 (capt)	Smith *et al.* (2003); De Magalhaes & Costa (2009)
Bdeogale omnivore **										
Crossarchus alexandri	1.5	?	?	?	?	?	?	?	?	Smith *et al.* (2003)
Crossarchus ansorgei	0.7-1.0	?	?	?	?	?	?	?	?	Smith *et al.* (2003)
Crossarchus obscurus	0.7-1.2	9	4	?	2.5 /?	58	23	?	13.3	Goldman (1987); Kingdon (1997); Ernest (2003); De Magalhaes & Costa (2009)
Crossarchus platycephalus	1.0-1.5	?	?	?	?	?	?	?	?	Kingdon (1997)
Cynictis penicillata	0.6	24	2	?	2 /?	56	61	~70 /?	15.2 (capt)	Earlé (1981); Cavallini & Nel (1995); Ernest (2003); De Magalhaes & Costa (2009)
Dologale dybowskii	0.3-0.4	?	?	?	?	?	?	?	?	Kingdon (1997)
Galerella flavescens	?	?	?	?	?	?	?	70(?) /?	?	Rathbun *et al.* (2005); Rathbun & Cowley (2008)
Galerella ochracea	?	?	?	?	?	?	?	?	?	-

Table 2 continued

Species	BM [kg]	ASM [m]	LS	BirthM /EmM [g]	LY/ IB-I [d]	G [d]	W [d]	I [d]* /D [m]	L [y]	References
Galerella pulverulenta	0.6-0.86	?	2.6	?	?	61	58	?	>11 (capt)	Cavallini & Nel (1995); Ernest (2003); Weigl (2005)
Galerella sanguinea	0.5-0.8	12	2	?	2 /?	65	55	~70 / ~12	>12 (capt)	Rood & Waser (1978); Waser *et al.* (1994); Ernest (2003); Weigl (2005)
Helogale hirtula	0.3	?	?	?	?	?	?	?	?	Smith *et al.* (2003)
Helogale parvula	0.35	13.5-15	3.3; 1-6	21 /?	3 /~120	49-54	56	153 /12-36 (48)	18 (capt)	Rood (1980, 1987, 1990); Rasa (1987a); Creel & Creel (1991); Ernest (2003); Weigl (2005)
*Herpestes auropunctatus****	0.47-0.8	♀:10 ♂:4(-5)	2.2	26/?	2-3 /151	49	50	?	>16	Roberts (1997); Ernest (2003); Hays & Conant (2003); De Magalhaes & Costa (2009)
Herpestes brachyurus	1.4; 1-3	?	?	?	?	?	?	?	?	Smith *et al.* (2003); Jennings *et al.* (2010)
Herpestes edwardsii	1.0-1.8	9	2.6	?	2-3 /?	60	?	?/6	>12	Roberts (1997); Santiapillai *et al.* (2000); Ernest (2003); Veron *et al.* (2004); Weigl (2005)
Herpestes fuscus	?	?	?	?	?	?	?	?	?	-
Herpestes ichneumon	2.9	24	2.7	?	1.5 /?	74	61	?	12	Palomares & Delibes (1992, 1993); Ernest (2003); De Magalhaes & Costa (2009)
*Herpestes javanicus****	0.47-0.8	♀:10 ♂:4(-5)	2.2	26/?	2-3 /151	49	50	?	>16	Roberts (1997); Ernest (2003); Hays & Conant (2003); De Magalhaes & Costa (2009)
Herpestes naso	1.9-4.2	?	?	?	?	?	?	?	>11	Kingdon (1997); Ray (1997); Weigl (2005)

Table 2 continued

Species	BM [kg]	ASM [m]	LS	BirthM /EmM [g]	LY/ IB-I [d]	G [d]	W [d]	I [d]* /D [m]	L [y]	References
Herpestes semitorquatus	?	?	?	?	?	?	?	?	?	-
Herpestes smithii	1.8	?	?	?	?	?	?	?	>17 (capt)	Smith *et al.* (2003); Weigl (2005)
Herpestes urva	1.8	?	?	?	?	?	?	?	>13	Smith *et al.* (2003); Weigl (2005)
Herpestes vitticollis	2.2-2.9	?	2.5	?	?	?	?	?	>12	Smith *et al.* (2003); Weigl (2005); De Magalhaes & Costa (2009)
Ichneumia albicauda	3.2- >5	?	2.3	?	1 /~360	60	?	~270 /?	>10	Taylor (1972); Waser & Waser (1985); Nowak (1991); Ernest (2003)
Liberiictis kuhni	2.3	?	?	?	?	?	?	?	?	Goldman & Taylor (1990)
Mungos gambianus	1.5	?	?	?	?	?	?	?	?	Smith *et al.* (2003)
Mungos mungo	1.5-1.9	12 (♀ 321 days)	3.2 (1-6; fetal)	20-50 /?	4 /88	59-63	65	90 /♀ 6-48, ♂12-36	12	Creel & Creel (1991); Cant (2000, 2003); Cant *et al.* (2001); Smith *et al.* (2003); Gilchrist *et al.* (2004)
Paracynictis selousi	1.8	?	2.5	?	?	?	?	?	?	Ernest (2003)
Rhynchogale melleri	1.7-3.0	?	2-3	?	?	?	?	?	?	Kingdon (1997)
Suricata suricatta	0.7 (max 1.02)	12	3.6; 1-7	31 /100	1-4 /82	60-70	42	90 /18-30	>12	Clutton-Brock *et al.* (1998, 1999c, 2006); Ernest (2003); Russell *et al.* (2003); http://www.kalahari-meerkats.com

Table 2 continued

Species	BM [kg]	ASM [m]	LS	BirthM /EmM [g]	LY/ IB-I [d]	G [d]	W [d]	I [d]* /D [m]	L [y]	References
Eupleridae										
Cryptoprocta ferox	♂7.4 ♀6.1;6-12	49	2.5; 1-6	100 /-	?	50-60	122	? /12-24	>23	Albignac (1975); Ernest (2003); Hawkins & Racey (2005); Weigl (2005); Kirschner (2009); Lührs & Dammhahn (2010) Lührs, pers. comm.
Eupleres goudotii	3.0	?	1-2	150 /-	?	?	64	?	?	Albignac (1972b); Ernest (2003); Goodman *et al.* (2003)
*Eupleres major*****	3.0 (?)	?	1-2(?)	150(?) /-	?	?	64 (?)	?	?	See *Eupleres goudotii*
Fossa fossana	1.7; 1.5-2.1	♀24 ♂?	1	100 /-	1 /365	82-89	76	?	>21 (capt)	Albignac (1972b); Ernest (2003); Goodman *et al.* (2003); Kerridge *et al.* (2003); Weigl (2005); De Magalhaes & Costa (2009)
Galidia elegans	0.7-0.9	♀24 ♂?	1	40-50 /-	1 /~365	72	60	?	26 (capt)	Albignac (1972b, 1973); Nowak (1991); Ernest (2003); Goodman (2003b); De Magalhaes & Costa (2009)
Galidictis fasciata	0.6	?	1	?	?	?	?	?	?	Albignac (1973); Goodman *et al.* (2003)
Galidictis grandidieri	1.2-1.64	?	1-2	?	1 /~365	?	?	?	?	Goodman (2003a); Goodman *et al.* (2003); Marquard *et al.* (2011)

Table 2 continued

Species	BM [kg]	ASM [m]	LS	BirthM /EmM [g]	LY/ IB-I [d]	G [d]	W [d]	I [d]* /D [m]	L [y]	References
Mungotictis decemlineata	0.4-0.7	♀24 ♂?	1-2	50 /?	?	74-106	39	? /24-36	>11	Albignac (1972b); Ernest (2003); Razafimanantsoa (2003); De Magalhaes & Costa (2009) ; Klös, pers. comm.
Salanoia concolor	0.7	?	1	?	?	?	?	?	?	Albignac (1972b); Goodman *et al.* (2003)
Salanoia durrelli	0.6	?	?	?	?	?	?	?	?	Goodman & Helgen (2010)

BM: Body mass; ASM: Age at sexual maturity [months]; LS: Litter size (mean; min-max); BirthM/EmM:Body mass at birth/Body mass at emergence, in denning species; LY: Number of litters per year/IB-I: Inter-birth interval [days]; G: Gestation length [days]; W: Weaning age [days]; I: Age of independence*[days]/D: age of dispersal [months]; L: Longevity [years]; (capt): in captivity; ?: not known; (?): conflicting statements in literature or concluded from anecdotal descriptions; *: Definition according to Gittleman (1986); **: species status uncertain (not regarded as a distinct species by Wozencraft (2005), but as a subspecies of B. crassicauda); ***: taxonomic conflict regarding previous taxonomy (*H. auropunctatus* and *H. javanicus* should be considered as two distinct species; Patou et al. (2009); *H. auropunctatus* not recognised as a distinct species byNyakatura & Bininda-Emonds (2012); ****: after Goodman & Helgen (2010).

Fig. 1 Phylogenetic classification and reconstruction of the ancestral state of social organisation, based on the recent phylogeny of Nyakatura & Bininda-Emonds (2012), conducted in MacClade Version 4.08a (Maddison & Maddison 2005). White branches indicate solitary, dotted ones pair-living and black ones group-living taxa. The social classification of species not marked by squares is still unknown.

CHAPTER 2

Gregarious sexual segregation: The unusual social organisation of the Malagasy narrow-striped mongoose (*Mungotictis decemlineata*)

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Abstract

Sex-specific costs and benefits of sociality are rarely evaluated, even though the main fitness determinants differ between the sexes. The Carnivora include some of the few mammalian species in which the sexes differ in social organisation, providing an opportunity to study male and female sociality separately. Anecdotal reports indicated that Malagasy narrow-striped mongooses (*Mungotictis decemlineata*) appear to have unusual and flexible association patterns. We therefore conducted a 3-year field study in western Madagascar to delineate the social organisation of this forest-dwelling species and to obtain insights into sex-specific determinants of sociality. We conducted systematic radio-tracking on 40 adult individuals (20 males, 20 females) and collected additional data during regular censuses and behavioural observations. We found males and females to live in small, same-sex social units. Males formed associations of up to 4 individuals, except for the short annual mating season, when they roamed by themselves. Male home ranges exhibited high mutual overlap and encompassed those of up to four female social unit ranges. Female social units were on average composed of 2 adult females, 1 juvenile and 1 infant offspring of the dominant female and occupied exclusive territories. Female units were stable year-round and their numerical size was unrelated to home range size, but home range sizes were significantly larger during the lean dry season. Our analyses indicate that both male and female associations are likely stabilized by anti-predator benefits, with females accruing additional benefits from joint resource defence. Males trade off the safety in associations for temporary reproductive opportunities. Thus, anti-predator benefits favour group living in both sexes, but sex-specific fitness limiting factors affect the stability of units differently.

Introduction

Although most mammals are solitary, some are pair-living (Lukas & Clutton-Brock 2013) and virtually all orders of mammals also contain species that live in groups of variable composition and stability (e.g., Jarman 1974; Gittleman 1989a; van Schaik & Kappeler 1997; Jarman 2000; Ebensperger & Cofré 2001; Kerth *et al.* 2001; Mitani *et al.* 2012). Identification of the factors affecting this variation in social organisation, i.e. the size, composition and spatio-temporal cohesion of species-specific social units, has been one of two major goals of socio-ecological research for more than five decades (Crook 1964; Crook 1970; Kappeler & van Schaik 2002; Clutton-Brock & Janson 2012; Koenig *et al.* 2013). Various environmental factors, such as resource characteristics and predation risk, but also life-history traits, such as body size and activity pattern, as well as phylogenetic signals have been found to explain part of the social variation observed among species (Jarman 1974; Clutton-Brock & Harvey 1977; Macdonald 1983; van Schaik 1983; Shultz *et al.* 2011; Kappeler *et al.* 2013; Thierry 2013). Much less is known about social variation within species and its underlying causes (Lott 1991; Schradin 2013). In some species, different subsets of a population may live in pairs or groups, or a given social unit may fluctuate between these categories over time (Maher & Burger 2011; Garber *et al.* 2015). In other species, an entire population may switch between a solitary and a gregarious life, typically in response to variation in environmental variables (Schradin & Pillay 2005; Schradin *et al.* 2012).

In addition, more sex-specific factors such as parental care, infanticide risk or resource dispersion appear to be of variable importance in different lineages, contributing to social variation among taxonomic groups (Macdonald 1983; Clutton-Brock 1989; van Schaik 2000). As a result, adult males and females may differ in their social organisation, with one sex being gregarious and the other solitary (Conradt & Roper 2000; Ruckstuhl & Neuhaus 2002; Lührs & Kappeler 2013). For the purpose of identifying the sex-specific factors that favour one or the other form of sociality, these species are particularly interesting because males and females of a species typically share all fundamental biological features and ecological requirements, providing natural controls for many of the factors that complicate interspecific comparisons.

The Carnivora have played a salient role in our understanding of patterns and processes in social evolution because they exhibit not only great interspecific variation in social organisation, ranging from solitary species to cooperative breeders (Macdonald 1983; Bekoff *et al.* 1984; Sandell 1989), but they also include species in different taxonomic groups that are socially particularly flexible (Waser & Waser 1985; Moehlman 1989) or exhibit gregarious male tendencies despite solitary females (Caro & Collins 1987; Waser *et al.* 1994; Kays & Gittleman 2001; Lührs *et al.* 2013). The mongooses (Herpestidae) are a small clade of 34 species that epitomize all these aspects of social variation (Schneider & Kappeler 2014). Long-term field studies of *Helogale parvula, Mungos mungo* and *Suricata suricatta* have characterised the social systems of the highly social members of this family in great detail, providing important general insights about cooperation, reproductive skew and other aspects of sociality (Creel *et al.* 1993; Clutton-Brock *et al.* 2001a, b, 2006; Clutton-Brock 2002, 2009a, b; Cant *et al.* 2013). However, the social systems of their sister group, the Eupleridae, remain poorly studied (Brooke *et al.* 2014; Schneider & Kappeler 2014). Because they evolved in isolation on Madagascar for the past 24 million years (Yoder *et al.* 2003), they can be regarded as a natural experiment in carnivore social evolution whose outcome can potentially reveal evolutionary transitions between different levels of carnivore sociality as well as insights into the mechanisms driving social evolution in general (Schneider & Kappeler 2014).

Current information on euplerid social systems is limited to a handful of studies, however. In the fosa, *Cryptoprocta ferox*, the largest euplerid species, solitary females are territorial and some, but not all males form long-term associations with 1-2 other males (Lührs & Kappeler 2013). Members of male associations may or may not be relatives, they exhibit larger body size than solitary males (Lührs *et al.* 2013), and they enjoy a mating advantage over the latter (Lührs & Kappeler 2014). In the giant-striped mongoose, *Galidictis grandidieri,* females also appear to be solitary and territorial and males appear to have much larger ranges than females (Marquard *et al.* 2011). The narrow-striped mongoose (*Mungotictis decemlineata*) was reported to exhibit a highly variable social system, including seasonally large groups, which split up into pairs, maternal groups, all male groups and solitary individuals (Albignac 1976). Another study reported social units consisting of one or two adult females, and occasionally a single adult male (Razafimanantsoa 2003). Because these reports were based on opportunistic short-term observations, we aimed to (i) characterise the social organisation of the narrow-striped mongoose based on multiple-year follows of known individuals, (ii) examine the effects of social unit size and season on home range size, and to (iii) provide basic life-history data for comparison with other mongooses and carnivores, focusing on sex-specific determinants of social organisation.

Materials and Methods

Study site

The study was conducted in Kirindy Forest/CNFEREF (Centre National de Formation d'Etude et de Recherche en Environment et Foresterie; 44°39'E, 20°03'S), a seasonal dry deciduous forest covering an area of about 12,500 ha, located 60 km northeast of Morondava in western Madagascar. This region is characterised by pronounced seasonality with a long, cool dry season between May and October and a hot rainy season with an average of 900 mm of annual precipitation (Sorg & Rohner 1996; Kappeler & Fichtel 2012). From 2011 to 2014, we conducted live-trapping and observations on narrow-striped mongooses in two grid systems (locally known as N5 and CS7; about 2 km apart) of small footpaths that are 25 or 50 m apart, spanning a total of 121 km and covering an area of 102 and 117 ha, respectively.

Trapping

Narrow-striped mongooses were trapped in live-traps (20x7x7 in., Tomahawk®, WI, USA) baited with rotten fish. Traps were set during the day along footpaths at a distance of 50 m and were checked every 2.5 h. Captured animals were briefly anaesthetized, using an individually adjusted dosage of 0.12 ml per kg body mass of ketamine [10%] solution, and individually marked with a Trovan® Euro ID-100 micro transponder. We obtained morphometric data on body mass, body size, tooth status, and took small (< 5mg) ear biopsies for genetic analyses. Based on these morphometric data, we classified animals into three age categories: adult (> 450 g and sexually mature), juvenile (> 300 g and older than 6 months) and infant (< 300 g and younger than 6 months). A total of 40 adult individuals (20 males, 20 females) were equipped with Sirtrack® ZV2C 149 VHF radio collars (18 g) with a programmed daily 16 h duty cycle. All other individuals were marked with individual colored plastic collars (adults) or unique tail-fur shaving (infants and juveniles) for visual identification.

Radio tracking and behavioural observations

Marked animals were generally located on a daily basis, but at least twice per week, by direct observation or via triangulation. The radio-collared individuals were tracked using a Telonics TR4-Receiver (Telonics Inc., AZ, U.S.A.) and a Yagi 3-element antenna (MWF-Service, Germany). GPS locations were collected using a handheld Garmin® GPS 60CSx device. We calculated triangulation fixes from bearings using the software LOAS ver. 4.0 (Ecological Software Solutions; Sallee 2004). We conducted regular census and continuous 1-h tracking sessions in order to collect data on life-history events and behaviour. During continuous tracking, we conducted instantaneous scan sampling, noting the location, state (*lie, sit, stand, walk, trot, run, climb* or *out of sight*) and activity (*travelling*, *foraging* and *resting*) every 5 minutes (Martin & Bateson 1993). Furthermore, we noted all social interactions (affinitive, affiliative, agonistic, parental, infantile, olfactory, vocal, vigilance and mating behaviour) during scans and *ad libitum*. Agonistic behaviour was defined as aggressive (*threat*, *chase*, *bite*) and submissive (*give ground*, *crouch*, *flee*). Olfactory behaviours included *smell*, *scent-mark* and *overmark*. Vocalizations were differentiated as *chortle*, *grumble* and *pup vocal*. Mating behaviour included *sexually approach*, *mount* and *copulate*. In total, we conducted 497 h of behavioural observations, recorded 10,411 scan observations, and collected 1,879 triangulation fixes.

We used data from 15 females and 17 males collected between 2012 and 2014 for the spatial analyses. We used several methods to calculate annual home ranges (May 2013 - April 2014): 100% MCP (=minimum convex polygon; Mohr 1947) as a measure of maximum space use; 95% MCP in order to avoid the influence of outlying points, which are possibly based on triangulation error and contribute a large additional area; 95%, 90% and 50% kernel home ranges (Worton 1989) in order to avoid overestimation of size, space use, and overlap, a dependence of size on the number of locations, and to display space use and core areas. Kernel density estimations have been shown to be robust and unbiased even with a relatively small number of data points (Kenward 2001; Börger *et al.* 2006).

In order to ensure independence of data points, we checked for autocorrelation among successively collected locations. Estimations using Schoener's ratio (t^2/r^2; t^2: mean squared distance between successive observations; r^2: mean squared distance between each observation and the center of activity) revealed that data points collected at a minimum of 40-min intervals were independent of each other (Schoener 1981; Swihart & Slade 1985; De Solla *et al.* 1999). Based on travel distances, this period is sufficient to cross an average home range (Doncaster & Macdonald 1997; Kays & Gittleman 2001). In practice, this resulted in 2 data points per animal per 1 h continuous tracking session. We calculated kernel home range sizes with *ad hoc* smoothing (Silverman 1986) by using the Animal Movement extension in ArcView ver. 3.3 (ESRI Inc.; Hooge & Eichenlaub 2000). For further analyses, we used the 90% and 50% kernel home ranges because 95% kernel home range sizes exceeded 100% MCPs, and thus generated even larger false overlap. To explore possible effects of ecological seasonality (i.e. food availability), we compared female 90 and 50% kernel home range areas and overlap of the dry (May-October 2013) and wet season (November 2013-April 2014). Following the extinction of one female social unit (see below), we also compared centroids and shifts of kernel home ranges of neighbouring units before and after this event.

Population biology, demographic and life-history characteristics

We recorded the social history of tagged narrow-striped mongooses from 2011 to 2014. We recorded all life-history events such as *birth*, *first seen*, *last seen*, *immigration*, *dispersal*, *group encounters*, *mating*, *pregnancy*, *death*, *cause of death* (if known). We estimated total population density and for the two grid systems separately. We based our estimations on the number of observed marked and unmarked individuals (the latter were observed in association with marked individuals) present on April 1 of each year in the total area of all annual 90% kernel female home ranges (minus overlap areas). To take into account fluctuations in male sociality (see below), we calculated ratios of compositional change of units for the middle and end of each month, resulting in a monthly rate over all units.

We estimated annual sex ratios and mortality rates in total and separately for the different age categories, thus accounting for variation among years. We estimated annual mortality based on the number of observed deaths per number of animal days (the number of days between the time the animal first appeared in the population and either its death or the last day of the sample; Small & DeMaster 1995; Clutton-Brock *et al.* 1999b, c):

$$\text{Daily Survival Rate} = 1 - (\text{number of deaths/number of animal days})$$
$$\text{Annual Survival Rate} = [\text{Daily Survival Rate}]^{365.25}$$
$$\text{Annual Mortality Rate} = 1 - [\text{Annual Survival Rate}]$$

As we did not find carcasses in many cases of disappearances, we calculated the minimum annual mortality rate based on the number of verified deaths, and the maximum mortality rate based on the number of cases when animals disappeared and were not re-sighted again. Juveniles of unknown sex were excluded from this analysis. We calculated the percentage of infant survival 3, 6 and 12 months after birth as measures of successful reproduction, including only pups emerging from the shelter.

For a comparative evaluation of life-history traits of *M. decemlineata*, we plotted (a) mean litter size and (b) number of litters per year in relation to body mass for group-living and solitary herpestids and euplerids, based on data in Schneider & Kappeler (2014).

Statistical analyses

We report mean ± SD throughout all analyses. We checked the distribution of residuals of home range area and overlap data for normality with a Shapiro-Wilk test. Overlap data were calculated in percentages and arcsine-square-root transformed for analyses. We averaged overlap estimations for each dyad. In case of multiple comparisons, significant levels were Bonferroni-corrected. Values of 90% kernel home range areas were not distributed significantly different from normality. We investigated the influence of sex on annual home range size by using a linear mixed-effects model (LMM) as provided by the package *nlme* in R (Pinheiro *et al.* 2014). A female dispersal event resulted in more than one individual home range value. In order to control for possible effects of habitat differences between the N5 and CS7 grid system and individual effects, individual was nested in grid system and both were included as random factors in the model. We used the weight argument of an exponential function to meet the assumptions of homoscedasticity and approximate normality of the residuals. Home range overlap among females and among males was compared between the sexes with a Mann-Whitney *U*-test. We investigated the effects of season and unit size and their possible interaction on home range size with a LMM. We incorporated total unit size (including young animals) and number of adults per unit as separate fixed factors after checking for independence. In the course of model simplification, non-significant terms were dropped from the initial model (backward elimination). In order to investigate male association patterns, we compared frequencies of daily scans of associated and solitary males during and outside the mating season with a McNemar test. Furthermore, we compared the minimum and maximum annual mortality between males and females, and between adults and juveniles using a paired *t*-test after arcsine-square-root transformation of the mortality ratios. We used the software R 3.1.2. (R Core Team 2014) and set an α-level of 0.05 for all statistical analyses.

Results

Social organisation: size and composition of social units

In total, we captured 63 narrow-striped mongooses on a total of 168 trapping days with a mean of 40 traps/day. The average population density at both sites was 20 individuals per km^2 and 15 adult individuals, respectively, with a slightly higher density at N5 (25 individuals/km^2) than at CS7 (17 individuals/km^2). Females formed permanent social units consisting of adults, juveniles and infants. On average, these units comprised 3.7 ± 0.4 individuals (mean ± SD), including 2 adult females (Table 1). The maximum recorded unit size was 6 individuals. The turn-over in unit composition was on average 49.2% from 2012 to 2014, with 20 to 75% of the original individuals still present at the end of the study period (Table 1; Fig 1).

We documented seven cases of dispersal involving 5 juvenile males and 2 juvenile females. Males dispersed from their mother's unit at the age of approximately 2 years. Females dispersed later than males, at the age of more than 3 years, or stayed in their natal unit for breeding. We observed female immigration into other female units (*N*=1) after the dominant female of that unit had died, and after fission of a unit, followed by the formation of a new unit (*N*=1; Fig. 1).

Table 1 Mean composition of female units of narrow-striped mongooses in Kirindy Forest/CNFEREF from 2012 to 2014 [a)].

Unit	Adult females	Juveniles (male or female)	Infants (male or female)	Total unit size	Percentage of individuals present since 2012
A	1.5	0.5	1.0	3.0	- [b)]
B	2.3	0.7	1.0	4.0	75
C	1.7	1.3	1.0	4.0	75
D	2.5	0.5	0.5	3.5	40
E [a)]	2.5	1.0	0.5	4.0	20
F	2.0	0.5	1.5	4.0	20 [c), e)]
G	2.0	1.0	1.0	4.0	75 [c)]
H	2	-	1	3	- [d)]
J	2	1	1	4	- [d)]
Mean	**2.0 ± 0.3**	**0.7 ± 0.4**	**1.0 ± 0.3**	**3.7 ± 0.4**	**50.8**

Means ± SD based on censuses on April 1 of subsequent years. [a)] For unit E, census from April 2011 included; [b)] unit A became extinct in April 2013; [c)] studied since November 2012; [d)] studied since June 2013; thus only data from 2014 included; [e)] after split of the unit, dispersal.

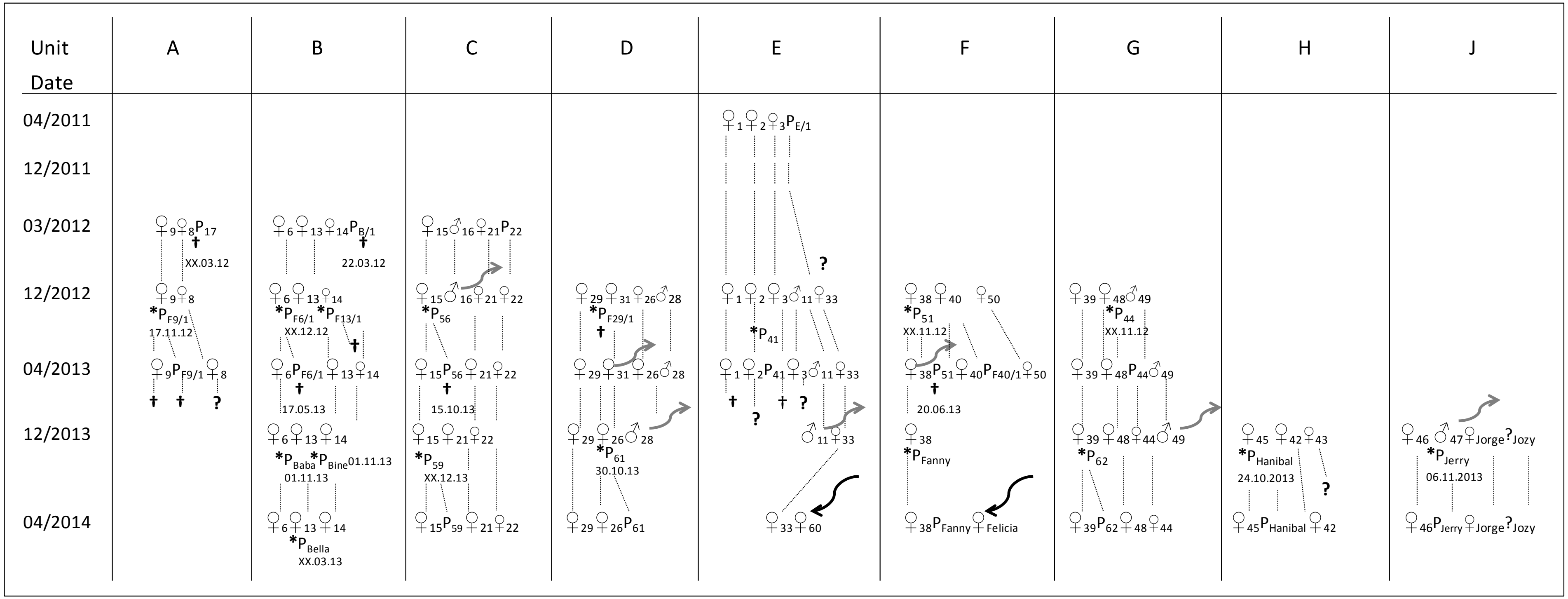

Fig. 1 Social histories of female units of *M. decemlineata* between 2011 and 2014.
♀: adult female; small ♀: juvenile female; ♂: adult male; small ♂: juvenile male; small ?: juvenile of unknown sex; P: infant (=pup); *****: birth, with date; †: death, with date; **?** (end of line): lost, reason of disappearance unknown; grey arrows to the right: dispersal; black arrows to the left: immigration; numbers and names in subscripts indicate animal identities. Names refer to animals which could not be marked with transponders.

Adult males formed less stable associations than females. They associated with 1 to 3 other males (Fig. 2). The composition of male associations was variable among years, and their stability differed among seasons (Fig. 3). Between November and June (i.e. during the non-mating season), radio-collared males (N=18) were in associations with other males on average in 58% (± 24) of N=671 daily scans, roamed alone in 36% (± 23), and were seen with female units in 6% (± 7) of scans. During the mating season (July-October), males were most often sighted alone (61% ± 20 of N=573 daily scans) and were associated with 1-3 other males in 17% (± 18) and with female units in 22% (± 13) of scans. Excluding the number of visits to female units by males in both seasons, males were significantly more frequently sighted alone during the mating season (79% ± 21 of N=427 daily scans) than outside the mating season (39% ± 24 of N=621 scans; McNemar test, χ^2=8.68, P=0.003).

Spatial distribution and home range patterns of social units

Mean annual home range size of females and males based on different estimation methods are presented in Table 2. Both 90% and 50% kernel home ranges (KHR) of males were significantly larger than those of females (LMM for 90% KHR: F=29.69, df=22, P<0.0001; LMM for 50% KHR: F=12.33, df=22, P=0.002). The spatial arrangements of home ranges indicated exclusive territories in females and sexual segregation in ranging patterns (Fig. 4a, b). Males covered up to 4 female ranges. The overlap of both 90% and 50% KHRs was significantly larger among dyads of overlapping males (N=52) than among female dyads (N=10; 90% KHR overlap: Mann-Whitney U-test: Z=-2.48, P=0.014; 50% KHR overlap: Mann-Whitney U-test: Z=-2.29, P=0.022; Table S1, supplement Chapter 2).

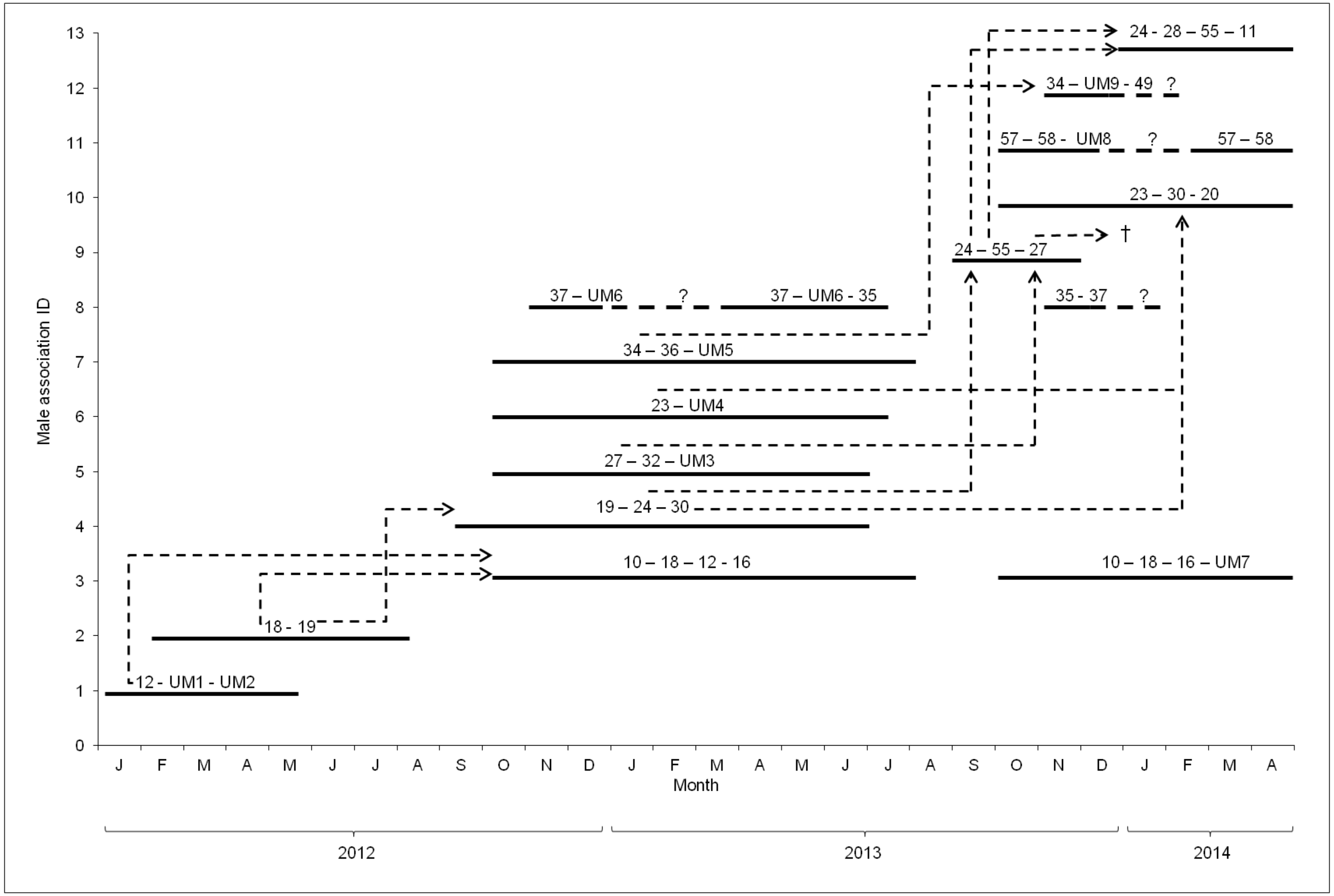

Fig. 2 Temporal stability and individual relocation among 13 male associations between January 2012 and April 2014. Associations were considered as new if they differed in composition from a previous one by at least 50%. Black bars depict male associations along the time axis, numbers indicate animal identities, with UM=unmarked male. In gaps between bars, males were solitary. Order of individual numbers within associations indicates the temporal sequence in which members associated. ?: periods of unknown stability and composition; †: death.

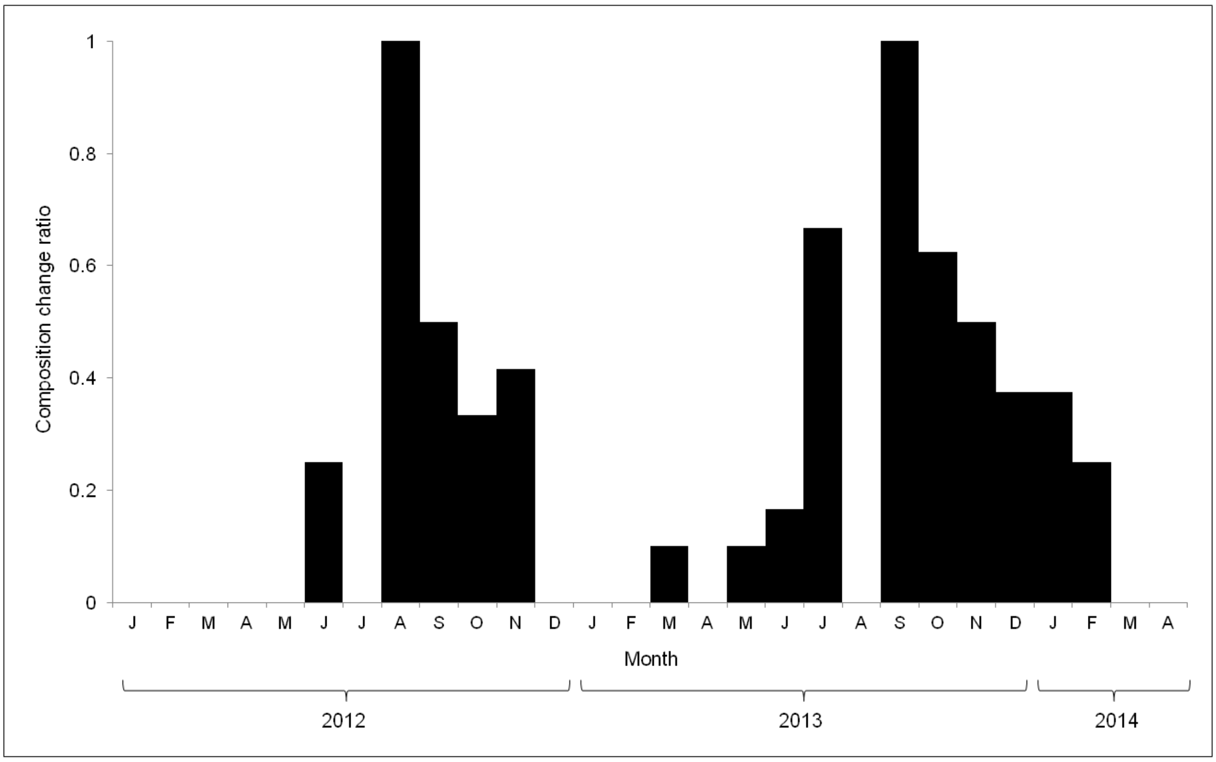

Fig. 3 Monthly fluctuation in composition of male associations between January 2012 and April 2014. Depicted is the proportion of a total of 13 male associations that changed in composition between successive months (0: no change, 1: change in composition). Thus, a ratio of 1 represents a change in composition of all associations. Note that not all associations were present every month.

Table 2 Annual home range estimates of narrow-striped mongooses in Kirindy Forest/CNFEREF between May 2013 and April 2014.

	100% MCP	**95% MCP**	**95% kernel**	**90% kernel**	**50% kernel**
Females	35.5 ± 12.3 (25.0-58.8)	28.7 ± 9.7 (16.4-47.1)	37.2 ± 11.9 (23.7-58.9)	30.4 ± 9.6 (20.0-48.0)	5.4 ± 4.3 (1.9-14.8)
Males	81.2 ± 23.9 (49.2-119.3)	63.2 ± 21.6 (36.3-102.8)	83.4 ± 23.7 (46.4-134.2)	63.9 ± 21.7 (34.1-114.4)	14.3 ± 8.7 (2.4-37.1)

Mean ± SD (min-max) in ha. Females: *N*=9; males: *N*=17.

We compared home range overlap of male dyads that were in association between May 2013 and April 2014 with those dyads with overlapping ranges, but that were never seen in association. The overlap of both 90% and 50% KHRs was significantly larger among associated (*N*=9 dyads) than non-associated males (*N*=43 dyads; 90% KHR overlap: Mann-Whitney *U*-test: *Z*=4.50, *P*<0.001; 50% KHR overlap: Mann-Whitney *U*-test: *Z*=4.72, *P*<0.001, both after Bonferroni-correction; Table S1, supplement Chapter 2). Home range overlap of dyads of female units did not differ among seasons either in 90% (paired *t*-test: *t*=1.80, *df*=13, *P*=0.096) or in 50% KHRs (Wilcoxon signed rank test: *V*=0, *P*=0.371; Table S2, supplement Chapter 2).

Both 90% and 50% KHRs of females were significantly larger during the dry season (May-October) than during the rainy season (November-April; 90% KHR: LMM: $F=6.97$, $P=0.034$, $df=7$; 50% KHR: LMM: $F=5.69$, $P=0.049$, $df=7$; Table S2, supplement Chapter 2). Total social unit size and number of adults per unit did not correlate ($t=0.32$, $df=14$, $P=0.754$), and were thus separately included into the model. Our model did not reveal a significant effect of either total unit size or number of adults per unit on home range size. There were no interaction effects between season and size of unit or number of adults, respectively, and interactions were thus removed in the process of model simplification.

The extinction event of female unit A in 2013 was followed by the partitioning of its home range by the neighbouring units. The shift of centroids of both 90 and 50% kernel home ranges revealed that particularly female unit B extended its former range (Fig. S1a, b, supplement Chapter 2). Female territorial behaviour was expressed by regular scent-marking and aggression during occasional direct encounters. We observed only four direct encounters between neighbouring female units, resulting in the displacement by one of the units ($N=3$), or withdrawal by one unit before direct interactions took place.

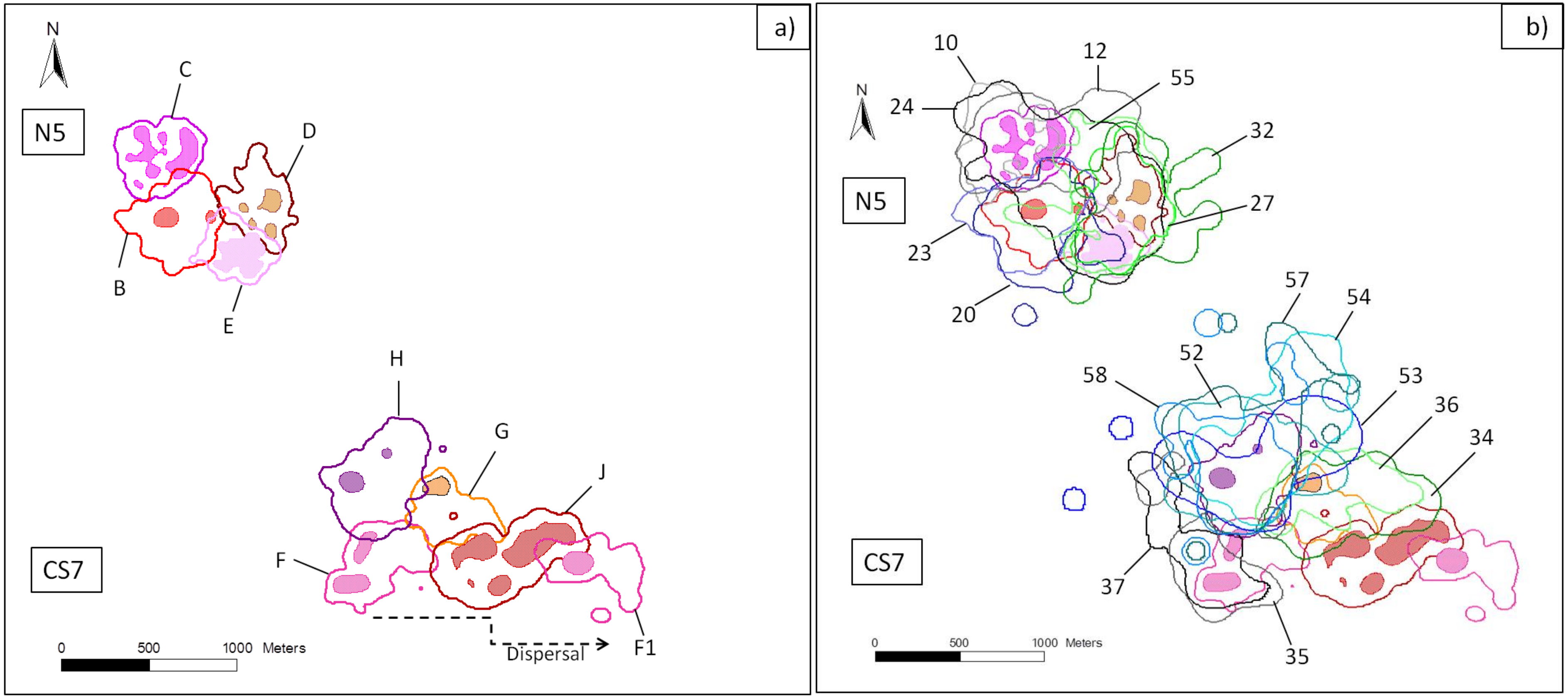

Fig. 4a, b Annual home range distributions of 9 female units (a, b) and 17 males (b) of narrow-striped mongooses in Kirindy Forest/CNFEREF from May 2013 to April 2014. Lines represent 90% kernel home ranges, filled areas represent 50% kernel home ranges (=core areas) of females. Letters label female units, numbers label male individuals. N5 and CS7 denote grid systems of pathes in the forest.

Demography and life-history characteristics

Between 2012 and 2014, the overall sex ratio of all identified individuals was close to even (M/F=1.13; 34 males, 30 females; mean ± SD among years in adults: M/F=1.27 ± 0.22; in juveniles: M/F=0.56 ± 0.25). The adult sex ratio was consistently male-biased, however, despite a consistently female-biased juvenile sex ratio (Fig. 5).

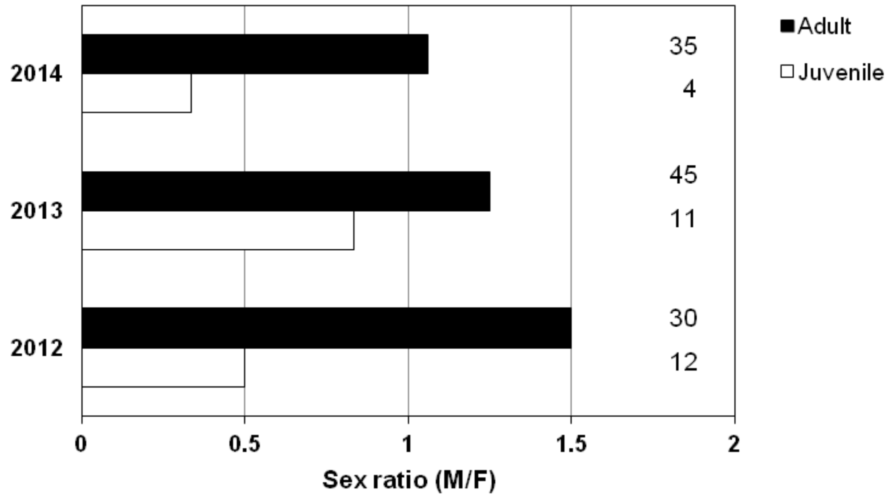

Fig. 5 Sex ratio of adult and juvenile narrow-striped mongooses over 3 years. The adult sex ratio (black bars) is biased towards males. The numbers (right) indicate sample size of identified individuals for each age category and year.

Reproduction was seasonal (Fig. S2, supplement Chapter 2). Sexual interactions, including 4 copulations, were observed between July and October, with a peak in August. However, two females that lost their pup within a month after birth became receptive again and mated again (in December and February, respectively). The estimated age of the youngest pregnant female was 2.8 years.

In all observed litters, females gave birth to only one pup. Of 21 infants that emerged between 2011 and 2013, per year, on average 85% survived to the age of 3 months, 50% to 6 months and 28% to 1 year. The pups surviving at least the first year were all born to the oldest, dominant female of a unit (*N*=3; born in 2011 and 2012).

In adults, the minimum mean annual mortality rate between 2011 and 2014 was 0.07 ± 0.09 (based on verified deaths), the maximum one was 0.23 ± 0.15 (based on presumed death, but carcass not found). We detected no significant difference in annual mortality between the sexes (min.: *t*=-2.30, *df*=3, *P*=0.10; max.: *t*=-2.44, *df*=3, *P*=0.09). In juveniles, the minimum mean annual mortality was 0.06 ± 0.07, the maximum one 0.22 ± 0.20 during the same period. Again, we detected no significant sex differences (min.: *t*=1.0, *df*=2, *P*=0.42; max.: *t*=1.0, *df*=3, *P*=0.42). We also did not detect any significant difference in minimum (*t*=0.14, *df*=3, *P*=0.90) or maximum (*t*=0.62, *df*=3, *P*=0.58) annual mortality between adults and juveniles (Table 3).

Table 3 Annual mortality (per year and mean±SD) by age and sex of the narrow-striped mongoose population in Kirindy Forest/CNFEREF from 2011 to 2014.

Year	**Juvenile male**		**Juvenile female**		**Adult male**		**Adult female**	
	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.
2011	-	-	0	0.47	0	0.90	0	0
2012	0	0	0	0	0.14	0.14	0	0
2013	0	0	0.17	0.43	0.22	0.40	0.12	0.23
2014	0	0	0	0	0.20	0.20	0	0
Annual mean	0.0±0.0	0.0±0.0	0.04±0.09	0.23±0.26	0.14±0.10	0.41±0.35	0.03±0.06	0.06±0.11
Mean by age min.	0.06 ± 0.07				0.07 ± 0.09			
Mean by age max.	0.22 ± 0.20				0.23 ± 0.15			

min.: minimum observed mortality, based on the number of verified deaths; max.: maximum observed mortality, including cases of disappearance due to unknown reasons. Mean by age including juveniles of undetermined sex.

The comparisons of (a) litter size and (b) number of litters per year (both corrected for body mass) among herpestids (group-living: N_a=5, N_b=5; solitary: N_a=13, N_b=7) and euplerids (N_a=9, N_b=3) showed a tendency for highest mean values for group-living herpestid species, followed by solitary herpestids and euplerids (Fig. 6), indicating relatively slow life histories in *M. decemlineata* and other Malagasy carnivores.

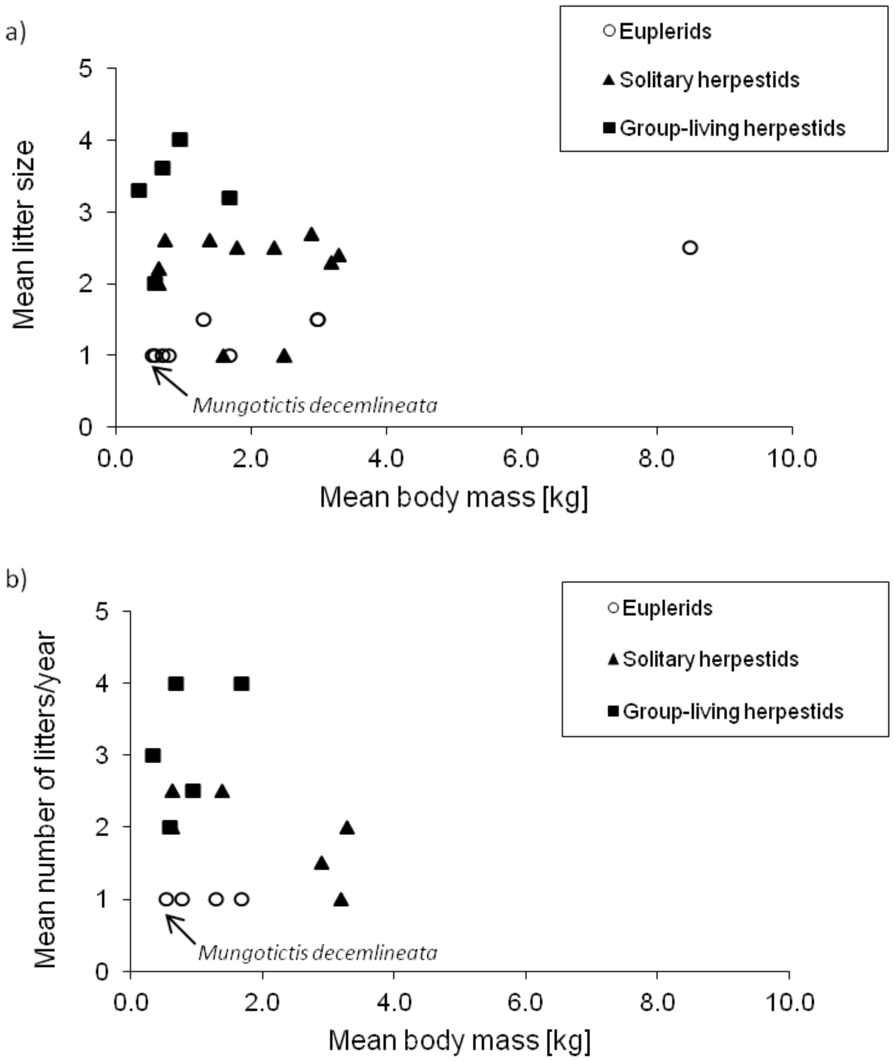

Fig. 6a, b Life-history traits of euplerid and herpestid mongooses in relation to body mass. a) Mean litter size, b) Number of litters per year. Euplerids: N_a=9, N_b=3; solitary herpestids: N_a=13, N_b=7; group-living herpestids: N_a=5, N_b=5.

Discussion

Sexually segregated sociality was the most striking aspect of the social organisation of *M. decemlineata*. Social units of males and females also differed in stability and ranging dynamics, suggesting that the sexes respond to partly different selective forces. Comparisons with herpestids indicate some similarities with other species in aspects of their social organisation as well as relatively slow life histories. We discuss these aspects in more detail below, focusing on sex-specific patterns and adaptations.

Sociality and sexual segregation

Two selective pressures, the advantages of cooperative hunting and the need for defence against other predators, have traditionally been considered to favour group living in carnivores. There is disagreement about whether cooperative hunting should be considered as a cause of sociality (Creel & Creel 1995) or a consequence thereof (Packer & Ruttan 1988), but, in any case, it does not appear to play a significant role in *M. decemlineata*, who forage independently for small prey items in the leaf litter and top soil (Rasolofoniaina 2014). Thus, potential benefits of cooperative hunting cannot be invoked to explain male and female units in narrow-striped mongooses.

Group-living in African herpestids is particularly pronounced in relatively small-bodied species inhabiting open habitats for which predation risk is high (Waser 1981; Rood 1986; Clutton-Brock *et al.* 1999a; Schneider & Kappeler 2014). Shared vigilance (Manser 1999), cooperative predator mobbing (Rasa 1977; Rood 1983b; Graw & Manser 2007) and elaborate sentinel systems (Clutton-Brock *et al.* 1999c) all attest to the ecological importance of predation risk for these species. Although *M. decemlineata* is a terrestrial inhabitant of dense forests, who suffer lower mortality rates compared to some African mongooses inhabiting open habitats (Rasa 1987b; Rasa 1989; Clutton-Brock *et al.* 1999a), they nonetheless appear subject to intense predation risk, they emit alarm calls against raptors (Madagascar harrier-hawk, *Polyboroides radiatus*) and they collectively mob snakes (Razafimanantsoa 2003; Schneider, pers. observation). We recorded six predation events (on 4 males and 2 females); two by ground boa (*Acrantophis madagascariensis*) and four by fosa (*C. ferox*; or possibly by stray dogs, *Canis lupus familiaris;* see also Hawkins and Racey 2008). Thus, the anti-predator benefits of gregariousness, which are especially high in small associations, may have contributed to the formation of small groups in narrow-striped mongooses of both sexes.

The spatio-temporal organisation of social units of *M. decemlineata* can be best described by sexual segregation. Sexual segregation has been mainly investigated in ungulates (Ruckstuhl & Kokko 2002; Ruckstuhl & Neuhaus 2002), but it has been noted in other taxa as well. Among various explanations for sexual segregation, the activity-budget hypothesis, which proposes that males and females segregate into different groups due to incompatibilities of activity budget and movement rate, has gained the strongest support, in particular in species displaying sexual dimorphism. Among carnivores, sexual segregation in daily activity rhythms has been found in the sexually dimorphic European polecat, *Mustela putorius* (Marcelli *et al.* 2003). *M. decemlineata* lacks sexual dimorphism in body mass, however (M/F: 1.03; Schneider and Kappeler, unpublished data; Rood & Waser 1978; Gittleman 1985; Clutton-Brock *et al.* 1999a) and the sexes do not differ in their diet (Rasolofoniaina 2014), so that sexual dimorphism in body mass and/or diet cannot explain sexual segregation in this species. Sexual segregation in non-dimorphic vertebrates requires further research (Ruckstuhl 2007). Moreover, the alternative predation-risk and forage-selection hypotheses (Ruckstuhl & Neuhaus 2002), which predict segregation of reproducing females and mixed-sex groups of non-reproducing females and males, are also not consistent with our findings. We therefore discuss female and male social units separately below.

Female spacing and social organisation

Apart from predation risk, the relative importance of other ultimate factors promoting mongoose sociality remains elusive. In solitary and facultatively social mongooses (*C. penicillata*: Cavallini & Nel 1995; Blaum *et al*. 2007; *H. ichneumon*: Ben-Yaacov & Yom-Tov 1983; Palomares & Delibes 1993), resource-based explanations of variation in sociality were founded on proxies such as habitat type and vegetation structure, failing to provide compelling evidence for comparison (Clutton-Brock & Janson 2012). In *M. decemlineata*, female social units maintained exclusive core areas, exchanged aggression with neighbouring units during encounters, and responded to the extinction of a neighbouring unit with territorial expansion. Female home range size did not correlate with female unit size, however, following the prediction of the resource dispersion hypothesis (Macdonald 1983). The observed seasonal variation in female home range size indicates that due to the higher abundance of arthropods, snails, small reptiles and eggs, which make up the bulk of *M. decemlineata*'s diet (Albignac 1976; Razafimanantsoa 2003; Schneider and Kappeler, unpublished data), foraging costs decreased during the wet season in spite of a potentially similar per-capita intake rate (Johnson *et al.* 2002). However, female mobility also decreased following parturition in late October, when members of units restricted their foraging to the area around the shelter (e.g. tree or ground hole) of newborns pups. Thus, joint resource defence appears to be an important driver of female sociality, but additional studies are required to determine foraging costs and feeding competition.

Proximate factors affecting social unit composition and dynamics include various life-history traits and patterns of dispersal. In general, reproductive rates of euplerids are relatively low in comparison to herpestids (Fig. 6). In *M. decemlineata*, only one female per social unit reproduced successfully during each breeding season (i.e. the pup survived more than a year), even though one or two additional females could give birth. Pup survival was comparable to mongooses with cooperative infant care, although higher during the first three months (*Helogale* *parvula*: 50% after 2 months; Rood 1990; *Mungos mungo*: 51% of emergent pups to 3 months of age; 18% to independence; Gilchrist 2001, 2006; *Suricata suricatta*: 38-62%; Clutton-Brock *et al*. 1999a). A low potential for reproduction within groups may represent a determinant of female competition and possible eviction or dispersal of females (see below), limiting female social unit size in *M. decemlineata*.

Philopatry of young females appears to be the main mechanism generating female gregariousness (see also Waser & Waser 1985; Palomares & Delibes 1993; Waser *et al.* 1994). In eusocial mongooses, females mainly disperse after eviction, and in meerkats even not voluntarily (Clutton-Brock *et al.* 1998, 2002; Cant *et al.* 2001; Stephens *et al.* 2005). In *M. decemlineata*, all females remained in their natal unit after two years, and dispersing females were older than 3 years. We only observed female immigration into vacant breeding territories where the dominant female had died or disappeared before. However, the observed separation of secondary females from units when giving birth (Schneider & Kappeler, unpublished data; cf. also Razafimanantsoa 2003) suggests female reproductive competition, so that eviction by dominants remains a possible proximate mechanism contributing to some cases of female dispersal. Thus, the presence and size of female units in *M. decemlineata* may be best explained as resulting from a frail trade-off between the anti-predator benefits of grouping and the costs of reproductive competition.

Male social organisation

The formation of male associations in other carnivores and mammals has been explained by four hypotheses: cooperative hunting or foraging, reproductive coalitions among kin, bachelor groups, and benefits of group augmentation. First, fitness benefits of cooperative hunting are unlikely to be an ultimate cause for male associations in *M. decemlineata*. In contrast to larger carnivores (lions: van Orsdol 1984; African wild dogs: Creel & Creel 1995; fosas: Lührs & Dammhahn 2010; Lührs *et al.* 2013), associated *M. decemlineata* mainly forage individually on hidden invertebrates. Larger prey, such as reptiles and mouse lemurs, were captured alone, aggressively defended against conspecifics and not shared (Schneider & Kappeler, unpublished data). In those mongoose species where cooperatively foraging or hunting have been reported anecdotally (*Galerella nigrata*: Rathbun & Cowley 2008; *H. ichneumon*: Palomares & Delibes 1993), social tolerance in areas of high food abundance and gregariousness in high-density populations seem to be more likely explanations for male sociality (Ben-Yaacov & Yom-Tov 1983; Rood 1989). Among Herpestids and Euplerids, only in the fosa is there strong evidence for benefits from cooperative hunting that male cooperative hunting provides tangible somatic benefits to associated males (Lührs *et al.* 2013).

Second, male sociality in *M. decemlineata* can also not be explained by reproductive coalitions. Cooperation among male kin in order to exclude rivals has been reported in some carnivores (e.g. *Acinonyx jubatus*: Caro & Collins 1987; *C. ferox*: Lührs *et al*. 2013; *Panthera leo*: Bygott *et al*. 1979; Packer *et al*. 1991), and it has been suggested for slender mongooses and the small Asian mongoose (Waser *et al.* 1994; Hays & Conant 2003). In slender mongooses, associations of up to four males immigrated from outside territories. Their MCP ranges overlapped by 80-98% and covered the ranges of up to 6 females, while being exclusive from other adjacent males (0-5% overlap). These associations were stable in composition for several years. Their inclusive fitness benefits were indicated by close kinship (half-siblings) and mixed paternity, resulting in low reproductive skew among coalition members (Waser *et al.* 1994), but detailed records of male behaviour during periods of female estrus are lacking. We recorded considerable range overlap also among non-associated males, even using the more conservative 90% kernel home range estimates. Furthermore, cohesion and composition of male associations were variable among seasons and years. In particular, their disintegration during the mating season contradicts the expected benefit implied by this hypothesis. Moreover, previously associated males showed aggression towards each other when entering female units for mating.

Third, because narrow-striped mongooses have litters of only one young (confirmed by captivity reports; A. Ochs, Berlin Zoo, pers. communication) and only one female reproduces successfully, male association partners of the same age cannot be littermates. Young males who left their natal units initially joined male associations within their natal range, thus creating opportunities for dispersing males to join up with relatives. In this respect, male associations resembled bachelor groups in some ungulates (Prins 1989; Ruckstuhl 1998). However, there were in fact marked age differences among unit members, and we found no indication of solitary, more competitive territorial males driving younger males into bachelor groups (Jarman 1974; Ruckstuhl & Neuhaus 2002). Moreover, male associations dissolved during the mating season, and all males sought reproductive opportunities, leaving no bachelors behind. Thus, male associations in *M. decemlineata* cannot be explained by male competition either.

Finally, the fundamental anti-predation benefits of group formation and augmentation discussed above presumably accrue for male associations of *M. decemlineata* as well (cf. Rasa 1987a; Clutton-Brock 2009c). This benefit is underlined by the preliminary observation based on small sample sizes that males, who spend less time in association, also appear to suffer higher mortality risk. Most male fatalities were also recorded during the mating season when males roam by themselves. Cooperative defence against predators provides another predation-related benefit of group formation (Rood 1983b). Thus, male *M. decemlineata* seek the vicinity of other males to enhance each other's survival, but this fragile association disintegrates temporarily as the reproductive component of individual fitness is at stake.

Conclusions

The unusual social organisation of *M. decemlineata* is characterised by sexually segregated gregariousness as both males and females live in small same-sex units. The factors favouring group living can therefore be studied separately in each sex. Shared vigilance, alarm-calling, dilution effects at small group sizes and collective predator mobbing seem to provide the crucial benefits that stabilize male and female associations. Joint territorial defence appears to provide another potential benefit to female associations, whereas males temporarily trade off safety against reproductive opportunities. Thus, the social organisation of this endemic Malagasy mongoose reflects the fundamental effects of anti-predator benefits for gregariousness as well as those of sex-specific fitness-limiting factors. Future investigations of female competition for resources and reproduction and the genetic basis of social units may reveal further insights into the mechanisms regulating unit sizes and composition.

Supplementary Material of Chapter 2: Tables

Table S1 Home range overlap of neighboring ranges within and between the sexes of narrow-striped mongooses in Kirindy Forest/CNFEREF from May 2013 to April 2014.

	90% kernel	**50% kernel**
Female-Female (*N*=10)	8.4 ± 6.4 (0.8-20.8)	0.0 ± 0.0 (0)
Female-Male (*N*=56)	41.0 ± 39.0 (0.3-100)	19.3 ± 29.6 (0-100)
Male-Female (*N*=56)	18.8 ± 18.9 (0.4-67.7)	5.7 ± 10.3 (0-41.4)
Male-Male (*N*=52)	30.2 ± 28.3 (1.4-97.0)	13.8 ± 22.8 (0-91.7)
Associated males (*N*=9)	71.6 ± 18.6 (36.5-97.0)	46.1 ± 27.3 (8.2-91.7)
Non-associated males (*N*=43)	21.6 ± 21.5 (1.4-78.7)	7.0 ± 14.6 (0-64.5)

Mean ± SD (min-max) in percentages. *N*=number of dyads.

Table S2 Seasonal home range sizes and overlap of female units of narrow-striped mongooses in Kirindy Forest/CNFEREF in the years 2013-2014.

	Dry season (May-Oct)		**Rainy season (Nov-April)**	
	Home range size (ha)	Overlap (%)	Home range size (ha)	Overlap (%)
90% kernel	32.7 ± 11.8 (19.2-50.5)	9.1 ± 7.0 (1.0-22.5)	25.7 ± 7.7 (18.8-41.4)	6.5 ± 7.4 (0.0-23.3)
50% kernel	9.1 ± 5.8 (1.9-17.9)	0.2 ± 0.6 (0.0-2.5)	3.8 ± 2.3 (1.9-7.6)	0.1 ± 0.3 (0-1.2)

Mean ± SD (min-max). *N*=8 female units.

Supplementary Material of Chapter 2: Figures

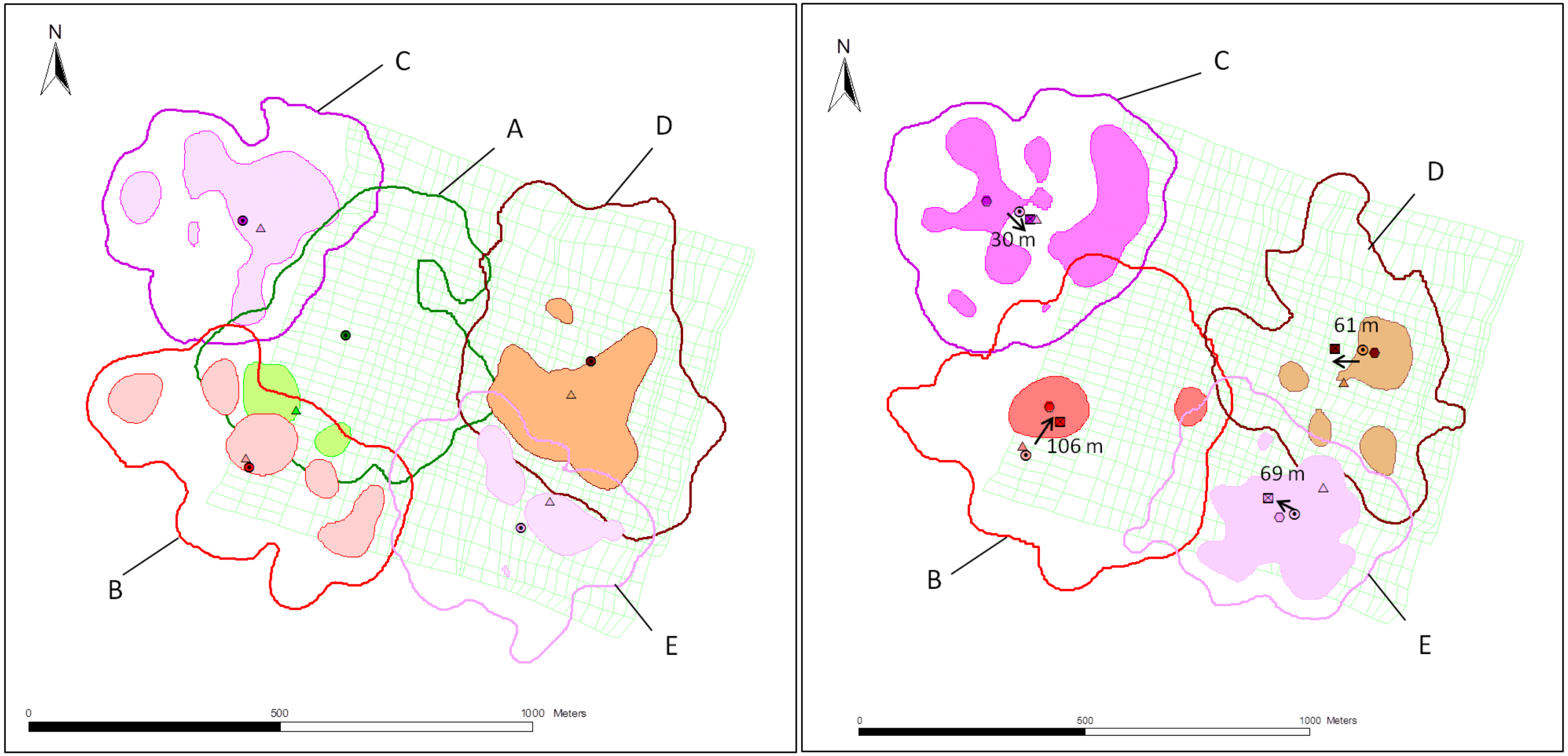

Fig. S1 Home range dynamics following extinction of a female social unit (A). **a** Annual 90% and 50% kernel home range distributions of female units of narrow-striped mongooses in the N5-site from May 2012 to April 2013. Dots indicate centroids of 90% kernel ranges, triangles those of 50% kernel ranges. **b**: Annual 90% and 50% kernel home range distributions of female units at the same sub-site from May 2013 to April 2014. Squares indicate centroids of 90%, hexagons those of 50% kernel ranges. Arrows and distances in meters indicate the shift of centroids of 90% kernel ranges among years. Underlying lines depict the path grid system.

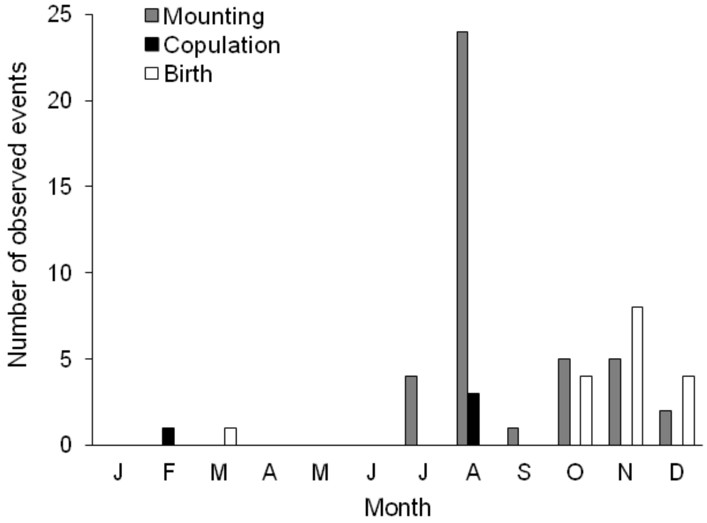

Fig. S2 Annual distribution of observed mating and birth events in narrow-striped mongooses from 2012 to 2014.

CHAPTER 3

Genetic population structure and relatedness in the narrow-striped mongoose (*Mungotictis decemlineata*), a social Malagasy carnivoran with sexual segregation

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Abstract

Information on the genetic structure of animal populations can allow inferences about mechanisms shaping their social organisation, dispersal and mating system. The mongooses (Herpestidae) include some of the best studied mammalian systems in this respect, but much less is known about their closest relatives, the Malagasy carnivores (Eupleridae), even though some of them exhibit unusual association patterns. We investigated the genetic structure of the Malagasy narrow-striped mongoose (*Mungotictis decemlineata*), a small forest-dwelling carnivore exhibiting gregarious sexual segregation. Based on mtDNA and microsatellite analyses, we determined population-wide haplotype structure and sex-specific and within-group relatedness. Furthermore, we analysed parentage and sibship relationships and the level of reproductive skew. We found a matrilinear population structure, with several neighboring female units sharing identical haplotypes. Within-group female relatedness was significantly higher than expected by chance in the majority of units. Haplotype diversity of males was significantly higher than in females, indicating male-biased dispersal. Relatedness within the majority of male associations did not differ from random, questioning the significance of kinship in reproductive coalition formation. We also found indications for a polygynous mating system and low levels of reproductive skew in both sexes. Low relatedness within breeding pairs confirms immigration by males and suggests similarities with patterns in social mongooses, providing a starting point for further investigations of mate choice and female control of reproduction and the connected behavioural mechanisms.

Introduction

The social organisation of vertebrates is defined by the composition of species-specific social units with regard to the number of individuals, their sex, age, cohesion and the resulting genetic structure (Kappeler & van Schaik 2002). Behavioural and demographic data can be used to describe how individuals are distributed in space and time, and solitary, pair- and group-living species are recognised as fundamental units of categorization of interspecific variation in social organisation (Crook 1970). The resulting genetic structure of a given population and, in particular, the relatedness within and among social groups is not straightforward to predict from a particular type of social organisation, however, because species vary in sex-specific reproductive skew and dispersal patterns, in adult sex ratios and other demographic characteristics (Greenwood 1980; Nonacs & Hager 2011; Di Fiore 2012; Liker *et al.* 2013; Nidiffer & Cortés-Ortiz 2015). Information on genetic structure can therefore reveal insights about social units, population structure and social behaviour that are not obvious from behavioural and demographic data alone (Gompper *et al.* 1997; Kappeler *et al.* 2002; Caniglia *et al.* 2014). Because sex differences in reproductive success affect the balance between local resource competition and local mate competition (Perrin & Mazalov 2000), information on local genetic population structure also allows characterisation of these components of the mating system (Ross 2001).

Among mammals, the Carnivora exhibit fascinating inter-specific diversity in social organisation and breeding systems (Macdonald 1983; Bekoff *et al.* 1984). Molecular studies have contributed to the illumination of social organisation and reproductive patterns of some enigmatic carnivores such as lions, cheetah and spotted hyenas (Packer *et al.* 1991; Gottelli *et al.* 2007; Holekamp *et al.* 2012). In several species, reproductive skew within social units has been estimated explicitly, tackling diverse questions about the extent of breeding competition, mate choice, kin selection among competitors and alternative reproductive strategies (e.g. African wild dogs: Girman *et al.* 1997; badgers: Dugdale *et al.* 2008; Ethiopian wolves: Randall *et al.* 2007; lions: Packer *et al.* 1991, 2001; spotted hyenas: Engh *et al.* 2002; East *et al.* 2003; white-nosed coatis: Gompper *et al.* 1997). Much less is known about genetic consequences of social organisation and mating system in solitary and forest-dwelling carnivores, however, because they are typically elusive, wide-ranging and have high dispersal capabilities (e.g. Dutta *et al.* 2013; Rodgers *et al.* 2015).

The sister-taxa Herpestidae (mongooses) and Eupleridae (Malagasy carnivores, including the Galidiinae, Malagasy mongooses) are socially and ecologically diverse groups of carnivores

(Schneider & Kappeler 2014). Genetic studies of eusocial herpestids have focused on breeding success and patterns of inbreeding (Keane *et al.* 1996; Griffin *et al.* 2003; Nielsen *et al.* 2012; Leclaire *et al.* 2013a). Insights into their social and genetic mating systems have contributed significantly to the development and testing of reproductive skew models (Cant *et al.* 2001, 2010; Clutton-Brock *et al.* 2001b; Clutton-Brock *et al.* 2008). Recent studies have focused on within-group relatedness in order to identify the links between extra-group paternity, mate choice and female control of paternity on the one hand, and inbreeding on the other hand (Nichols *et al.* 2015; Sanderson *et al.* 2015). In contrast, the local genetic structure among neighboring groups remains largely unresolved. Still much less is known about genetic structure and reproductive systems of the so-called ‘solitary’ mongooses, which often display gregarious tendencies (e.g. *G. sanguinea*: Waser *et al.* 1994). For the Malagasy carnivores, information on genetic structure is entirely missing (Schneider & Kappeler 2014). Existing molecular studies in euplerids have focused on a higher organisational level, i.e. phylogeographic and taxonomic questions (Veron *et al.* 2004; Bennett *et al.* 2009; Durbin *et al.* 2010; van Vuuren *et al.* 2012). Because they have evolved in isolation on Madagascar for more than 20 myr (Yoder *et al.* 2003), potential convergences with African herpestids are particular interesting for behavioural ecologists, however.

Genetic structure can differ between the maternally inherited mitochondrial and the diploid inherited nuclear DNA, even on small geographic scales, and differences can be maintained between social groups in spite of nuclear gene flow (Avise *et al.* 1987; Hoelzer *et al.* 1994). Therefore, the combined use of mtDNA and nuclear microsatellites has been worthwhile to detect sex-specific genetic structure and different processes on evolutionary and ecological time scales (Rassmann *et al.* 1997; Gerloff *et al.* 1999; Haavie *et al.* 2000; Martien *et al.* 2014).

In the present study, we characterise the local population genetic structure, relatedness and reproductive system of the Malagasy narrow-striped mongoose, *Mungotictis decemlineata*. The social organisation of this small diurnal, forest-dwelling carnivore has only recently been described (Chapter 2) and revealed unique social patterns. Spatial and behavioural data of 40 radio-collared individuals collected over 4 years revealed that 1-3 adult females and their offspring form stable social units that defend exclusive home ranges. Adult males form separate social units, which also contain 2-4 individuals, but which cover the home ranges of on average 3 female social units and which disintegrate during the annual mating season. The adult sex ratio and natal dispersal are male-biased, while females often staying and breeding in their natal units. The general goal of this study was to glean additional information on this unusual type of social organisation from a genetic study. Specifically, we aimed to clarify whether (i) there are population-wide sex differences in haplotype distribution and relatedness, (ii) the higher observed rate of male dispersal was reflected by greater haplotype diversity, (iii) members of male and female social units were more closely related to each other than expected by chance, and (iv) to characterise the genetic mating system and the level of reproductive skew in both sexes. By providing more details on the genetic structure and reproductive system of this representative of a largely unstudied group of carnivores, we also aim to contribute to the understanding of the evolutionary pathways from solitariness to gregariousness.

Materials and Methods

Study site and data collection

The study was conducted in Kirindy Forest/CNFEREF (44°39'E, 20°03'S), a dry deciduous forest of about 12,500 ha located 60 km northeast of Morondava in western Madagascar. Narrow-striped mongooses were regularly trapped in two local study areas about 3 km apart. Morphometric, behavioural, life-history and spatial data were collected from radio-collared individuals of 9 female units and 13 male associations between 2011 and 2014 (Chapter 2). For the present study, we also obtained small skin biopsies from anaesthetized individuals and transferred them in 90% ethanol to the genetics laboratory of the German Primate Center.

Genetic analyses

mtDNA

DNA for all analyses was extracted from tissue samples using the Qiagen QIAamp Tissue Kit (Qiagen, Hilden, Germany). For mtDNA analyses, we used samples from a total of 84 individuals, 33 of which were collected during a previous study between 2000 and 2010. We amplified a fragment of the mtDNA control region (d-loop) via PCR, using the mammalian primers ProL-He (5'-ATACTCCTACCATCAACACCCAAAG-3') and DLH-He (5'-GTCCTGAAGAAAGAACCAGATGTC-3'; Seddon *et al.* 2001). In a 30 µl reaction, 2 µl DNA extract (50 ng), 18.4 µl H_2O, 3 µl 10x buffer (containing $MgCl_2$ 15 mM), 0.1 µl of each primer (100 pmol/µl), 0.2 µl dNTP (25 mM), 4.0 µl BT (10 mg bovine serum albumin [BSA] + 0.5% Triton) and 0.2 µl BioTherm^{TM} Taq DNA polymerase (5 units/µl) were used. Cycling conditions in Thermocycler 2720 (Applied Biosystems®) were as follows: an initial step of 92°C for 10 min, followed by 40 cycles of 1 min at 92°C, 1 min at 60°C and 1 min at 72°C, followed by an elongation step of 5 min at 72°C. Amplification success was validated by visualization of PCR products under UV light (312 nm) after electrophoresis on a 1% agarose gel (Gelred^{TM}, Biotium Inc., Hayward, CA, U.S.A.).

To reduce the chance of sequencing mitochondrial pseudogenes in the nuclear genome (numts), we also amplified 31 (37%) of the sequences by long-template PCR. We targeted a region of about 2kbp using a newly designed primer, L14724C (CGACTAATGATATGAAAAACCATCGTTG; modified from Irwin *et al.* 1991) and one of the primers reported above, DLH-He. Results from LR-PCRs and short fragment amplifications were then compared to validate our approach. PCR products were purified using Microcon® UFC7 PCR centri filters (Merck Millipore, Billerica, MA, U.S.A.). For sequencing, in a 10 µl reaction, 6.5 µl purified PCR product (20 ng), 1.5 µl 5x BigDye® buffer, 1.0 µl primer (3.3. pmol/µl) and 1.0 µl Big Dye® were used. PCR products were precipitated by a natrium-acetate-ethanol mix and sequenced on an ABI 3130xL Genetic Analyzer (Applied Biosystems®).

Chromatograms were checked by eye and consensus for each individual was generated from sequences in forward and reverse directions using Geneious R6.1.4 (Biomatters Ltd, NZ). We aligned the final sequences using MUSCLE (Edgar 2004) and estimated mitochondrial genetic diversity including total number of haplotypes, haplotype diversity (Hd) and nucleotide diversity (π) using DNaSP 5.10.1 (Librado & Rozas 2009). In order to assess haplotype and nucleotide diversity between males and females, we tested for significance using the ‘difference test’ in Statistica ver. 9.1 (StatSoft Inc. 2010). Finally, we created a minimum spanning network (Bandelt *et al.* 1999) using PopArt ver. 1.7 (Leigh & Bryant 2015).

Amplicons varied in length due to the presence of multiple indels across samples. We performed long-range PCRs on multiple samples to minimize the risk of including numts in our analyses. Long and short template PCRs showed identical sequences, therefore we are confident that our dataset contains only true mitochondrial sequences. Given the difficulty of dealing with gaps in estimating mitochondrial haplotypes, we employed a conservative approach in which sites with gaps were excluded from the analyses. The final alignment included 325 bp. MtDNA sequences were uploaded to GenBank and can be accessed through the following accession numbers KU696553-KU696636.

Amplification and analyses of microsatellites

For this analysis, we isolated genomic DNA from 96 individuals. We tested 26 microsatellite markers isolated for the fosa (*Cryptoprocta ferox)* to characterise genetic variation (Vogler *et al.* 2009). Thirteen markers were polymorphic with an average number of 8 alleles (range: 3-12;

Table S1, supplement Chapter 3). One of each primer pair was end-labeled with a FAM-fluorescent tag. In a 30 µl reaction, 2 µl DNA extract (50 ng), 20.4 µl H_2O, 3 µl 10x buffer (containing $MgCl_2$ 15 mM), 0.1 µl of each primer (100 pmol/µl), 0.2 µl dNTP (25 mM), 4.0 µl BT (10 mg bovine serum albumin [BSA] + 0.5% Triton) and 0.2 µl BioTherm^{TM} Taq DNA polymerase (5 units/µl) were used. The amplification was carried out as following: 92°C for 10 min, 35 cycles of denaturation at 92°C for 30 s, annealing at primer-specific temperature (Table S1, supplement Chapter 3) for 30 s, extension at 72°C for 30 s; final extension step at 72°C for 10 min. Microsatellites were analysed on an ABI 3130xL Genetic Analyzer (Applied Biosystems®). Fragment length was assessed relative to GeneScan^{TM}-400HD Size Standard using PEAK SCANNER^{TM} v1.0 (Applied Biosystems®).

We tested for deviations from Hardy-Weinberg equilibrium (HWE) and linkage disequilibrium (LD) using the package ‘pegas’ ver. 0.7 (Paradis 2010) in R 3.2.1 (R Core Team 2015). For HWE, Chi^2 tests and for LD, the T_2 test (Zaykin *et al.* 2008) were implemented in this package. F_{is} estimates according to Weir & Cockerham (1984) and Robertson & Hill (1984) were calculated in GENEPOP ver. 4.3. (Raymond & Rousset 1995; Rousset 2008). We conducted estimations of expected and observed homozygotes and tests for the presence of null alleles using MICRO-CHECKER (Van Oosterhout *et al.* 2004).

Relatedness analyses based on microsatellite data

We conducted parentage and relatedness analyses for 73 individuals sampled between 2010 and 2014. Based on the preliminary microsatellite analyses (see above), locus 41HDZ71 was excluded in the following analyses due to many null alleles (up to 41%; Table S2, supplement Chapter 3).

Several methods to estimate relatedness among individuals have been proposed in the literature, however their performance is influenced by many factors, including the characteristics of the molecular markers used (e.g., number of loci, heterozygosity, allele frequency) and the pedigree of the individuals being examined (Csilléry *et al.* 2006; Pew *et al.* 2015). In order to select the best relatedness estimator based on our data, we used the R package *related* (Pew *et al.* 2015). This package implements the functionality of COANCESTRY (Wang 2011) but it also allows for an explicit comparisons across seven different relatedness estimators, five moment estimators (Queller & Goodnight 1989; Li *et al.* 1993; Ritland 1996; Lynch & Ritland 1999; Wang 2002) and two likelihood-based estimators, the dyadic likelihood estimator - dyadml (Milligan 2003) and the triadic likelihood - trioml - estimator (Wang 2007). Using the allele frequencies observed in our data set, we first simulated data sets of 100 pairs for four known relatedness categories (parent-offspring, full-sibling, half-sibling, and unrelated). Then, for each of the seven relatedness estimators, we calculated the correlation coefficient (“Pearson’s”) between observed and expected relatedness values.

We then calculated the average level of relatedness within groups at three different levels: 1) adult males *versus* adult females (two groups); 2) among adult females within the same social group (eight units with two or more adult females); and 3) among males belonging to the same male association (11 associations with at least two genotyped individuals). To determine whether individuals within groups were more related than expected, we compared the observed values for each group against a distribution of ‘expected’ relatedness values generated by randomly shuffling individuals between groups for 1000 permutations and keeping group size constant.

Parentage and sibship analyses

We used COLONY V2 (Jones & Wang 2010) to infer parentages and full and half sibship. COLONY is robust against deviations from HWE (J. Wang, pers. communication). Therefore, the two other loci showing deviations from HWE and marginal signs of null alleles (41HDZ105 and 41HDZ626) remained in the analysis. However, we set a higher genotyping error rate of 0.03 for these two loci (J. Wang, pers. communication). For all other loci, a genotyping error rate of 0.01 was set, according to estimations based on a number of resampled individuals (c. 7% of the study population; Hoffman & Amos 2005). We implemented the recommended settings of full-likelihood method and a polygamous mating system without inbreeding (appropriate when analysing parentages for offspring from several breeding seasons; Jones & Wang 2010). The probability that fathers and mothers were included in the candidate samples was assumed to be 80% for males and 90% for females, based on the mean proportion of sampled individuals of all marked and unmarked ones per year. Cohorts included animals born at the end (Oct-Dec) of the respective year or at the beginning (Feb-Mar) of the following year. The offspring sample included the cohorts 2010 to 2013. Four females of the cohort 2010 were included in both the offspring and the mother candidate sample. We accepted parentage and full and half-sibling assignments with a probability >0.80.

Furthermore, we compared relatedness based on the trioml estimator and haplotypes (individually determined, not concluded from matrilines) within all breeding pairs that were assigned with a probability >0.80.

Analyses of reproductive skew

We calculated eight indices of reproductive skew (S: Reeve & Ratnieks 1993; S_c: Keller & Krieger 1996; S_3: Pamilo & Crozier 1996; Q: Ruzzante *et al.* 1996; λ: Kokko & Lindström 1997; I_δ and I_p: Tsuji & Tsuji 1998; B: Nonacs 2000) using the software SKEW CALCULATOR 2003 (Nonacs 2003). We conducted analyses for males and females based on three cohorts born between 2011 and 2013. For these cohorts, we could confirm the presence of the included candidate males and females based on capture dates, age, and observations. We based our conclusions on the *B* index and its corresponding confidence intervals and *P*-values (Nonacs 2000). In contrast to all other indices, *B* is the only one that takes into account differing lengths of time individuals were present in the parent sample, i.e. varying number of cohorts (Nonacs 2000, 2003). *B* can range from -1 to +2. When reproductive skew is greater than expected, *B* is positive; when it is randomly distributed, *B* is 0; when it is more evenly distributed than expected, *B* is negative. We pooled all males for this analysis because paternities indicated that males also sired offspring in cases in which there was no regular spatial overlap with the respective female, supported by direct observations of single excursions of males from their usual range.

We based skew calculations only on genetic paternities, because it was not possible to infer paternities from copulation events or other social traits due to the lack of paternal care. For females, we referred to all emerged pups for which we could assign genetic and/or social maternities. We excluded 2 units (H and J) because SKEW CALCULATOR 2003 cannot detect reproductive skew in units with less than 2 pups. We conducted a power analysis implemented in SKEW CALCULATOR 2003 to determine the power of the dataset to detect skew, estimating significance levels based on 10,000 simulations. We based this analysis on the following demographic means: 2 mature females; 3 pups within 3 cohorts per unit; a probability of 0.7 and 0.3 for the first and second female, respectively, based on the average presence during breeding seasons.

For comparison with the available genetic samples, we also calculated the mean percentage of conceiving females, and the mean percentage of pups emerging from the observed pregnancies based on direct observations of pregnancies available for the cohorts 2012 and 2013.

Results

mtDNA haplotypes

We identified 10 distinct mtDNA haplotypes from 84 *M. decemlineata* (43 males, 33 females, and 8 individuals of unknown sex). All 10 haplotypes were also recovered in a previous phylogeographic study (van Vuuren *et al.* 2012). Out of 325 bp, 24 sites were polymorphic. Overall nucleotide diversity (π) was estimated at 0.02429 ± 0.00079 and the overall haplotype diversity (Hd) was estimated at 0.786 ± 0.021. The parameter theta, θ, was 4.798 and the value of Tajima's D was positive, but not significant (D=1.95545, P>0.05), suggesting no significant deviation from neutrality.

The frequency distribution of the mtDNA haplotypes was relatively skewed with four haplotypes (I, III, IV, and V) being very common (13-25 individuals) and the remaining ones (II, VI, VII, VIII, IX, and X) occurring at low frequencies (1 or 2 individuals; Fig. 1). Females and males differed strongly in haplotype identity and diversity. Only five different haplotypes were found among females, while nine distinct haplotypes were present among males. While only one haplotype (VI) was unique in females, five haplotypes were exclusively represented by males, suggestive of male migration into the study area. Moreover, haplotype V was found in 12 males but only in one female (Fig. 1 and 2). Although there was no significant difference in π between the sexes ($\pi_{♂}$= 0.02423 ± 0.00166, $N_{♂}$=43; $\pi_{♀}$= 0.02401 ± 0.00098, $N_{♀}$=33; P=0.501, haplotype diversity was significantly higher in males ($\mathrm{Hd}_{♂}$= 0.818 ± 0.030, $N_{♂}$=43; $\mathrm{Hd}_{♀}$= 0.714 ± 0.038, $N_{♀}$=33; P<0.001). All individuals of the female units A, B and C displayed haplotype IV; D, E and H shared haplotype I; F, G and J displayed haplotype III (Fig. 2a). Female immigration resulted in one unit comprising different haplotypes (Fig. 2a, unit E). Members of male associations differed in haplotypes. In 10 associations in which the haplotypes of at least two males were identified, maximally 50% of males shared the same haplotypes, including five associations of two males.

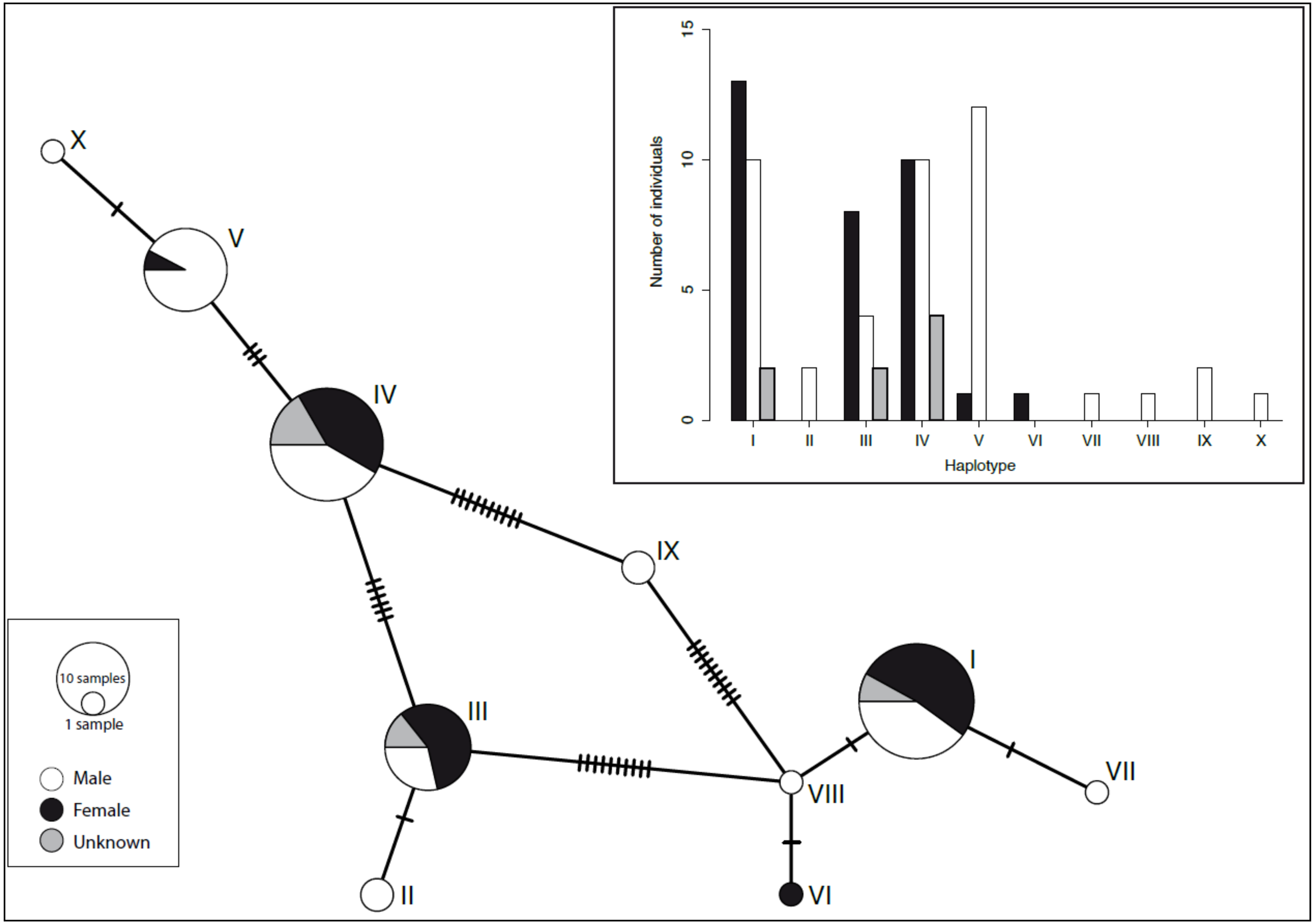

Fig. 1 Haplotype network and haplotype frequencies of male and female narrow-striped mongooses in Kirindy Forest/CNFEREF. Roman numerals refer to different haplotypes.

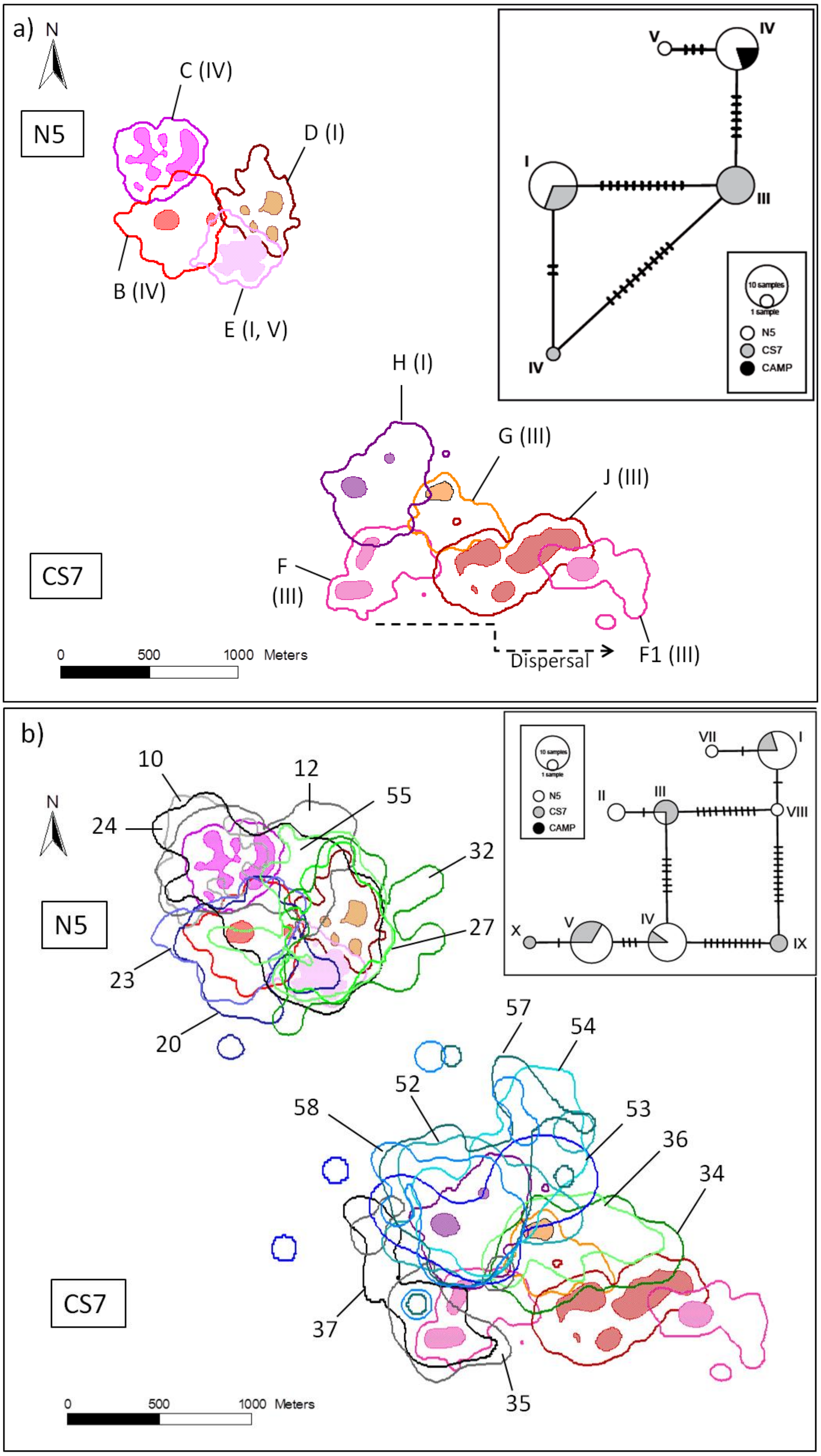

Fig. 2 Annual home range and haplotype distributions of 9 female units (a, b) and 17 males (b) of narrow-striped mongooses. Lines represent 90% kernel home ranges, filled areas represent 50% kernel home ranges (=core areas) of females. Letters label female units, numbers label male individuals. Haplotypes are indicated in brackets. N5 and CS7 denote local study areas.

Microsatellite analyses

Three out of 13 loci showed significant deviations from HWE and signs of null alleles (Table S2, supplement Chapter 3). The test for LD did not reveal non-random associations of alleles among different loci (T_2=23.97; *df*=22; *P*=0.349).

Relatedness within sexes, female units and male associations

The correlation coefficients of the seven estimators ranged between 0.745 for ritland (Ritland 1996) and 0.855 for trioml (Wang 2007). Hereafter, we describe results only based on trioml, the estimator with the highest correlation coefficient. Values for all estimators are reported in Table 1. Overall, females were found be more closely related to each other than males; however, based on our permutation approach, only four estimators out of seven showed a significant difference from a random distribution (*P*<0.05). Average pairwise relatedness among adult females belonging to the same social unit was generally higher than expected, with values ranging between 0.251 in unit F and 0.542 in unit C. The only unit in which the relatedness value obtained by trioml was not significantly different from the random distribution was unit G (*R*=0.318; *P*=0.057). However, three other estimators (wang, lynchli, and quellergt) found this difference statistically significant (*P*<0.05).

Two male associations (2 and 12) had higher relatedness estimates than that of the mean of the permuted relatedness estimates, 0.534 (*P*=0.023) and 0.447 (*P*=0.040) respectively. In the other nine cases, males forming associations were not more closely related to each other than expected by chance. The mean observed relatedness of males within associations ranged between 0 and 0.063 and were not found to be significantly greater than that of randomly generated groups.

Table 1 Relatedness within sexes, female units and male associations of narrow-striped mongooses, based on seven different relatedness estimators.

		N	**trioml**	**wang**	**lynchli**	**lynchrd**	**ritland**	**quellergt**	**dyadml**
Correlation coefficients			0.855	0.846	0.837	0.842	0.745	0.840	0.849
Relatedness within sexes									
Males		23	0.068	-0.055	-0.064	-0.027	-0.028	-0.026	0.082
Females		24	0.088	**0.050**	**0.040**	**-0.011**	**-0.012**	0.010	0.102
Adult females within social unit									
	A	3	**0.536**	**0.564**	**0.533**	**0.458**	**0.445**	**0.464**	**0.559**
	B	3	**0.415**	**0.438**	**0.428**	**0.380**	**0.242**	**0.361**	**0.432**
	C	2	**0.542**	**0.472**	**0.510**	**0.346**	**0.250**	**0.510**	**0.547**
	D	3	**0.340**	**0.260**	**0.218**	**0.222**	**0.230**	0.180	**0.368**
	E	3	**0.412**	**0.348**	**0.345**	**0.459**	**0.561**	**0.363**	**0.487**
	F	3	**0.251**	**0.266**	**0.265**	0.154	**0.181**	**0.311**	**0.302**
	G	2	0.318	**0.420**	**0.475**	0.164	0.089	**0.392**	0.353
	H	3	**0.385**	**0.446**	**0.428**	**0.348**	**0.254**	**0.448**	**0.435**
Male associations									
Year									
2012	2	2	**0.534**	**0.423**	**0.405**	**0.396**	**0.171**	**0.416**	**0.536**
2013	3	4	0.059	-0.052	-0.079	-0.017	-0.049	-0.055	0.067
	4	3	0.043	-0.152	-0.155	-0.162	-0.152	-0.140	0.057
	5	2	0.000	-0.207	-0.225	-0.104	-0.047	-0.140	0.000
	7	2	0.000	-0.210	-0.190	-0.058	0.067	-0.090	0.000
	8	2	0.322	0.295	0.335	**0.334**	**0.286**	0.280	0.392
2014	9	3	0.010	-0.151	-0.167	-0.061	-0.061	-0.094	0.015
	10	3	0.031	-0.115	-0.062	-0.068	-0.033	-0.057	0.039
	11	2	0.063	0.157	0.055	0.027	0.026	0.012	0.087
	12	2	**0.447**	**0.364**	0.335	**0.385**	**0.454**	**0.356**	**0.461**
	13	4	0.032	-0.185	-0.231	-0.105	-0.127	-0.163	0.046

N: number of individuals; A-H: unit identity; 2-13: identity of male association; in **bold**: significantly higher related than expected by random combination of individuals; negative relatedness values indicate lower relatedness than expected by random combination. Female unit F1 (which derived from unit F) was not included here because only one female was genotyped.

Parentages and sibling relationships

Of 22 offspring, paternity and maternity, respectively, could be assigned to 19 infants and juveniles with a probability >0.80, thereof 18 with a probability >0.95 (Table 2). For one juvenile (Md26), none of the candidate fathers was assigned. For two infants, Md51 and Md62, only low probabilities of candidates, including the observed probable social mothers (Md38 and Md39) were obtained (mothers: 0.486 and 0.163; fathers: 0.293 and 0.025, respectively). For one juvenile (Md50), the adult females of the unit were not assigned as mothers, suggesting that it was presumably offspring of a female previously breeding in this unit, but which had disappeared before the observation period and could not be sampled.

Full- and half-sibling relationships are summarised in Table 3 and 4. There were five full-sibling pairs. Ten half-sibling pairs shared a common father, while eight pairs shared a common mother. All shared maternities of half-siblings were within the same social unit, while all shared paternities were distributed among different units.

Relatedness within breeding pairs (*N*=15) was low (mean *R*=0.054; range: 0-0.386), with only one pair displaying relatedness comparable to the level within female units (Md1 – Md4: *R*=0.386; Table 2). For all breeding pairs for which haplotypes could be determined for both parents (*N*=7), 5 pairs differed while 2 ones showed identical haplotypes.

Table 2 Parentage assignments for 22 narrow-striped mongoose offspring sampled from 2011 to 2014.

Offspring ID	Sex	Unit ID	Unit size	Cohort	Assigned mother	Probability mother	Assigned father	Probability father	*R* (m/f)
A: Infants									
Md17	N/A	A	3	2011	Md9	1.0	Md19	0.998	0.103
Md56	N/A	C	4	2012	Md15	1.0	Md12	1.0	0
Md59	N/A	C	4	2013	Md15	1.0	Md12	1.0	0
Md61	N/A	D	3	2013	Md26	0.999	Md27	1.0	0
Md41	F	E	6	2012	Md1	0.965	Md19	0.892	0
Md51	N/A	F	5	2012	(Md38)	(0.486)	(Md19)	(0.293)	(0.077)
Md44	F	G	4	2012	Md48	1.0	Md35	1.0	0
Md62	N/A	G	4	2013	(Md39)	(0.163)	N/A	N/A	N/A
B: Infants and juveniles									
Md8	F	A	3	2010	Md9	1.0	Md19	1.0	0.103
Md14	F	B	4	2010	Md6	1.0	Md4	1.0	0
Md21	F	C	4	2010	Md15	1.0	Md19	1.0	0
Md22	F	C	4	2011	Md15	1.0	Md19	1.0	0
Md26	F	D	4	2010	Md_MLL11	1.0	N/A		N/A
Md28	M	D	4	2011	Md_MLL11	0.997	Md32	1.0	0.174
Md3	F	E	4	2010	Md1	1.0	Md_MLL9	0.999	0
Md11	M	E	5	2010	Md1	1.0	Md4	1.0	0.386
Md33	F	E	5	2011	Md2	1.0	Md5	1.0	0.079
Md50	F	F	4	2011	(Md63)	(0.749)	Md34	1.0	(0.186)
Md49	M	G	4	2010	Md48	1.0	Md35	1.0	0
Md42	F	H	3	2010	Md45	0.873	Md57	0.967	0.006
Md43	F	H	3	2011	Md45	1.0	Md57	1.0	0.006
Md47	M	J	4	2011	Md46	1.0	Md34	1.0	0

A: 8 infants born during the observation period of the respective unit; B: 14 infants and juveniles already present at the beginning of the respective observation period. Parentages with a probability < 0.80 in brackets. R (m/f): relatedness within breeding pairs according to the trioml estimator.

Table 3 Full-sibling assignments for 10 narrow-striped mongoose offspring including the cohorts from 2010 to 2013.

Full-sibling IDs	Unit	Full-siblings probability	Full-siblings mother	Full-siblings father	Half-siblings IDs
Md8, Md17	A	0.998	Md9	Md19	Md21, Md22, *Md41*
Md21, Md22	C	1.0	Md15	Md19	Md8, Md17, *Md41*, Md56, Md59
Md56, Md59	C	1.0	Md15	Md12	Md21, Md22
Md44, Md49	G	1.0	Md48	Md35	-
Md42, Md43	H	0.854	Md45	Md57	-

IDs in *italics* denote half-sibship probabilities lower than 0.95.

Table 4 Half-sibling assignments for 14 narrow-striped mongoose offspring including the cohorts from 2010 to 2013.

Half-siblings IDs	Unit(s)	Half-siblings probability	Half-siblings mother(s)	Half-siblings father(s)	Cohort(s)
Md8, Md21	A, C	1.0	Md9, Md15	Md19	2010
Md8, Md22	A, C	1.0	Md9, Md15	Md19	2010, 2011
Md8, Md41	A, E	0.892	Md9, Md1	Md19	2010, 2012
Md17, Md21	A, C	0.998	Md9, Md15	Md19	2011, 2010
Md17, Md22	A, C	0.998	Md9, Md15	Md19	2011
Md17, Md41	A, E	0.889	Md9, Md1	Md19	2011, 2012
Md14, Md11	B, E	1.0	Md6, Md1	Md4	2010, 2011
Md21, Md56	C, C	1.0	Md15	Md19, Md12	2010, 2012
Md21, Md59	C, C	1.0	Md15	Md19, Md12	2010, 2013
Md21, Md41	C, E	0.892	Md15, Md1	Md19	2010, 2012
Md22, Md56	C, C	1.0	Md15	Md19, Md12	2011, 2012
Md22, Md59	C, C	1.0	Md15	Md19, Md12	2011, 2013
Md22, Md41	C, E	0.892	Md15, Md1	Md19	2011, 2012
Md26, Md28	D, D	0.997	Md_MLL11	N/A, Md32	2010, 2011
Md3, Md11	E, E	1.0	Md1	Md_MLL9, Md4	2010, 2011
Md3, Md41	E, E	0.964	Md1	Md_MLL9, Md19	2010, 2012
Md11, Md41	E, E	0.965	Md1	Md4, Md19	2011, 2012
Md50, Md47	F, J	0.994	N/A, Md46	Md34	2011

Reproductive skew

The 22 offspring were fathered by 10 males (i.e. 34.5% of all 29 candidate fathers). Genetic mothers represented 10 of 27 (37.0%) candidate mothers. Indices of reproductive skew are reported in Table 5. *B* skew indices revealed no significant reproductive skew within males or females. 95% confidence intervals (CI) included zero for all sample units, and thus were not significantly different from a random distribution. 95% CIs also overlapped between males and females in both analyses; thus the sexes were not significantly different in parentage distribution functions (Table 5). However, for two female units (A and C) CIs included maximum *B* values. Thus, monopoly by one female could not be excluded. Our power analysis revealed that 36 units would be necessary to discriminate a skewed distribution from a random one.

Based on observations for the cohorts 2012 and 2013, on average 91.7 ± 8.4% of mature females (*N*=24) conceived, thereof two females twice within the 2013 season. In 78.7 ± 20.0% of observed pregnancies (*N*=26), pups emerged. However, from these two cohorts, on average, only 27.7% of pups survived the first year of life (Chapter 2).

Table 5 Indices of reproductive skew among 25 male and 17 female narrow-striped mongooses based on the genetic parentages (in males) and emerged pups (in females) of the cohorts 2011 to 2013.

Units	N	N_b	S	S_c	S_3	Q	λ	I_δ	I_p	B	95% CI (B)	p level (B)	*Equal*	*Monopoly*
Males – genetic paternities	25	9	0.65	0.14	0.74	0.03	0.24	1.60	0.24	0.03	-0.07, 0.12	0.066	-0.07	0.90
Females - emerged pups														
A	2	1	1	1	1	1	1	2	0.12	0.06	-0.17, 0.06	0.579	-0.17	0.06
B	3	2	0.33	0.06	0.50	0	0.62	1	0	-0.07	-0.13, 0.49	0.833	-0.13	0.60
C	2	1	1	1	1	1	1	2	0.25	0.04	-0.08, 0.04	0.552	-0.08	0.04
D	3	2	0.33	-0.41	0.50	-0.50	0.62	0	-0.26	-0.13	-0.25, 0.62	1.0	-0.25	0.63
E	3	2	0.41	0.05	0.60	0	0.69	1	0	-0.08	-0.20, 0.35	0.824	-0.20	0.36
F	2	2	0	-1	0	-1	0	0	-1	-0.25	-0.25, 0.24	1.0	-0.25	0.25
G	2	2	0	-1	0	-1	0	0	-1	-0.25	-0.25, 0.24	1.0	-0.25	0.25
Female mean	2.4	1.7	0.44	-0.04	0.51	-0.07	0.56	0.86	-0.27	-0.10		0.958		

N: number of individuals; N_b: number of individuals that gained at least one parentage within all cohorts; skew indices: S: Reeve & Ratnieks (1993); S_c: Keller & Krieger (1996); S_3: Pamilo & Crozier (1996); Q: Ruzzante *et al.* (1996); λ: Kokko & Lindström (1997); I_δ and I_p: Tsuji & Tsuji (1998); B: Nonacs (2000). *Equal*: minimum B value possible (equal sharing of parentages); *Monopoly*: maximum B value possible if all parentages are monopolized by the individual with the highest parentage rate.

Discussion

Our study revealed a strong effect of sex on genetic structure. Haplotype diversity was significantly higher in males than in females. Female units were based on matrilines, and some neighboring units showed identical haplotypes. Similarly, relatedness within female units was higher than expected by chance and higher than among males. Members of male associations differed in haplotypes and average pairwise relatedness of associated males was not significantly different from chance. The mating system of *M. decemlineata* is best characterised by polygyny, with some indications for mate choice but no evidence for reproductive skew in either sex. We discuss these main findings in more detail below.

Haplotype distribution and relatedness in females

Our findings on haplotype distribution indicate a matrilinear structuring of female social units. Identical haplotypes among neighboring units indicate that matrilines exist beyond the level of mother-daughter relationships, and suggest that philopatry is female-biased. Similar examples of groups based on matrilines occur in several other carnivores, including procyonids, hyaenids and felids (Waser & Jones 1983; Frank 1986b; Packer *et al.* 1991; Van Horn *et al.* 2004). Matrilinearity is also prominent among mongooses. In meerkats, which are mainly composed of a dominant breeding pair and subordinate first-order relatives, breeding tenure lasts longer for females than for males, and dispersal is male-biased, while females do not leave the group voluntarily (Clutton-Brock *et al.* 2006; Russell *et al.* 2007; Young *et al.* 2007). In *Ichneumia albicauda*, a ‘solitary’ mongoose with strong gregarious tendencies in high-density populations, matrilinearity of clans was suspected as well (Waser & Waser 1985). However, studies of herpestids have more often focused on within-group relatedness, to investigate the level and effects of inbreeding (Keane *et al.* 1996; Nielsen *et al.* 2012) and breeding strategies (e.g. extra-pair paternity) in societies with different levels of reproductive skew (O’Riain *et al.* 2000; Leclaire *et al.* 2013a, b; Nichols *et al.* 2015; Sanderson *et al.* 2015). Sociality among adult females in *M. decemlineata* is therefore higher than in some solitary herpestids such as *Herpestes ichneumon* and *Galerella sanguinea*, where groups do not contain more than one adult female (Rood & Waser 1978; Palomares & Delibes 1993).

In *M. decemlineata*, the significant within-group relatedness of adult females for the large majority of estimators and female units is in accordance with our conclusions based on mtDNA haplotypes and suggests that units are generally formed by mothers and their offspring. However, several estimators found relatedness values not significantly different from a random combination, in particular for two units (F and G), indicating that other mechanisms can influence social organisation. Indeed, we observed single cases of dispersal of and immigration by relatively young mature females into units in which breeding positions were vacant after dominant females had died (Chapter 2). This process resulted in one unit (E) of mixed haplotypes. Thus, not only eviction by dominants is a possible explanatory mechanism for female dispersal here. Because usually only the pup of the dominant breeding female survives the first year of life, overall fitness benefits for voluntarily dispersing females can be higher when breeding territories are vacant than from staying in their natal group (Clutton-Brock & Lukas 2012). The haplotype structure among neighboring units and the consistently higher average relatedness among females for all estimators suggest that female dispersal is spatially more limited than in males.

Male relatedness and implications for dispersal and association patterns

The higher haplotype diversity and the relatedness estimations indicate that male *M. decemlineata* disperse more widely away from their natal unit. Male-biased dispersal has been also observed in solitary and eusocial mongooses (Waser & Waser 1985; Rood 1987; Clutton-Brock *et al.* 2002), where the probability of attaining breeding opportunities within the natal group is much lower for males than for females, which presumably drives male bias in dispersal rates (Rood 1987; Cant *et al.* 2001; Clutton-Brock *et al.* 2001c).

In striking contrast to findings and speculations reported from other carnivore species, associated male *M. decemlineata* were not more closely related than expected by chance in most cases. Five out of 10 associated male dyads showed different haplotypes. Only 3 out of 11 associations revealed significantly higher relatedness than randomly expected, one of them for only 2 of the 7 estimators (association 8). Association 12 included a recently dispersed young male, which joined a male within the range of its natal unit. Because narrow-striped mongooses have litters of only one young, association partners cannot be littermates. Additionally, we observed disintegration of male associations at the beginning of the mating period and strong variation of their composition among years (Chapter 2). This pattern argues against inclusive fitness benefits of male coalitions such as in fosas (Lührs *et al.* 2013), lions (Bygott *et al.* 1979; Packer *et al.* 1991), slender mongooses and small Indian mongooses (Waser *et al.* 1994; Hays & Conant 2003). More mutualistic benefits, such as reduction in predation risk (Chapter 2), may therefore explain the formation of male associations in this species.

Reproductive patterns and implications for the mating system

Based on parentage data, some males fathered offspring of up to two female units in one breeding season, indicating polygynous mating. Because females were also observed to mate with other males than the genetic father, the mating system is best characterised as mild promiscuity. The spatio-temporal distribution of males during the mating season also revealed that males roamed among the ranges of up to 3 female units instead of monopolizing specific females. However, the presence of full-siblings in consecutive breeding seasons reflects the effects of either female choice or male monopolization in the general context of promiscuous mating.

Conclusions regarding the level of reproductive skew are difficult due to the small number of units and pups sampled. Accordingly, the power of *B* index calculations was low, not revealing significant skew, although statistically not excluding monopoly by females in some units. Proportions of conceiving females and emerging pups are comparable to low skew societies such as banded mongoose females, where 83% of females conceived and 71% carried to term (Cant 2000). However, from 2012 to 2014, on average only 28% per cohort of emergent narrow-striped mongoose pups survived the first year of life, all of them born by the dominant female of the unit. The only exception was revealed by genetic maternities of the cohort 2011, when offspring of two females survived, however born at an interval of several months from each other, and before a turn-over in unit composition. In conclusion, *post partum* mechanisms are apparently responsible for regulating reproductive success in females, but we have no evidence regarding a possible role of female infanticide, which has been documented in social herpestids (Gilchrist 2006b; Young & Clutton-Brock 2006; Young *et al.* 2008).

In contrast to eusocial mongooses, in which one or a few dominant males sire almost all pups (Griffin *et al.* 2003; Nichols *et al.* 2010), the potential of male narrow-striped mongooses to monopolize access to receptive females is limited by two main factors. First, sexual segregation, including female aggression towards males, in combination with large female ranges impede a stable association of males with receptive females (Orians 1969; Lukas & Clutton-Brock 2013). Second, male associations disintegrate at the beginning of the mating period and vary markedly in composition, and thus do not provide a reproductive advantage for association partners. In combination with a male-biased adult sex ratio and the occasional intrusion of outside males into ranges of their conspecifics (Chapter 2), this apparently creates a scramble competition which prevents high reproductive skew among males.

Conclusions

This rare socio-genetic investigation in a Malagasy mongoose species revealed similarities to the matrilinear structure found in other carnivores, despite sexual segregation. The lack of high relatedness within male associations indicates that male sociality can also arise independent of inclusive fitness benefits. Finally, despite a formal lack of evidence for significant reproductive skew, female reproductive competition is also evident in much smaller social units than in group-living herpestids, but the mechanisms appear to operate mostly post-natally.

Supplementary Material of Chapter 3: Tables

Table S1 Primer sequences, repeat motifs and annealing temperatures of the 13 microsatellite loci (Vogler *et al.* 2009).

Locus ID	Primer sequence 5’-3’	Repeat motif	Annealing temp. (°C)	Size range
41HDZ1	F: GTCAGCGCAGAACCCAAC R: ATTCACCCAAGATTGCCC	$(CA)_9TA(CA)_{10}$–AAACT$(CA)_5$	58	217-244
41HDZ67	F: CAGTTTGGCAGTTCCTCAGTAAG R: TCATTCCTTTTGCGGCTG	$(CA)_{22}$	54	268-304
41HDZ71	F: GGTCCATCCATTCCGTCA R: CACAAAAACAGTGCGAACCT	$(GT)_{17}$	52	197-235
41HDZ78	F: GTCTGCCAAGTCTGGATGC R: ATTTTGTGAAGGTCTGATGGG	$(CA)_{20}$	58	88-131
41HDZ90	F: TGTGCCCAATCCATAACCC R: CACTCCAGACAGCAAACCAAG	$(GT)_{21}$	60	137-162
41HDZ105	F: GGTGTCCGAGAACTCAAGAATA R: AGCCTGCTATCACATTTACCAA	$(CA)_{29}$	54	147-196
41HDZ112	F: TCACAGAACAAGTTACTCACAAGC R: TCTCACATTTTCAAAGGACCTC	$(CA)_4CCAA(CA)_5$–CCAA$(CA)_{17}$	54	156-192
41HDZ122	F: GACACATACACAGTTTCTCTACATCC R: CTTTGAAGGGAATGACCAGTG	$(CA)_{19}$	54	112-151
41HDZ261	F: TGAATCCATCCCAGGCTG R: CATCTGAAGGAAGGTTGAAGC	$(TG)_5C(GT)_{13}$	52	210-250
41HDZ592	F: ACTGTAACATAGTAGGAAATGGATACG R: TGAGGTTTTTGACTTTTGCTTG	$(CA)_{15}$	52	170-186
41HDZ626	F: GGTTCTGTGTCTCCCTCTCC R: CTCACTTATCAAACAAAACGGG	$(CA)_4TT(CT)_{18}$	54	175-225
41HDZ633	F: GGTTATTGCAGGCTATTCTAGGTC R: CAACTAAATACTCATAAAAAACCAAGC	$(CA)_{17}$	52	140-183
41HDZ960	F: CAACCACTGACTTCTTACTGACAA R: GGACTTATTTATGTTTAGGAATGTAGAG	$(CT)_{10}(CA)_{14}T(AC)_{18}$	56	178-222

Table S2 Summary statistics for microsatellite loci including probabilities of deviation from Hardy-Weinberg Equilibrium and null allele frequency estimations.

			Homozygotes		F_{is}		HWE			Null allele frequency estimations			
Locus	*k*	*N*	Exp.	Obs.	W&C	R&H	Chi^2	*df*	*P* (exact)	Oo.	Ch.	Br. 1	Br. 2
41HDZ1	3	96	52.0	54	0.051	0.087	3.887	3	0.273	0.018	0.023	0.014	0.014
41HDZ67	12	96	15.6	10	-0.064	-0.047	77.770	66	0.143	-0.035	-0.034	-0.032	0
41HDZ71	9	85	17.5	56	0.574	0.561	274.177	36	0.000	0.275	0.399	0.253	0.409
41HDZ78	7	96	16.9	11	-0.069	-0.046	18.899	21	0.582	-0.039	-0.036	-0.034	0
41HDZ90	6	96	36.1	35	-0.013	-0.029	9.908	15	0.724	-0.001	-0.009	-0.007	0
41HDZ105	11	96	19.8	34	0.192	0.201	190.283	55	0.000	0.094	0.103	0.083	0.083
41HDZ112	8	96	31.2	32	0.018	0.027	54.321	28	0.135	0.002	0.006	0.005	0.005
41HDZ122	8	96	21.2	17	-0.051	-0.048	66.764	28	0.083	-0.026	-0.027	-0.025	0
41HDZ261	10	96	14.7	12	-0.028	-0.005	35.613	45	0.482	-0.018	-0.016	-0.015	0
41HDZ592	6	96	22.8	25	0.036	0.009	11.538	15	0.607	0.017	0.016	0.013	0.013
41HDZ626	8	96	32.0	44	0.193	0.163	35.820	28	0.030	0.089	0.104	0.075	0.075
41HDZ633	10	95	14.3	12	-0.023	-0.009	48.931	45	0.117	-0.017	-0.014	-0.013	0.031
41HDZ960	11	96	14.1	13	-0.008	0.015	48.952	55	0.384	-0.009	-0.007	-0.006	0

k: number of alleles; *N*: number of individuals; Exp., Obs.: expected and observed number of homozygotes; F_{is}: inbreeding coefficient according to Weir & Cockerham (1984), and Robertson & Hill (1984); null allele frequency estimations based on different algorithms: Oo.: Van Oosterhout *et al.* (2004); Ch.: Chakraborty *et al.* (1992); Br. 1 and Br. 2: Brookfield (1996).

GENERAL DISCUSSION

In the present thesis, I delineated the social organisation (**Chapter 2**) and the genetic structure and reproductive characteristics (**Chapter 3**) of the Malagasy narrow-striped mongoose (*Mungotictis decemlineata*) in Kirindy Forest/CNFEREF. I hereby considered the characteristics of social systems and life-histories of the Herpestidae and Eupleridae and their implications for socio-ecological theory (**Chapter 1**), aiming to establish a valuable basis for inter-specific comparisons.

In the following, I summarise and discuss my results in a comparative perspective to mongoose, carnivore and mammalian social systems. The striking pattern of gregarious sexual segregation found in *M. decemlineata* provides the opportunity for a distinct inference and evaluation of the factors determining social patterns in males and females, considering the sex-specific predictions of socio-ecological theory. Finally, I draw conclusions from my findings in the context of social evolution in the herpestids and euplerids.

Social organisation of the narrow-striped mongoose: determinants and mechanisms leading to sexually segregated gregariousness

Sexual segregation associated with gregariousness in both sexes was the key finding characterising the social organisation of *M. decemlineata*. This configuration of sociality is mirrored in the sex-specific ranging patterns, local genetic structure and relatedness patterns. Female social units were based on matrilines, comprised on average two adult females, one juvenile and one infant, and occupied exclusive territories. The members of these stable units synchronised their activity, i.e. they roamed in close proximity and denned together, and interacted socially through various forms of behaviour. In contrast, male social organisation displayed strong variability. Males were associated with one to three other males. They roamed together in close proximity and socially interacted. Male associations disintegrated during the mating period, when males roamed primarily as solitary individuals, and also varied in composition among years. Male home ranges overlapped extensively with other males year-round and with up to four female units (**Chapter 2**). Relatedness was relatively high in females and within female units, but not higher than expected by chance in males and within the majority of male associations. Haplotype diversity was also higher in males, whereas several neighbouring female units showed identical haplotypes (**Chapter 3**).

The formation of social units in *M. decemlineata* in both sexes was indicated to result from the benefits facilitating group-living in small-sized carnivores. Of the two major selective forces hypothesised to determine group-living in carnivores, cooperative hunting and the need for defence against larger predators, I consider predation risk as a likely factor driving gregariousness in *M. decemlineata*. Although Albignac (1976) reports occasional group-hunting of mouse lemurs, cooperative hunting as a selective force such as has been observed in large-sized carnivores (African wild dogs: Creel & Creel 1995; fosas: Lührs *et al*. 2013, lions: van Orsdol 1984; see Bailey *et al*. 2013 for a review) is unlikely to play a major role in *M. decemlineata,* because despite the synchronised activities of associated individuals, the animals forage on their own and mainly on arthropods, and observations showed that prey is not shared (**Chapter 2**; Rasolofoniaina 2014).

Predation risk and the benefits of group augmentation have been mainly related to group-living mongooses in African open savannahs and deserts, where the co-evolution with diverse predator communities (e.g. large cats, larger mongooses, poisonous snakes, raptors) has generated highly developed systems of shared vigilance, sentinel behaviour, alarm calling and communal predator mobbing (Rasa 1977; Clutton-Brock *et al.* 1999c; Manser 1999; Graw & Manser 2007). The significance of predation risk was also found in the narrow-striped mongoose, in spite of the forest-dwelling life style and lower mortality rates than those in African mongooses. I recorded predation events in males and females by fosa (*Cryptoprocta ferox*; see also Hawkins & Racey 2008) and ground boa (*Acrantophis madagascariensis*) and frequent vigilance behaviour and alarm calls particularly against the harrier-hawk (*Polyboroides radiatus*; **Chapter 2**). In other vertebrate taxa in island ecosystems (van Schaik & van Noordwijk 1985; Beauchamp 2004), group sizes correlate positively with predation risk as well. I deduce that the formation of small social units in both sexes in *M. decemlineata* increase survival chances.

The sexual segregation in the ranging patterns of *M. decemlineata* corresponds to important predictions of socio-ecological theory. Several hypotheses of sexual segregation have been developed, mainly based on ungulate studies (Main & Coblentz 1996; Ruckstuhl & Neuhaus 2002). In particular, for social segregation of male and female units within the same habitat, which is the case for *M. decemlineata* here, the activity-budget and the social-preference hypothesis have gained support from sexually size-dimorphic species (Bon & Campan 1996; Conradt 1998). While the activity-budget hypothesis has been tested in non-dimorphic ungulates as well (Neuhaus & Ruckstuhl 2002), the proximate and ultimate mechanisms of social preference in this context, e.g. learning or developmental determination, remain unclear (Ruckstuhl 2007). For non-dimorphic species, it was predicted that males and females would be found in mixed-sex groups year-round (Ruckstuhl & Neuhaus 2002). However, empirical testing of the hypotheses on sexual segregation is rare for other vertebrates.

M. decemlineata does not show sexual dimorphism in body mass, but distinct sexual segregation in spatio-temporal distribution within the same habitat, i.e. social sexual segregation (**Chapter 2**). As a consequence, the patterns were inconsistent with the activity-budget hypothesis (Ruckstuhl & Neuhaus 2002), although sex differences in movement rates and travel distances were potential proximate factors facilitating sexual segregation here.

The empirical basis for comparisons with other carnivores is limited. Marcelli *et al.* (2003) showed sex differences in broad categories of activity in European polecats (*Mustela putorius*), a sexually size-dimorphic carnivore. Although sexual segregation is widespread in terrestrial and marine mammals (Wolf *et al.* 2005; Wearmouth & Sims 2008), hypotheses of sexual segregation have only been investigated explicitly in a few terrestrial carnivore species. Predominantly, the risk of male infanticide has been indicated to determine the social avoidance of males by females with offspring and thus consistent sexual segregation, particularly when males immigrate from other areas (*Ursus arctos*: Wielgus & Bunnell 1995; Rode *et al*. 2006; *Puma concolor*: Keehner *et al*. 2015). Male infanticide is an important mechanism determining reproductive strategies in carnivores and other mammals (van Schaik 2000). In herpestids, both extra-group and within-group infanticide by males has been observed in banded mongooses (Cant 2000). However, in group-living mongooses, infanticide risk is predominantly found to be a major mechanism determining suppression of subordinates and reproductive skew among females as a consequence of intense female breeding competition (*H. parvula*: Keane *et al*. 1994; *S. suricatta*: Clutton-Brock *et al*. 1998, 2010; Young & Clutton-Brock 2006; **Chapter 1**) and apparently generates characteristic life-history traits and reproductive strategies such as oestrus and birth synchrony (*M. mungo*: Cant 2000; Hodge *et al*. 2011). Infanticide is difficult to observe and evidence from less intensively studied mongooses is lacking. In species such as *M. decemlineata*, where the sexes are socially and spatio-temporally segregated, it is likely to be difficult for males to determine the parentage of infants (Pagel 1997). Since no infanticide has been reported so far from *M. decemlineata*, this aspect cannot be fully analysed here.

However, considering the mechanisms relevant for reproductive strategies opens an interesting area of study, because it links the observed spatio-temporal segregation of males and females to the characteristics of the mating system. The general distribution of females and males of *M. decemlineata* follows the predictions of socio-ecological theory in this respect (Emlen & Oring 1977). Females defend access to resources by maintaining exclusive territories, and males respond to the distribution of females. The mating system is closely related to female ranging patterns, and thus the access to and defensibility of females by males (Clutton-Brock 1989). In *M. decemlineata*, the spatial distribution of males roaming among several female units (**Chapter 2**) as well as the distribution of paternities (**Chapter 3**) indicate a polygynous or mildly promiscuous mating system, in which males are unable to monopolise access to particular females. It has been argued that polygyny is the most conspicuous trait shared by species exhibiting sexual segregation, and specific behaviours are connected to this mating system (Wolf *et al.* 2005). Sexual harassment by males, followed by frequent female aggression towards the male was the most striking behaviour of mating interactions observed in *M. decemlineata* (Sehner 2014; Schneider & Kappeler, unpublished data). The benefits of this form of sexual coercion to males are high when they succeed in mating and the related costs due to energetic expenditures and potential injuries are inevitable in a system in which monopolisation of females is difficult. In contrast, the costs for females are indicated to be high and result in consequences for female movements and social behaviour (Clutton-Brock & Parker 1995). As a consequence, female avoidance of sexual harassment by males has been considered to be one important explanation for sexual segregation in mammals (Trillmich & Trillmich 1984; Wolf *et al.* 2005). It is indicated that it also plays an important role for sexual segregation in *M. decemlineata*.

Within the sexually segregated units of *M. decemlineata*, I found interesting sex-specific patterns of sociality, life history and genetic structure, which provide further implications for the social and genetic mating system and interesting comparisons with other species. In the next section, I will discuss these patterns, their determinants and consequences in both sexes.

The determinants of female social organisation

The distribution and territoriality of female units in *M. decemlineata*, including exclusive core areas, indicate a response to the distribution of resources and joint resource defence. Home range extensions largely exceeded previous estimations (cf. Razafimanantsoa 2003). The seasonal variation in home range size displays variation in the abundance of resources between dry and rainy season (**Chapter 2**).

The defence of an area large enough to meet the resource requirements with a critical probability is a basic assumption of the resource dispersion hypothesis (Macdonald 1983). According to the predictions of this hypothesis, female home range size did not correlate with the number of group members in *M. decemlineata*. Although older offspring and secondary adult females might experience a lower level of food security than older residents, this mechanism can reduce the costs of sharing a territory with conspecifics (Johnson *et al.* 2002). Gregariousness has been also related to food resource characteristics in facultatively social (*Cynictis penicillata*: Cavallini & Nel 1995; Blaum *et al*. 2007) and solitary mongooses (*Herpestes ichneumon*: Ben-Yaacov & Yom-Tov 1983; Palomares & Delibes 1993), reflecting the high potential for intra-specific variation in social organisation in these species. However, the level of feeding competition and its effect on group size in different species remain unclear because an accurate distinction between distribution, abundance and predictability of resources is lacking and differences in population densities hamper comparisons. Furthermore, female philopatry and dispersal, as important factors shaping organisation and group size, are not found to be closely related to food resource characteristics (Clutton-Brock & Janson 2012).

Overall, the number of adult females within units and their relatedness suggest that female sociality in *M. decemlineata* is higher than in several solitary herpestids (Rood & Waser 1978; Palomares & Delibes 1993). Low haplotype diversity and relatively high average relatedness within female units indicate female-biased philopatry in the narrow-striped mongoose population (**Chapter 3**), confirmed by observational data (**Chapter 2**). Clustering of identical haplotypes in neighbouring female units and the low number of unique female haplotypes suggests that female dispersal is restrained in comparison to males. In contrast, higher haplotype diversity and more unique haplotypes in males suggest that males immigrate into the area. Similarly, female philopatry is indicated to facilitate gregariousness in 'solitary' herpestids (Waser & Waser 1985; Waser *et al.* 1994). In eusocial mongooses, females mainly disperse after eviction by dominants, and in meerkats and banded mongooses they even do not disperse voluntarily (Rood 1987; Clutton-Brock *et al.* 1998; Cant *et al.* 2001, 2013). In these species, subordinated females, in contrast to males, can occasionally breed and potentially inherit dominance status within their natal group (Keane *et al.* 1994; Griffin *et al.* 2003). Thus, in spite of suppression by dominants, long-term fitness consequences favour philopatry instead of dispersal for breeding opportunities elsewhere, and its associated costs such as particularly high predation risk (Stephens *et al.* 2005).

In *M. decemlineata*, patterns of observed pregnancies and reproductive skew estimations showed that all mature females could potentially breed within their unit (**Chapter 2** and **3**). However, the slow reproductive rate, i.e. low litter size and frequency, represent a crucial finding in this species. In combination with the recorded substantial mortality of newborns, especially pups of young subordinate females (**Chapter 2**), these traits limited inclusive fitness benefits of subordinates. The constraints on group size appeared to be strong enough to limit reproduction to one pup per year per group.

In meerkats and dwarf mongooses, although groups are mainly composed of a dominant breeding pair and their first-order relatives, indirect inclusive fitness of subordinate helpers cannot explain natal philopatry and cooperative breeding behaviour alone (Clutton-Brock *et al.* 2001a; Clutton-Brock 2002). Although female units of *M. decemlineata* were generally based on mother-daughter relationships and mean relatedness within units was high, the overall reproductive output of units was presumably too low to generate sufficient indirect inclusive fitness benefits for young subordinate females. As a result, female narrow-striped mongooses dispersed from their natal unit in some cases, particularly when breeding territories in the local area were vacant (**Chapter 2**).

I found that breeding territories became available due to predation on a dominant breeding female, resulting in a strong turn-over in unit composition and a critically reduced number of adult females capable to breed (cf. **Chapter 2**, Fig. 1, unit E, year 2013). This finding shows how the impact of extrinsic factors can lead to a change in broad categories of social organisation (cf. Schradin 2013). Predation avoidance is highly pronounced in eusocial mongooses, in which the death of dominant breeders can dramatically lower the survival chances of groups, which lead to group extinction in dwarf mongooses when group size drops below five individuals (Rasa 1987a).

The determinants of male social organisation

The formation of male associations and sexual segregation except for direct approaches to receptive females for mating are the two crucial characteristics which I found in male social organisation. As in females, predation risk was indicated to play a major role for the social organisation of males. Although based on a small sample size, males suffered higher losses due to predation during the mating period, when they roamed primarily on their own (**Chapter 2**). Shared vigilance, alarm calling and dilution effects were important indicators for the benefits provided by male associations to avoid predation. Especially for young males which I observed dispersing from their natal unit, associating with older males can increase survival chances in this respect. Despite the striking differences between Malagasy tropical dry forest and the more open habitats of African group-living herpestids, the risk of predation can be assumed to be particularly high for dispersing or evicted individuals in both systems (Rood 1983a; Rasa 1987a).

Alternative hypotheses explaining male associations in other carnivores and mammals include cooperative hunting (Bailey *et al.* 2013), the formation of bachelor groups (e.g. in ungulates: Jarman 1974; Ruckstuhl 1998) and reproductive coalitions among kin. Based on the above-mentioned foraging patterns and mainly arthropod-based diet of *M. decemlineata* (Rasolofoniaina 2014), group hunting is unlikely to determine male association patterns (**Chapter 2**). Based on the observed age structure and the lack of separation of groups of young males and older, more competitive males, the concept of bachelor groups does not correspond to the observed patterns as well (**Chapter 2**).

Male coalition formation based on kinship represents another major hypothesis to explain male association patterns in carnivores, but has been studied in varying extent. Joint defence of territories (e.g. *Acinonyx jubatus*: Caro & Collins 1987) and inclusive fitness benefits for coalitions of male kin by defending the access to females against unrelated competitors (*C. ferox*: Lührs et al. 2013; *Galerella sanguinea*: Waser et al. 1994; *Herpestes javanicus*: Hays & Conant 2003; *Panthera leo*: Bygott et al. 1979; Packer et al. 1991) have been indicated as ultimate reasons determining this pattern of male social organisation. In *M. decemlineata*, the low proportion of identical haplotypes among associated males and the low average relatedness within the large majority of male associations argue against kin selection and inclusive fitness benefits for coalitions partners as a determinant for male sociality (**Chapter 3**). In particular, the tendency of increasing within-coalition relatedness with increasing association size (Packer *et al.* 1991) was not indicated in *M. decemlineata*. Additionally, spatial, demographic and behavioural observations were inconsistent with findings on slender mongooses, in which male coalitions have been investigated in some detail. There, males were found to be littermates immigrating together into another area and their ranges were exclusive from non-associated males (Waser *et al.* 1994). In contrast, *M. decemlineata* male home ranges extensively overlapped not only with associated, but also non-associated males. In addition, associated males were not littermates as a result of the low reproductive rate, i.e. a litter size of one and usually only one young which was raised per unit and year. Furthermore, male associations disintegrated in the beginning of the mating period, contradicting a potential role in the exclusion of rivals. Finally, they varied in composition among years (**Chapter 2**), while male units in slender mongooses were stable for several years (Waser *et al.* 1994). However, intra-specific variation is significant also among other species. For example, male reproductive skew in lions increased with increasing coalition size (Packer *et al.* 1991), while in slender mongooses, paternities appeared to be evenly distributed within male coalitions (Waser *et al.* 1994). Thus, the fitness consequences of male coalition formation are not universal.

The mating system of the narrow-striped mongoose

Considering the determinants of sexual segregation described above, it seems reasonable to discuss the spatial and behavioural patterns particularly in connection to the mating system. As mentioned, male spatial distribution in *M. decemlineata* indicates a strong link to a predominant roaming strategy. Due to the wide distribution of females in relatively large ranges, the potential for monopolisation and defensibility of access to females is supposed to be low (**Chapter 2**). The pattern is in accordance with predictions of socio-ecological models (Emlen & Oring 1977; Kappeler 2013), and predicts a polygynous or promiscuous mating system (see above and **Chapter 3**).

As I discussed above, behavioural aspects such as the general aggression of females towards males in order to avoid harassment appears to be a mechanism facilitating sexual segregation in *M. decemlineata*. In particular, due to asynchrony in oestrus and the seasonal receptivity of females, which is reflected in the delimited duration of the peak mating season from end July to end October and the records of births (**Chapter 2**, supplement Fig. S2), males allocate their energy expenditures to roaming in search of receptive females rather than investing in the monopolisation of particular female units. The latter situation would presumably result in higher costs related to aggressive female response and potentially to contest competition with male rivals. In particular, when considering the low litter size and survival rate of newborns in *M. decemlineata* (**Chapter 2**), only males roaming among different female units can presumably achieve sufficient reproductive fitness outcomes.

The observed adult sex ratio in the population, asynchronous oestrus in females, low potential for monopolisation, roaming of males among different female units, and additionally observed occasional male intrusions into territories of receptive females which otherwise did not show regular overlap indicate a male-biased operational sex ratio and scramble competition among males (Emlen & Oring 1977; Clutton-Brock & Parker 1992). The potential for monopolisation of reproduction by *M. decemlineata* males was relatively low, in contrast to patterns found in group-living herpestids, in which dominant males sire almost all infants (Griffin *et al.* 2003; Nichols *et al.* 2010).

The distribution of subsequent parentages by specific individuals in different seasons and the low relatedness within breeding pairs suggest that males that had immigrated from outside areas sired offspring more often than locally originating males (**Chapter 3**). Although based on a relatively small dataset, this outcome may indicate a possible role of female mate choice. In eusocial mongooses, recent evidence suggests that odor-based kin discrimination by breeding females occurs (Leclaire *et al.* 2013b). Considering the distinct sexually segregated organisation, it will be interesting to examine the existence of similar mechanism in *M. decemlineata*.

Conclusions and reflections with regard to carnivore social evolution

In the present thesis, I have demonstrated the characteristics of an unusual carnivore social organisation. Predation is the most probable determinant for gregariousness in both sexes of *M. decemlineata*. However, there are distinct sex-specific mechanisms resulting in differences in stability and genetic composition in male and female social units. I have also found indications for relatively slow life histories, especially generally low reproductive success in females.

An extensive phylogenetic reconstruction has shown that the patterns such as the one found in *M. decemlineata,* i.e. male distribution and mating strategies responding to females distributed in large ranges, represent the ancestral state in mammals (Lukas & Clutton-Brock 2013). This result is in accordance with the strong signal of sociality within the phylogeny of herpestids and euplerids, in which the group-living herpestids form a separate clade (Mungotinae) from the solitary mongooses (Veron et al. 2004; **Chapter 1**). Under a parsimonious assumption, the signal of solitary organisation has remained in the Eupleridae.

However, we can notice remarkable inter-specific variation in social patterns in mongooses. It can be assumed that the euplerids evolved under partially different selection pressures compared to several species on the African mainland, for example with regard to habitat characteristics and the co-evolution with other predators (cf. Dewar & Richard 2007). Importantly, the comparison revealed relatively slow life histories in *M. decemlineata* and other Eupleridae in contrast to the Herpestidae (**Chapter 1**). Similar patterns have been found in other mammalian groups on Madagascar, and have been related to their hyper-variable environment due to climatic unpredictability (Dewar & Richard 2007).

I conclude that *M. decemlineata* represents a transitional evolutionary level between solitary and group living. Its social organisation shows characteristics of a higher organisational level than reported from several mongooses of the ‘solitary’ clade, especially with regard to female sociality. This finding is particularly interesting considering the indicated ancestral phylogenetic signal of sociality and the apparently slow life history in comparison to many herpestids. Whether this understanding represents only an artefact of the shallow state of knowledge about many other species, or a new evolutionary hypothesis is currently unclear In his review, Rood (1986) mentioned species such as *Cynictis penicillata* (Herpestidae) or *M. decemlineata* (Eupleridae) as important candidates in the study of evolutionary transitions from solitariness to group-living. Because phylogenetic proximity and life-history traits are indicated to be better predictors of social patterns than broad ecological categories (Clutton-Brock & Janson 2012), further investigations of relatively unknown herpestid and euplerid species may provide substantial information regarding the determinants and pace of social evolution in these and other carnivores.

Outlook

Sexual segregation in organisation offers the opportunity to study the factors determining sociality in males and female separately. In general, considering the longevity of *M. decemlineata* of more than 11 years, further long-term studies would be desirable to reveal more details of life-histories, demographic patterns.

Based on the presented results of social organisation, genetic structure and reproduction, it will be also particularly interesting to examine further details about the social structure in general. Although observations of inter-individual relationships contributed significantly to deduce the factors potentially leading to sexual segregation in *M. decemlineata* such as sexual harassment and aggression between males and females, many specific subsets of behavioural interactions offer additional research opportunities. Further explicit testing of the hypotheses on social segregation between the sexes based on detailed behavioural data may shed more light on the operating mechanisms and the evolutionary outcome of sexual coercion for female mating preferences and social relationships.

With regard to the observed patterns of female unit composition, dispersal and reproductive skew, it will be particularly interesting to identify the behavioural mechanisms of female competition and the determinants of low reproduction rates in detail. Since female reproductive success was found to be largely influenced by *post partum* mechanisms, determining whether infanticide by dominant females occurs will be important. Furthermore, female dispersal is indicated to be a trade-off between benefits provided by the natal units and the potential for own breeding opportunities in vacant territories, although under the risks associated with dispersal. Thus, it will be interesting to investigate the relative impact of reproductive suppression. Connected to this topic, the existence of eviction of females would be another important aspect related to maximum sizes of units and reproductive skew, also with regard to more detailed comparisons with herpestids.

Regarding male social organisation, more details on the behaviour of association mates may reveal interesting patterns about dominance structures and factors stabilising these associations. Relating male behaviour to their relatedness may also provide additional information about the determinants of male sociality in *M. decemlineata* and allow further comparisons with other carnivore species.

The mating system of *M. decemlineata* still offers a large diversity of research opportunities. Although the general nature of inter-sexual relationships has been related to some morphological and age characteristics of males and females in a preliminary analysis (Sehner 2014), more detailed studies of additional morphological and behavioural traits and their relationship to potential mate choice and reproductive success would be highly beneficial for comparisons with the identified reproductive strategies in mongooses.

Finally, taking into account the relatively slow life histories and low reproduction in species such as *M. decemlineata*, the remaining populations are presumably subject to decline in the course of habitat loss. Considering the alarming rate of deforestation in Madagascar, more detailed knowledge about the social systems, spatial requirements, demography as well as population genetics of Malagasy carnivores is crucial with regard to conservation because they represent endemic flagship species of highly threatened, unique ecosystems.

ETHICAL NOTE

During the research within the frame of this thesis, all applicable international, national, and institutional guidelines for the care and use of animals were followed. Research protocols and capture procedures were approved by the Ministry for the Environment, Water and Forests of Madagascar, MINEEF.

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SUMMARY

The diversity of ecological and behavioural adaptations of the Carnivora makes them an exemplary group for studying patterns of mammalian social evolution. In particular, species displaying sex-specific forms of social organisation offer the opportunity for investigating sex-specific costs and benefits in order to reveal the determinants and mechanisms of sociality. The mongooses (Herpestidae) are one group of small-bodied carnivores in which studies on a small number of highly social, cooperatively breeding species have significantly contributed to the understanding of group living and reproductive skew in mammals. In contrast, much less is known on the social systems of the closest related taxon, the Malagasy carnivores (Eupleridae). However, this group provides a great potential to study the pace and mechanisms of carnivore social evolution in a comparative perspective, because it evolved in isolation on Madagascar for more than 20 myr.

In this thesis, I present the social organisation, life-history and genetic characteristics of the Malagasy narrow-striped mongoose (*Mungotictis decemlineata*) in Kirindy Forest/CNFEREF, a seasonal dry forest in western Madagascar. As a basis for inter-specific comparisons, I provide a comprehensive review summarising and evaluating the state of knowledge on the social systems and life-history traits of herpestids and euplerids and relate them to predictions of socio-ecological theory.

During field studies from 2011 to 2014, I trapped, measured, genetically sampled and individually marked 63 narrow-striped mongooses. I collected spatial, demographic and behavioural data on a total of 40 radio-collared individuals (20 males, 20 females) and their associated conspecifics during systematic tracking and census. In order to characterise the social organisation of *M. decemlineata*, I analysed the composition of social units with regard to sex and age of individuals, and their home range size and distribution. Additionally, I analysed sex ratios, mortality, and reproductive traits within the study population. Furthermore, I conducted mitochondrial DNA and microsatellite analyses based on samples of the 63 trapped individuals and further 33 ones from a previous study between 2000 and 2010. Microsatellite analyses were based on 13 loci reported from the fosa (*Cryptoprocta ferox*), which had shown to amply successfully in preliminary testing. In order to reveal the local genetic structure and dispersal patterns, I analysed haplotype diversity and distribution in males and females. Based on microsatellites, I analysed the relatedness within sexes and social units, and parentages and sibships.

I found males and females to live in small same-sexed social units. In total, I observed nine female units and 13 male associations during 497 h, collected 10,411 scans and 1,879 triangulation fixes. Female units were based on matrilines. Their members showed higher relatedness than expected by chance and comprised on average two adult females, one juvenile and one infant. They occupied exclusive territories. Their home range size (mean 90% kernel estimation: 30.4 ha) was not related to their numerical size, but larger during the lean dry season than during the rainy season. Males formed association of up to four individuals, which disintegrated during the mating period and varied in composition among years. In the large majority, associated males were not more closely related than expected by chance. Male home ranges (mean 90% kernel estimation: 63.9 ha) showed high overlap with associated and non-associated males, and encompassed those of up to four females.

Dispersal was male-biased, supported by higher haplotype diversity in males than females. Life-histories were indicated to be slow, with males dispersing at an earlier age than females. Mortality did not differ between sexes, but observations indicated that particularly solitarily roaming males were vulnerable to predation. Reproductive skew in females based on emerged pups was low, but *post partum* mortality limited successful reproduction to dominants. Paternity distribution, adult sex ratios and mating behaviour indicated mild promiscuity, with males fathering pups of different female units within the same season.

In conclusion, patterns in *M. decemlineata* followed important predictions of socio-ecological theory regarding the distribution of males and females. Anti-predator benefits probably determined gregariousness in both sexes. In contrast, kinship was not indicated as a major determinant of male sociality. The sexual segregation in *M. decemlineata* appears to be strongly related to reproductive strategies displayed in male roaming behaviour, the resulting differences in activity and sexual harassment by males and female aggression towards males. In females, occasional dispersal is indicated to be a trade-off between direct benefits of philopatric group living and opportunities for reproduction in vacant breeding territories.

In the comparative phylogenetic perspective, the sociality in *M. decemlineata* shows a higher organisational level than described for several species of the ‘solitary herpestid’ clade. However, general patterns of the mating system indicate a rather ancestral state in mammalian evolution. Characteristics of the social structure and mating system provide starting points for further research and comparisons to herpestids, e.g. regarding the intensity and mechanisms of female competition and the determinants of reproductive success as well as a potential role of mate choice.

ZUSAMMENFASSUNG

Aufgrund ihrer vielfältigen Anpassungen in Ökologie und Verhalten stellen die Carnivora eine geeignete Gruppe dar, um die Muster innerhalb der sozialen Evolution der Säugetiere zu studieren. Insbesondere Arten mit unterschiedlicher sozialer Organisation der beiden Geschlechter bieten die Möglichkeit, geschlechtsspezifische Kosten und Vorteile zu untersuchen, um die Determinanten und Mechanismen von Sozialität aufzuzeigen. Die Mangusten (Herpestidae) sind eine Gruppe kleiner Raubtiere, in der Studien zu einer kleinen Anzahl von hochsozialen Arten mit kooperativer Jungenaufzucht entscheidend zum Verständnis des Gruppenlebens und der Verteilung des Fortpflanzungserfolgs unter Gruppenmitgliedern bei Säugern beigetragen haben. Im Gegensatz dazu ist über die Sozialsysteme ihrer nächsten Verwandten, der Eupleridae (Madagassische Raubtiere) viel weniger bekannt. Diese Gruppe bietet jedoch ein großes Potenzial zur Untersuchung der Geschwindigkeit und Mechanismen der sozialen Evolution der Raubtiere in vergleichender Perspektive, weil sie sich für mehr als 20 Millionen Jahre isoliert auf Madagaskar entwickelt hat.

In dieser Dissertation lege ich die soziale Organisation, Lebenslaufstrategie und genetischen Eigenschaften des madagassischen Schmalstreifenmungos (*Mungotictis decemlineata*) im Kirindy-Wald/CNFEREF, einem tropischen saisonalen Trockenwald im Westen Madagaskars, dar. Als Grundlage für zwischenartliche Vergleiche bewerte ich des weiteren in einer umfassenden Betrachtung den Wissensstand über die Sozialsysteme und Lebenslaufstrategien der Herpestiden und Eupleriden und setze diese in Beziehung zu den Vorhersagen sozio-ökologischer Theorie.

Während meiner Feldstudien in den Jahren 2011 bis 2014 fing ich 63 Schmalstreifenmungos in Lebendfallen, vermaß und markierte diese und nahm Gewebeproben für genetische Untersuchungen. Von insgesamt 40 Individuen (20 Männchen, 20 Weibchen), die ich mit Radiosendern versehen hatte, sowie von den mit ihnen assoziierten Artgenossen sammelte ich durch systematische Radiotelemetrie und Zensus räumliche, demografische und Verhaltensdaten. Zur Charakterisierung der sozialen Organisation von *M. decemlineata* analysierte ich die Zusammensetzung sozialer Einheiten im Hinblick auf Geschlecht und Alter der Individuen und ihre Streifgebietsgröße und –verteilung. Außerdem analysierte ich das Geschlechterverhältnis, Mortalität und Reproduktionsmerkmale der Population. Des weiteren analysierte ich mitochondriale DNA und Mikrosatelliten der 63 beprobten sowie 33 weiterer Individuen aus einer vorherigen Studie zwischen 2000 und 2010. Die Mikrosatelliten-Analyse

basierte auf 13 Loci der Fossa (*Cryptoprocta ferox*), die in vorläufigen Tests erfolgreich amplifizierten. Um die lokale genetische Struktur und Abwanderungsmuster aufzudecken, analysierte ich die Haplotypendiversität von Männchen und Weibchen. Basierend auf der Mikrosatellitenanalyse untersuchte ich Verwandtschaft innerhalb der Geschlechter und sozialer Einheiten sowie Elternschaften und Geschwisterverhältnisse.

Männchen und Weibchen lebten in kleinen gleichgeschlechtlichen sozialen Einheiten. Insgesamt beobachtete ich neun weibliche Einheiten und 13 Assoziationen von Männchen in 497 h, sammelte 10,411 Verhaltensscans und 1,879 Triangulationspunkte. Weibliche Einheiten basierten auf Matrilinien. Ihre Mitglieder waren enger verwandt als unter Zufallsbedingungen erwartet und umfassten durchschnittlich zwei adulte Weibchen, ein Juveniles und ein Junges. Weibliche Einheiten behaupteten eigene Territorien. Ihre Streifgebietsgröße (90% Kernel, arithmetisches Mittel: 30.4 ha) stand nicht in Zusammenhang mit der Zahl ihrer Mitglieder, war aber größer während der kargen Trockenzeit als zur Regenzeit. Männchen bildeten Assoziationen von bis zu vier Individuen, die sich während der Paarungszeit auflösten und in ihrer Zusammensetzung zwischen Jahren variierten. In der großen Mehrheit waren assoziierte Männchen nicht näher miteinander verwandt als durch Zufall erwartet. Die Streifgebiete der einzelnen Männchen (90% Kernel, arithmetisches Mittel: 63.9 ha) überlappten stark mit solchen von mit ihnen assoziierten und nicht-assoziierten Männchen und mit denen von bis zu 4 weiblichen Einheiten. Es wanderten mehr Männchen als Weibchen ab, bestätigt durch höhere Haplotypendiversität bei Männchen als bei Weibchen. Die Lebenslaufstrategien waren überwiegend langsam, wobei Männchen in jüngerem Alter abwanderten als Weibchen. Die Mortalitätsraten unterschieden sich nicht signifikant zwischen den Geschlechtern. Beobachtungen lassen jedoch darauf schließen, dass besonders allein umherstreifende Männchen anfällig gegen Prädation waren. Der Fortpflanzungserfolg der Weibchen, gemessen an der Zahl der lebend erschienenen Jungen zeigte keine signifikante Ungleichverteilung, aber *Post-partum*-Mortalität beschränkte die erfolgreiche Fortpflanzung auf dominante Tiere. Die Verteilung der Vaterschaften, das Geschlechterverhältnis der Adulten zugunsten der Männchen und das Paarungsverhalten deuteten auf gemäßigte Promiskuität hin, wobei einige Männchen Junge in verschiedenen weiblichen Einheiten innerhalb derselben Paarungssaison zeugten.

Schlussfolgernd lässt sich sagen, dass die Muster der Verteilung von Männchen und Weibchen in *M. decemlineata* wichtigen Vorhersagen sozio-ökologischer Theorie folgten. Vorteile bei der Vermeidung von Fressfeinden bestimmten die Vergesellschaftung von Individuen in beiden Geschlechtern. Verwandtschaft war hingegen keine bestimmende Determinante der Sozialität unter Männchen. Die sexuelle Segregation in *M. decemlineata* schien stark mit Fortpflanzungsstrategien zusammenzuhängen, die sich im Umherstreifen der Männchen, daraus resultierender Aktivitätsunterschiede und in sexueller Belästigung der Weibchen durch die Männchen und darauf folgender Aggression der Weibchen ausdrückten. Bei Weibchen resultierte gelegentliche Abwanderung wahrscheinlich aus der Kosten-Nutzen-Abwägung zwischen philopatrischem Gruppenleben und der Möglichkeit der eigenen Fortpflanzung in unbesetzten Territorien.

In vergleichender Perspektive zeigt die Sozialität von *M. decemlineata* ein höheres Niveau als es für mehrere Arten der Klade der ‚solitären Herpestiden‘ beschrieben wurde. Allgemeine Muster des Paarungssystems deuten jedoch auf einen vergleichsweise ursprünglichen Zustand innerhalb der Säugetierevolution hin. Die Merkmale der Sozialstruktur und des Paarungssystems bieten Ansatzpunkte für weitere Forschung und Vergleiche mit den Herpestiden, z. B. im Hinblick auf die Intensität und Mechanismen weiblicher Konkurrenz und Determinanten des Fortpflanzungserfolgs sowie einer möglichen Rolle der Partnerwahl.

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CURRICULUM VITAE

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WORK EXPERIENCE

Since Jan 2016	**Guest scientist**, Behavioral Ecology and Sociobiology Unit, German Primate Center, Göttingen, Germany
Jan 2011-Dec 2015	**Research assistant** Department of Sociobiology/Anthropology, Georg-August University of Göttingen • **Behavioral ecological field studies, Kirindy Forest, western Madagascar** (17 months); research station of the German Primate Center; funded by the German Research Foundation (DFG) • **Research stay, Kalahari Meerkat Project, Northern Cape, South Africa**; in cooperation with the University of Cambridge, UK • Project planning and management • Third-party funding acquisition • Data collection; GIS analysis • Student supervision; teaching
Aug-Sep 2010	**Project, CEF measures,** Plan B Consulting, Neu-Eichenberg • Relocation of sand lizard populations (*Lacerta agilis*), railway Berlin-Cottbus
Jul-Sep 2009, Aug-Sep 2008 and Aug-Sep 2007	**Research internships,** European bison project, Mammal Research Institute, Polish Academy of Sciences, Białowieża, Poland • GIS-Analysis • Wildlife telemtery • Data processing
Oct 2008-Nov 2009, Sep 2006, Sep-Oct 2005,	**Internships abroad,** Bird Protection Committee, Göttingen, Germany • **Cyprus** and **Catalonia, Spain** (4 weeks each): Monitoring of illegal bird poaching (EU Directive 79/409/EWG), Data processing
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EDUCATION

Nov 2010-Dec 2015	**Doctoral studies, Department of Sociobiology/Anthropology, Georg-August University of Göttingen** Project: "Social organisation of the narrow-striped mongoose (*Mungotictis decemlineata*) in Kirindy Forest CNFEREF, Madagascar", Advisor: Prof. Peter M. Kappeler; Grade obtained: "magna cum laude"
Oct 2008-Oct 2010	**Master's studies in Biodiversity and Ecology, Georg-August University of Göttingen** Degree obtained: Master of Science (Grade A – Excellent).

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Apr-Sep 2005	**Study of medicine,** Georg-August University of Göttingen
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2004	**High school graduation: Allgemeine Hochschulreife** (general qualification for university entrance) Europaschule Theodor-Heuss-Gymnasium (grammar school), Göttingen

SCIENTIFIC FUNDING

Oct 2012-Dec 2015	Research grant of the German Research Foundation (DFG) to Prof. P. M. Kappeler, University of Göttingen, for the project „Social organisation and mating system of the narrow-striped mongoose (*Mungotictis decemlineata*)“ (KA 1082/23-1)
Jan-May 2010	Scholarship of the German Academic Exchange Service (DAAD) for a Master’s thesis abroad

PUBLICATIONS

Book chapters/studies

Kowalczyk, R., Kamiński, T., **Schneider T. C.** (2010). Influence of supplementary feeding on bison in Białowieża Primeval Forest. In: Kowalczyk R, Ławreszuk D, Wójcik JM (eds): European bison conservation in the Białowieża Forest - Threats and prospects of the population development. Zakład Badania Ssaków, Polskiej Akademii Nauk, Białowieża

Schneider, T. C. (2010). Microhabitat selection by European bison (Bison bonasus) in Białowieża Primeval Forest, Poland. Universität Göttingen, D., M.Sc. Thesis

Schneider, T. C. (2008). Influence of supplementary feeding on European bison ranging in winter in Białowieża Primeval Forest. Universität Göttingen, D., B.Sc. Thesis

Articles in scientific journals

Schneider, T. C., Kappeler, P. M. (2014). Social systems and life-history characteristics of mongooses. Biological Reviews 89:173-198.

Schneider, T. C., Kowalczyk, R., Köhler, M. (2013). Resting site selection by large herbivores – The case of European bison (*Bison bonasus*) in Białowieża Primeval Forest. Mammalian Biology 78:438-445.

Talks

Schneider, T. C. (2015) The Commitment of the Federal Government of Germany and civil society institutions to combating the causes and effects of organized poaching and the prevention of illicit wildlife trade. Information Tour at the invitation of the Federal Foreign Office. Visitors Program of the Federal Republic of Germany.

Schneider, T. C. & Kappeler P. M. (2014). Social organisation and demography of the narrow-striped mongoose. IV. Annual meerkat and mongoose meeting. University of Cambridge, UK.

Schneider, T. C. & Kappeler P. M. (2012). Social organisation of the narrow-striped mongoose: spatial and association patterns. II. Annual meerkat and mongoose meeting. Dept. of Zoology, University of Cambridge, UK.

Schneider, T. C. & Kappeler, P. M. (2011). The lost world in carnivore social evolution: social organisation of the narrow-striped mongoose (*Mungotictis decemlineata*). Talk. I. Annual meerkat and mongoose meeting. Dept. of Zoology, University of Cambridge, UK.

Schneider, T. C. (2010) Microhabitat selection by European bison (Bison *bonasus*) in Białowieża Primeval Forest. University of Hamburg.

Editorial activities

Ad hoc reviewer for *Journal of Mammalogy*

Others

Grüling, B., Gras, P., **Schneider, T. C.** www.nachhaltigwissen.de – An internet blog on topics from science and society, with a specific focus on conservation, environment and sustainable development

Tilman Carlo Schneider

DECLARATION

I hereby declare that I have written the submitted thesis with the title “Social organisation of the narrow-striped mongoose (*Mungotictis decemlineata*) in Kirindy Forest C.N.F.E.R.E.F., Madagascar” on my own and that I have not used any other than the permitted and cited sources and aids.

Tilman Carlo Schneider

Göttingen, November 2015

Signature