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Sociality in the African Woodland Dormouse



A thesis submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg in fulfilment of the requirements for the degree of Doctor of Philosophy

2017

DECLARATION

I declare that this thesis is my own, unaided work. It is being submitted for the Degree of Doctor of Philosophy at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any other University.



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ZJK Madikiza

May 23, 2017

ABSTRACT

Social systems describe the social organisation, mating system and social interactions of a species, and are revealing of the nature of how animals live and the underlying mechanisms of living alone or in groups. The social system of the African woodland dormice *Graphiurus murinus* has not been documented. The aim of my study was to investigate sociality, the mechanisms promoting sociality, and to *G. murinus* along the continuum of sociality in respect of rodents. Investigations on nest sharing in free-living woodland dormice showed that sleeping associations were common in females than males but changed seasonally (females all year round; males in breeding and winter seasons), reflecting the reproductive and thermoregulatory needs. The social structure of these sleeping associations was assessed using association indices and social network analysis. Woodland dormice exhibited a web of relationships between sex and age groups, with adult female groups and juvenile groups forming strong and exclusive relationships, while male groups showed ephemeral and weak relationships. In staged dyadic encounters of same sex dyads in captivity, females were amicable and tolerated unfamiliar females, whereas males displayed low tolerance and aggression towards unfamiliar. The three-chamber paradigm tests for sociability and social preferences revealed that both adult males and females had an intrinsic motivation to be social. However, this motivation differed by sex, with females showing a greater affinity for both strangers and unfamiliar females, whereas males showed an affinity for familiar males. Observations of huddling in female dyads revealed that, under decreasing Ta, females huddled together and combined nest material, thus changing the local microclimate and the insulation capacities of nests. In addition, long-associations were maintained even after Ta was increased, revealing that thermal challenges might promote group formation and enhance familiarity amongst females. Both my field and laboratory data suggest that woodland dormice form small seasonally transient sleeping associations. In females, limited aggression, tolerance, and nest sharing and construction under low temperatures could also lead to prolonged group-living. In males, aggression towards unfamiliar males, possibly maintains intra-sexual territoriality, yet familiarity creates tolerance, leading to group-living. Group-living in this arboreal rodent is mediated by the apparently phylogenetically constrained energetic demands of thermoregulation, coupled with an inherent need to associate with conspecifics. The level of familiarity between conspecifics or the presence of social partners facilitates group formation and is shaped by prevailing ecological conditions.

DEDICATION

Mom

Nomsa Mtimkulu

Thank you for the endless sacrifices you've made in order for me to get to where I am today.

"Kukufuphi ukuvuka …"

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This has been a bitter-sweet journey. However, I am forever grateful to the people who have been with me through it. Thank you for your presence, commitment and support towards turning my dream into reality.

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CHAPTER 1
General Introduction

Rationale for my study

This research was triggered by the lack of data on the social systems of the Glirids (family Gliridae). My over-arching aim was to position my study species, the woodland dormouse *Graphiurus murinus*, along the continuum of sociality for rodents, along the two extremes, namely "solitary" and "social", and to further understand the possible mechanisms driving its position along this continuum. As a consequence, I consider different types of social strategies potentially adopted by this species. Through this study, I will then be able to evaluate my findings with other studies on rodent species generally, thereby contributing to a better and inclusive understanding of rodent social evolution by incorporating poorly studied taxa. Below, I provide the background which is relevant to the aims and objectives of my thesis, including the definition of group-living, the mechanisms that define group-living, and the inherent benefits and costs attached to sociality.

In the following sections, I provide a summary of the current standing of sociality, focussing on the general theories pertaining to mammals generally and rodents in particular. Next, I provide an overview of social systems of the family Gliridae, summarising the findings of numerous dormice species. Finally, I provide currently available information regarding the biology of my study species, *Graphiurus murinus*, and end with the general aims of my study.

Sociality

The definition of sociality evolved over time. Lee (1994) defined sociality as a "tendency of animals to form groups or to live in groups". However, to simply define sociality as group-living is rather misleading since sociality occurs in a myriad of forms, and complex dynamics govern social groups. The latter may vary in terms of size, structure and degree of consistency (Ebensperger & Hayes 2008). Pitcher & Parrish (1993) elaborated that animals that live in groups are characterized as "a set of organisms, of the same species, that remain together for a period of time, interacting with one another to a distinctively greater degree than with other conspecifics" (p. 365). Lacey *et al.* (2003) defined social species as those that live in discrete

groups, within which there is an extensive spatial overlap among adults. Hare & Murie (2007) listed the components that exemplify sociality as follows: (1) multiple individuals that overlap in space and time, such that a social group is formed; (2) that there exist fundamental ecological and evolutionary factors promoting and maintaining group-living; (3) interactions (social behaviour) among group members that impart both benefits and costs; and (4) the emergent properties of groups themselves, and in particular, their success relative to other groups. Based on the definitions above, it appears that there is a general agreement that a certain degree of proximity in time and space between conspecifics is an essential prerequisite for grouping, with varying degrees of social interactions.

As highlighted by Lacey & Sherman (2007), one reason why it tends to be difficult to precisely define and identify the social systems of species is that the "solitary" and "social" labels are not dichotomous but rather represent endpoints along a continuum of spatial and social interactions among conspecifics, and species or even populations may fall anywhere along this continuum. Therefore, it is to be expected that variations in spatial overlap (small, intermediate, large) and social cohesions – this referring to the strength of the social ties or bonds between individuals (weak, intermediate or strong) will be present. In rodents, social systems range from mostly solitary species such as the vlei rat *Otomys irroratus* (Davis 1972) to eusocial species, such as the naked mole-rat *Heterocephalus glaber* (Jarvis 1981; Reeve & Sherman 1991; Bennett & Faulkes 2000). In some cases, this continuum may be observed among populations within a single species (intraspecific variation in sociality) as in prairie voles *Microtus ochrogaster* (Roberts *et al.* 1998) or even within a single population, as in the case of the striped mouse *Rhabdomys pumilio* (Schradin *et al.* 2012) and great gerbil *Rhombomys optimus* (Randall *et al.* 2005). This suggests that grouping (or group-living) is possibly governed by a particular set of ecological conditions, rather than phylogenetic constraints. Therefore, social systems may simply be a response to those ecological conditions, resulting in individuals shifting dynamically from solitary to group-living during the course of their life (Nevo *et al.* 1992; Jarvis *et al.* 1994; Spinks *et al.* 2000). Because group-living is interlinked with the environment and the life cycle of individuals of a species, it is thus not possible to categorize species, or individuals, as solitary or social without investigating and considering both the environment they inhabit and whether and how the timing at which group and solitary living occurs in relation to essential life history events, such as the mating period, presence and level of parental care, and occurrence and timing of natal dispersal.

In practice, an indication of group-living is based on the spatial and social interactions among conspecifics during the breeding period (Lacey & Sherman 2007). Spatially, individuals in a group are expected to demonstrate a high spatial overlap, and sharing of resting/nesting sites, e.g. Gunisson's prairie dogs *Cynomys gunnisoni* (Slobodchikoff 1984). Interactions between members of the same group are expected to differ from those with members of other groups: members of the same group are more likely to cooperate in activities, and illustrate some degree of nepotism or favouritism. For example, in plains viscachas *Lagostomus maximus*, allo-grooming has been observed among all age-sex classes within a social group but not between members of different social groups and, agonistic interactions occurred more often between members of different social groups than within a group (Branch 1993).

Models of sociality

A variety of hypotheses have been put forward to explain the occurrence of group-living in rodents and other mammals. Among these, three potential factors have been proposed as drivers of group-living in rodents, linked to phylogenetic constraints (Rowe & Honeycutt 2002), ecological constraints (Ebensperger 2001) and anatomical and life history traits. McKitrick (1993) defined phylogenetic constraints as "any result or component of the phylogenetic history of a lineage that prevents an anticipated course of evolution in that lineage" (p. 309). In other words, this hypothesis proposes that group-living will be expressed only in those lineages that share a common ancestry. For example, it has been proposed that group-living in some petrophilic rodents maybe phylogenetically constrained, in which the preference for rocky habitats by these rodents might be constrained genetically, which in turn may directly influence the degree of sociality, and therefore limit the forms of social behaviours that are observed (reviewed by Nutt 2007). In contrast, the ecological constraint hypothesis suggests that grouping in animals might be a consequence of specific environmental conditions. Therefore, this hypothesis suggests that individuals might be forced to share their space with conspecifics under particular environmental conditions, e.g. limited suitable nest sites in the striped mouse *Rhabdomys pumilio* (Schradin *et al.* 2011). Lastly, group-living may be driven by anatomical traits such as brain size and longevity of a species, with the former influencing the capability of individuals to engage in and sustain complex social relationships, and therefore shaping the degree of sociality (Dunbar & Shultz 2007). However, the causal relationship between sociality and brain size evolution is not often clear (Pérez-Barbería *et al.* 2007). Life history traits such as survival and longevity underpin

sociality in some species (Arnold & Owens 1998). High survival rates and longevity of adults has direct impacts on territory occupation by offspring, through limited breeding territories for offspring, thus leading to natal philopatry, and development of long term bonds and associations in groups, e.g. in breeding birds (Brown 1987).

When the aforementioned three evolutionary factors (phylogeny, ecological, life history) are considered, one is able to establish whether sociality among monophyletic groups is shaped by ecological constraints or whether sociality is bounded by phylogenetic history or life history traits. Additionally, when these factors are combined, environment and phylogeny can work together to connect prevailing ecological processes with historical contingency (e.g. Harvey & Pagel 1991). Emlen (1995) proposed an integrated theory of family social dynamics that seems to explain how these different factors may act together and determine animal sociality. Emlen (1995) hypothesized that the formation of family groups is essentially a consequence of natal philopatry and delayed dispersal, where descendants remain in their natal nests. Studies of the formation of social groups in rodents have largely adopted Emlen's hypothesis, emphasising the prominent role of natal philopatry in group formation (Lacey & Sherman 2007). Emlen's theory incorporates three major principles or concepts (i.e. ecological constraints, reproductive skew, kin selection) which are discussed below.

***Ecological constraints*.** This theory maintains that group formation can take place when the costs associated with dispersal are so high that offspring are forced to be philopatric (Emlen 1982; Koenig *et al.* 1992). Under such conditions, offspring gain higher fitness by continuing to stay in their natal areas rather than dispersing and establishing new territories. As an example, when offspring are born into good quality habitats that provide access to resources, such as food and mates, whereas the surrounding habitats are of poor quality, then offspring increase their fitness by remaining in their natal territories (Emlen 1982). However, the benefits of philopatry theory (Stacey & Ligan 1991) claims that it is the intrinsic benefits (e.g. predator defense, access to resource, cooperative foraging) of living in groups that encourage philopatry rather than dispersal. In both scenarios, this leads to the formation of kin groups.

***Reproductive skew*.** Social species are often classified according to their reproductive structure, whereby all group members take part in reproduction (i.e. egalitarian, low skew or plural breeders), versus groups where reproduction is limited to a single individual of each sex (i.e. despotic, high skew, singular breeders) (Keller & Reeve 1994). The principle idea behind the reproductive skew theory is that, following the formation of social groups due to natal philopatry and ecological constraints, the probability of these groups remaining together

or disbanding will be determined by the availability of breeding opportunities outside natal groups. This further suggests that competition for breeding opportunities will directly impact on the extent of reproductive skew, the cost and benefits to group members and, as a consequence, group stability (Emlen 1995).

***Kin Selection*.** Kin selection has been predicted to be the main driver of sociality (Solomon 2003), and that animal social theories are underpinned by kin selection and inclusive fitness (Emlen 1995). This theory maintains that due to formation of groups through natal philopatry, groups should be made up of kin mainly (Emlen 1995). Under such conditions, it is expected that group members will increase their indirect fitness through enhancing a close relative's direct fitness. This can be achieved by providing care to a relative's offspring, which share some genes with the individual providing care (Hamilton 1964). Therefore, the process by which group formation takes place has clear implications on the kin structure and the inclusive fitness.

Emlen's ecological constraints hypothesis does not have universal support. Some species, such as the striped mouse *Rhabdomys pumilio*, is group-living during the breeding season when population density is high, but leave groups and start solitary breeding when population density is low (Schradin *et al.* 2010). In other species, natal philopatry is not the only mechanism leading to formation of social groups. Group formation may exist through attraction to the same or similar stimulus (Parrish *et al.* 1997), and mutual attraction of individual members (Parrish *et al.* 1997; Romey 1997) in individuals of different ages, as a consequence, groups are comprised of non-kin. For example, in the common degu *Octodon degus* social group size is not correlated with population density or with the quantity or quality of burrow systems (Ebensperger *et al.* 2011).

Fitness benefits and costs of sociality

One hypothesis proposed to explain group-living in most mammals is that it may be to defend resources (Wrangham 1980; Macdonald 1983). For example, per capita resources (feeding areas, space, burrows) secured by individuals should be greater in group-living species as compared to solitary species. This therefore means that an individual is much more likely to secure resources in groups. For example, group sizes increased in Gunnison's prairie dogs *Cynomys gunnisoni* when food was experimentally increased (addition of seeds); the feeding territory of each rodent group contracted (Slobodchikoff 1984).

A second hypothesis proposed to explain sociality in rodents is the predatory risk avoidance (Alexander 1974; Hoogland 1995; Armitage 1998). This means that group-living

rodents have a greater chance of surviving predation than they would if they were living solitarily, through the so called "many eyes effect" (Hoogland 1981; Elgar 1989), and employing alarm calls, such as in Gunnison's prairie dogs *Cynomys gunnisoni* (Slobodchikoff 1984) and plains viscachas (Branch 1993). In addition, group-living individuals are able to hide among other group members (i.e. 'selfish herd effect') (Hamilton 1971), as has been shown in black-tailed prairie dogs *Cynomys ludovicianus* and yellow-bellied marmots (Armitage 1962; Hoogland 1981). Finally, prey animals may aggregate so as to create a "dilution effect" and confuse the predator, hence decreasing their own risk of being preyed upon, as found in the case of degu *Octodon degus* (Ebensperger & Wallen 2002).

A third hypothesis, the social thermoregulation hypothesis (Canals *et al.* 1989), states that endothermic species will nest communally to reduce energy expenditure on thermoregulation. This hypothesis predicts that the frequency of communal nesting will increase with decreasing ambient temperature (reviewed in Ebensperger 2001). Support for the social thermoregulation hypothesis in rodents is provided by evidence of increases in communal nesting during winter in many species and decreases in energy expenditure of individuals when huddling (reviewed in Ebensperger 2001), as found in striped mice (Scantlebury *et al.* 2006; Schradin *et al.* 2006), flying squirrels *Glaucomys volans* (Thorington & Weigl 2010), Alpine marmots *Marmota marmota* (Arnold 1988), and Siberian hamsters *Phodopus sungorus* (Jefimow 2011).

An important component of huddling is tolerance among participating conspecifics (Barash 1974). In many group-living rodents, such as marmots (Rausch & Rausch 1971; Barash 1973; Holmes 1984), huddling occurs in very large groups usually with very close relatives. However, several studies have shown that social huddling with non-related individuals may exist in some species, for example in deer mice *Peromyscus maniculatus* (Andrews & Belknap 1986) and striped mice (Schradin *et al.* 2006). There is evidence that even species that usually live solitarily (e.g. shrews and voles) engage in social huddling occasionally under cold stress (Webster & Brooks 1981; Hays & Lidicker 2000), highlighting a need for mutual tolerance and the emergent benefits of huddling.

While group-living offers many benefits to animals, there are also costs attached to living and sharing the environment with other individuals. For example, group-living can increase exposure to parasites and disease (Bryant *et al.* 2002), increase predation risk, and cause misdirected parental care (Alexander 1974; Barash 1974; Hoogland 1995). Another important disadvantage to grouping is reproductive competition (Alexander 1974; Ostfeld 1990), defined as a decrease in the reproductive output of an individual due to the presence of

conspecifics (Schradin *et al.* 2010). Reproductive competition is possibly the main reason why social animals may choose solitary living (Schradin *et al.* 2010).

Ebensperger & Blumstein (2007) mentioned that reproductive competition could involve conspecifics being chased out of groups during the breeding season, as well as reproductive suppression through behavioural, hormonal and olfactory mechanisms, and killing of offspring. Infanticide is perhaps the greatest cost for group-living animals. For females, infanticide by other lactating females is common in species where communal nesting takes place, such as in striped mice (Schradin & Pillay 2003; Schradin *et al.* 2009), white-footed mice *Peromyscus leucopus* (Wolff & Cicirello 1991; Jackquot & Vessey 1994), deer mice *Peromyscus maniculatus* (Millar & Derrickson 1992) and black-tailed prairie dogs *Cynomys ludovicianus* (Hoogland *et al.* 1989; Hoogland 1995). Infanticide by group-living females is apparently a strategy to avoid diverting parental effort and resources towards genetically unrelated offspring (Pierotti 1991). This is the case in highly social species, where several females are spatially clumped (e.g. bats; Kunz & Ebensperger 1999). For males, infanticide has been linked to the sexual selection hypothesis, which suggests that infanticide is a form of male-male competition, since killing a rival's offspring increases the killer's fitness or relatedness in the population, while reducing the fitness of rivals (Hrdy 1974).

Research on sociality in rodent species has mainly focused on explaining the benefits of group-living. Many studies have focused on between population variation in sociality in order to explain the adaptive benefits of group-living in different geographic locations, but have not always considered within population variations in sociality, such as the existence of kin groups or individual changes in social behaviour and sociality (but see Schradin *et al.* 2010). Studies within populations will reveal not only whether sociality changes under different environmental conditions but also whether the social system is not fixed but can change flexibly, independent of genetic changes in the population (Schradin *et al.* 2010).

Group-living in dormice

Observations of dormice forming groups are common. Group-living dormouse species are diverse geographically and within genera, and include the edible dormouse *Glis glis* (Pilastro 1992; Marin & Pilastro 1994; Scinski & Borowski 2008; Fietz *et al.* 2010; Koppmann-Ruf et al. 2012; Sevianu & David 2012), common dormouse *Muscardinus avellanarius* (Likhachev 1966; Morris *et al.* 1990; Bright & Morris 1996; Juškaitis 1997), garden dormouse *Eliomys quercinus* (Bertolino *et al.* 2007; Viñals *et al.* 2017), forest dormouse *Dryomys nitedula* (Juškaitis & Keturka 2016), Japanese dormouse *Glirulus japonicus* (Kawamichi *et al.* 2000;

Shibata *et al.* 2004), and African woodland dormouse *Graphiurus murinus* (Kingdon 1974; Madikiza 2010; Madikiza *et al.* 2010a, 2011; Madikiza & Do Linh San, in prep.).

In the woodland dormouse, adults of both sexes have been found in a single nest at the same time in different parts of its geographic range, namely East Africa (Kingdon 1974) and South Africa (Madikiza 2010). A population in a riverine *Combretum* forest in South Africa displayed both same-sex and opposite-sex home range overlaps (Madikiza *et al.* 2011), and evidence exists that individuals may share nest boxes with conspecifics throughout the year, although this was more apparent during the hibernation and reproductive seasons (Madikiza *et al.* 2010a; Madikiza & Do Linh San, in prep.). However, several studies in southern Africa suggest a lack of group-living in the genus *Graphiurus*. Ansell (1960) claimed that both free-living woodland dormouse and the rock dormouse *G. platyops* are primarily solitary. Field studies on the spectacled dormouse *G. ocularis* in the Western Cape have revealed territorial encounters accompanied by loud vocalisations, teeth bearing, raised claws and bushy tails (Channing 1984; Van Hensbergen & Channing 1989).

Some potential benefits and costs of group-living in dormice

Dormice aggregations may be linked to thermoregulation. One study suggested that the reason male edible dormice form aggregations is to assist in reproductive activities, such that they may utilize huddling to counterbalance high thermoregulatory costs associated with reproductive activity (Fietz *et al.* 2010). In the common dormouse, juveniles hibernate within home ranges of adults, and in some cases, with the adults (Juškaitis 1997). Similarly, in the woodland dormouse, winter aggregations of torpid adult individuals have been recorded in experimental nest boxes (Madikiza 2010).

It has been hypothesized that female dormice may form groups to increase their reproductive success. In a free-living population of edible dormice, breeding females communally nursed their pups (Pilastro 1992; Marin & Pilastro 1994; Sevianu & David 2012), this occurrence has further been observed in the forest dormouse *Dryomys nitedula* (Juškaitis & Keturka 2016). Non-breeding female edible dormice also raise their younger siblings in a communal nest, possibly to gain maternal care experience (Pilastro *et al.* 2006). Similarly, aggregations by females before, during and after the mating season (mostly in association with one or several young) were observed in the woodland dormouse (Madikiza *et al.* 2010a). In the garden dormouse one to three females were found together with different sized litter in nests (Viñals *et al.* 2017).

The African woodland dormouse *Graphiurus murinus*

The African woodland dormouse *Graphiurus murinus* is a small (24–34 g) arboreal forest dwelling rodent. It has a uniform grey to buffy-grey pelage with a buffy white underbelly. It is characterised by a grey bushy tail which is shorter (58 to 94 cm) than the head-body length (78 to 113 cm) (Skinner & Chimimba 2005). Sexual dimorphism is not distinct in the woodland dormouse (de Graaff 1981; Madikiza 2010). The woodland dormouse is arboreal and nocturnal, with peak activity concentrated around 20:00 to 21:00 (Lombard 2014). It is largely insectivorous with frugivory supplementing the invertebrate dominated diet (Lamani 2014).

Phylogeny

The African dormouse (*Graphiurus*) is classifed into the subfamily Graphirunae and based on morphological (Wahlert *et al.* 1993) and molecular (Montgelard *et al.* 2003) characteristics. *Graphiurus* belongs to the family Gliridae. Even though the number of species has varied over the years, this genus consists of 15 described or recognised species (Monadjem *et al.* 2015), which were once classified into four subgenera *Aethoglis, Gliriscus, Claviglis* and *Graphiurus* (Pavlinov & Patapov 2003; also reviewed in Holden 2005) all restricted to Sub-Saharan Africa. Recently, cranial and middle-ear morphology indicated that there was a divergence early in the evolution of African dormice, when first *G. nagtglasii* and then *G. crassicaudatus* separated from the remainder of the graphiurines (*angolensis, christy, kelleni, lorraineus, murinus, ocularis, parvus* and *surdus*), thus leading to the graphiurines being regarded as a monophyletic group (Pavlinov & Potapova 2003; Holden 2005). Based on this evolutionary evidence, the separation of the Graphiurinae into three subgenera was recognized: 1) *Aethoglis,* represented by *G. nagtglasii*; 2) *Claviglis,* comprised of *G. crassicaudatus*; and 3) *Graphiurus,* which incorporates the remainder of the graphiurine species (Pavlinov & Potapova 2003).

Karyotypic analyses show that woodland dormice have a diploid number of chromosomes of 2n = 46 (Taylor *et al.* 1994). Similar findings were reported by Kryštufek *et al.* (2004) for two populations in the Eastern Cape Province (i.e. Great Fish River Reserve; where the present study was conducted and Hogsback; 100 km from the Great Fish River Reserve), South Africa. However, Tranier & Gautun (1979) found the diploid number of chromosomes of *G. murinus* to be 2n = 76. Clearly, a systematic revision of the *G. murinus* species group is therefore needed.

Graphiurus species are distributed and restricted to the south of the Sahara Desert (Kingdon 1997; Monadjem *et al.* 2015). Six recognized *Graphiurus* species occur in southern Africa, including: 1) *G. microtis*, which is widespread in the savannah zone, but missing in West Africa; 2) spectacled dormouse *G. ocularis*, which is restricted to the southern parts of South Africa; 3) the lesser savannah dormouse *G. kelleni*, which occurs throughout the savannah zone, but lacking in the southern savanna of Botswana , Namibia and South Africa; 4) the rock dormouse *G. platyops*, is variably distribute in the north-eastern savannas of southern Africa; 5) *G. rupicola* occurs along the escaprpment of Namibia forming a long narrow belt into South Africa; and 6) the African woodland dormouse *G. murinus*, which is very widespread (Figure 1), occurring from eastern to southern parts of the African continent (Reviewed by Monadjem *et al.* 2015).



Figure 1. Geographic distribution of the African woodland dormouse (*Graphiurus murinus*) (after IUCN 2016).

The African woodland dormouse distribution range is in montane or temperate regions (Monadjem *et al*. 2015), and it is highly characterised by woodland and forests, where it uses tree holes of old *Acacia* (Smithers & Wilson 1979) and *Combretum* trees (K. Madikiza pers. obs. 2004–2012) as nesting sites (Kingdon 1974; Skinner & Chimimba 2005, Lamani *et al.* 2013). It has also been collected in Afromontane forests (Qwede 2003; Kryštufek *et al.* 2004).

Reproductive biology

Woodland dormice are seasonal breeders, starting from October (austral spring) up to the austral summer in February (Madikiza 2010), and seem to be associated with high availability and abundance of fruits, insects and high rainfall (De Graaff 1981). Trapping studies in two populations of woodland dormice by Qwede (2003) and Madikiza (2010) reported that pregnant females and scrotal males were exclusively trapped from October to February, indicating that young are born during summer, supporting observations reported by other authors (Ansell 1960, De Graaff 1981, Wirminghaus & Perrin 1993). After gestation of 24 days, females in natural populations give birth to 3–6 young (Lynch 1989), with a body weight, head–body length and tail length of 3.5 g, 40 mm and 18 mm respectively Kingdon (1974). However, observations that some adult females can produce up to two litters six to eight weeks apart, and different females came into oestrus at different times, thus indicating asynchronous receptivity in females, has been noted (Madikiza 2010). Allen 7 Loveridge (1933) reported occurrences of females with subadualts, thus indicative of tolerance between mothers and weaned offsprings.

Physiology

Of relevance to my study is the heterothermy that occurs in members of the family Gliridae, characterised by communal huddling, multiple-day torpor bouts, and hibernation under low ambient temperatures or in response to food deprivation (Ellison & Skinner 1991; Webb & Skinner 1996; Whittington-Jones & Brown 1999; Mzilikazi *et al.* 2012). Field studies of woodland dormice support the occurrence of winter and summer torpor (Madikiza 2010). The species is known to huddle and aggregate in torpor groups of 5–10 conspecifics in nest boxes (Madikiza 2010), where individuals were found torpid in nest boxes from end autumn (May) and throughout winter (August), when the minimal monthly temperature reached below 4 °C. Further, field studies also indicated that woodland dormice did not hibernate throughout winter, but rather entered into prolonged torpor bouts lasting up to 8 days, by lowering body temperatures to a minimum of 2.5 °C (Mzilikazi *et al.* 2012). Winter aggregations and

huddling in nests seems to reduce their thermoregulatory demands in winter. Furthermore, these findings led me to ask whether woodland dormice preferentially nested with (particular) individuals when ambient temperatures were low, and does a declining ambient temperature trigger the formation of winter groups (aggregations) in the species?

Social organisation and mating system

Woodland dormice can be described as primarily solitary (Ansell 1960). However, young adults and juveniles were trapped together in one trap, indicating that they possibly forage together or not too far apart from each other (Madikiza 2010). In East Africa, 11 adult male and female woodland dormice were found in a communal nest (Kingdon 1974). In South Africa, two or more adults of both sexes have been observed sharing nest boxes throughout all seasons, and this was more prominent in winter and breeding seasons (Madikiza 2010; Madikiza & Do Linh San, in prep.).

During the nursing period, sometimes, 1–3 adult females with young from one to two litters shared a nest box (Madikiza 2010). However, the reasons for these aggregations are yet to be established, and it is unclear whether there is any allo-parental care. Woodland dormice have extensive same- and opposite sex home range overlap throughout the year, which is more prominent before and during the breeding season. Madikiza *et al.* (2012) hypothesised that the species is promiscuous, based on home range overlaps and space use by both males and females.

While the social behaviour of woodland dormice is unknown, the previous findings are suggestive of group-living tendencies in woodland dormice and that the formation and reasons for groups may change spatio-temporally (Madikiza 2010; Madikiza *et al.* 2011). Woodland dormice are an important experimental subject for quantitative studies on sociality because of inconsistent reports of its sociality in the literature (solitary) and from some cursory field research (group-living during some periods) and anecdotal reports. As a model of sociality, woodland dormice might offer the opportunity to assess whether group-living is a constant feature of the species, if it is driven by environmental conditions, or rather a result of tolerance between familiar and unfamiliar individuals of both sexes, without the need for extraneous (e.g. environmental) drivers.

Motivation and aims of my study

Quantitative information about dormouse aggregation or social behaviour has been obtained in the edible dormouse (Pilastro 1992; Marin & Pilastro 1994). The one study on *G. murinus* simply inferred sociality based on conservative capture-mark-recapture methods or simultaneous locations (spatial relationships) of individuals in nest boxes (Madikiza 2010). These techniques do not provide information about whether dormouse groups are formed through attraction to a common resource or through individuals are inherently attracted to one another, regardless of resources. This means that the primary mechanisms that drive group composition or formation are unknown in woodland dormice, as well as the function or role of the aggregations.

The overall aim of my study was to establish the social system of the woodland dormouse by adopting a number of different approaches, focussing on the different aspects that may lead to group-living. The first two data chapters (Chapters 2 and 3) are based on trapping, radio-tracking and nest box monitoring of a free-living woodland dormouse population from the Great Fish River Reserve (Eastern Cape, South Africa). In Chapter 2, I documented the sleeping site use of dormice in order to determine the patterns of sleeping associations. In Chapter 3, I used the social network analysis to assess the social structure of the study population, thus revealing the patterns of social relationships that occur between different sex and age groups.

In my behavioural experimental chapters, the woodland dormice used originated from free-living populations in the Eastern Cape Province, South Africa. A total of 28 adult dormice (15 males, 13 females) were trapped and removed from five areas. Both males and females were used for the third and fourth data chapters (Chapters 4 and 5), while only females were used for the final data chapter (Chapter 6). Individuals had a rest period of 2 months between each re-use experiments.

In Chapter 4, I assessed the elements (e.g. amicable and aggression) of intra-sexual social behaviour of the woodland dormice using dyadic social interactions to gain insight into the causal factors of a social system. In Chapter 5, I ascertained whether there was an intrinsic motivation to be social and whether this motivation was modified through familiarity. Finally, in Chapter 6, I tested whether thermal challenges modified the social behaviour in female woodland dormice, thus promoting group-living, as proposed by the socio-thermoregulation hypothesis (Ebensperger 2001).

Layout of the thesis

This thesis is made up of seven chapters: an introductory chapter (Chapter 1), five data chapters (Chapter 2–6), exploring the themes defined above, followed by a main discussion and conclusion chapter (Chapter 7). All my data chapters are written in the format of a manuscript, with the intention to publish. Each data chapter has its own reference list. Unavoidably, there is slight to extensive repetition of material between chapters. The tables and figures of each chapter are numbered individually per chapter, and page numbers run throughout the thesis.

List of Terms

Sociality: a combination of the proximate and ultimate processes that result in the existence or absence of social groups.

Social behaviour: interactions among group members that impart both benefits and costs, and these interactions can be used as measures (metrics) to assess the nature of sociality.

Social network: measuring and charting of social interactions in space and time, reflecting the relationships between individuals, and the overall social structure of a particular population.

Social structure: the nature and patterns of social interactions between individuals.

Social system: describes how animals live in time and space, spanning solitary to group-living species.

Social organization: the demography of a social system in space and time, such as the number of individuals (group size), age structure and sex ratio.

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CHAPTER 2

Sleeping Associations in the African Woodland Dormouse *Graphiurus murinus*

Abstract

The tendency to form associations with conspecifics has been recorded in numerous animal species. Sleeping associations are particularly crucial in understanding sociality because several social activities (e.g. huddling, rearing of young, and possibly mating) take place within the nest and these may serve as a precursor to group-living (i.e. sociality). The African woodland dormouse *Graphiurus murinus* is an arboreal rodent (family Gliridae) that exhibits extensive intra- and intersexual home range overlap, and in which sharing of artificial nest boxes has been recorded throughout the year. Here, I studied the demographic and seasonal patterns of sleeping associations in a riverine *Combretum* forest (Great Fish River Reserve, South Africa), where dormice had access to natural sites only (tree trunk and branches) or both natural sites and nest boxes. I established the sleeping locations of 68 radio-collared dormice (21 adult males, 26 adult females, 21 juveniles) on an average of 47 days (range 8–174) from June 2010 to December 2012. I obtained 3193 locations (70% in natural sleeping sites and 30% in nest boxes) and recorded 390 sleeping site associations between an average of 2.18 (range 2–4) radio-collared dormice; 73% of these associations comprised adult females and 47% adult males. As predicted, throughout the year, females (24.6%) showed a slightly higher, but statistically significant, percentage of associations than males (20.9%). This study confirmed that male–male sleeping associations (common in a previous nest box study) take place almost exclusively during the mating season (92%). As expected, male–female sleeping associations were particularly high during the mating season (63%), but they were also recorded in autumn (24%) and winter (12%). Contrary to my expectations, juveniles did not only form sleeping associations with adult females (with females present in 65% of adult–juvenile interactions), but also with adult males (44%). Juvenile–juvenile associations were common (15%) and did not vary from summer to winter (no juveniles could be tracked in spring). With exception of male–male groups, high frequency of sleeping associations between all other main combinations of individuals were observed in winter, probably for thermoregulatory benefits. In conclusion, woodland dormouse sleeping

associations changed seasonally by sex but not by age, likely reflecting the changing reproductive and thermoregulatory priorities of the species.

Keywords: Nest sharing, resting site, seasonal variations, sociality, social huddling

Introduction

Individuals of many animal species have a tendency to form associations with conspecifics at some time during their lives (Lott 1991). The close proximity of conspecifics facilitates social activities (e.g. mating, huddling), leading to familiarity, and ultimately creating stable social relationships (Smolker *et al.* 1992). These social relationships can be described by the level (e.g. frequency) at which social interactions take place, their form (type and intensity) and the sequential patterns of social interactions between individuals (Hinde 1976).

Sociality (both loose aggregations as well as structured groups), affords individuals the opportunities to interact with conspecifics. Being in a group may also increase direct fitness of individuals, and the fitness gained will largely depend on the difference between the costs and benefits derived from living in close proximity to conspecifics (Krause & Ruxton 2002). For example, group-living individuals may profit from cooperative vigilance (many eyes hypothesis), reduced predation risk (dilution effect; Williams 1966), social thermoregulation (Ebensperger 2001), better access to resources (Pitcher *et al.* 1982) and social learning by means of interactions with conspecifics (Brown & Laland 2006). At the same time, under different environment conditions, detrimental effects of living in close proximity to other individuals may lead to costs, such competition for resources (e.g. food and mates) and increased probability of parasite and disease transmissions (Côté & Poulin 1995).

Environmental factors can explain the distribution and patterns of association of adult males and females in different taxa (reviewed in Ebensperger 2001). For example, the availability and distribution of suitable shelter and food, and predation risk will shape sociality (Lott 1991; Travis *et al.* 1995). Suitable resources especially when clumped might attract conspecifics to an area (e.g. degus *Octodon degus*, Ebensperger *et al.* 2012), leading to group-living. On the other hand, associations can also occur when conspecifics are constrained by environmental (ecological) factors with or without fitness benefits, for example, when sleeping sites are a limiting factor. In the grey mouse lemur *Microcebus murinus*, sleeping sites were found to be a limiting resource for females leading to group-living (Lutermann *et al.* 2010). Irrespective of these external forces leading to associations at

sleeping sites, sharing of sleeping sites may lead to an increased social association, tolerance and familiarization when individuals are inactive.

Sleeping site associations are important for understanding the social behaviour of animals, because most social activities, such as mating, huddling and rearing of young, take place within the nest (Shafique *et al.* 2009). These social activities in nests may serve as a foundational basis to sociality (Shah *et al.* 2003; Lancaster *et al.* 2006) by providing benefits that increase fitness. Association at sleeping sites could also have physiological advantages. For example, in heterothermic species such as the grey mouse lemur *Microcebus murinus*, associations between conspecifics at sleeping sites can potentially reduce heat and water loss from the body under unfavourable environmental conditions (Perret 1998). These benefits could therefore be the trigger that encourages reciprocal acceptance amongst conspecifics that share sleeping sites, and as a consequence facilitating familiarity and cooperation (i.e. two or more conspecifics that engage in activities, where group members benefit more than lose).

Association in nests has been documented in many dormice species. In free-living edible dormouse *Glis glis*, two or even three breeding females share a nest and communally nurse their pups (Pilastro 1992; Marin & Pilastro 1994). Pilastro *et al.* (1996) suggested that breeding females and offspring nest communally, and as a consequence, young females might gain experience in rearing of siblings, and offspring have an advantage of using their mothers home ranges prior to dispersal (Marin & Pilastro 1994). Male aggregations have also been observed in the edible dormouse, and these aggregations might compensate for costs linked to reproductive activity by providing thermoregulatory advantages (Fietz *et al.* 2010).

In a previous study, I investigated the sharing of artificial nest boxes in free-living African woodland dormice *Graphiurus murinus* in a riverine *Combretum* forest (Great Fish River Reserve, South Africa; Madikiza 2010). Nest box sharing between two or even more individuals was observed during all seasons. Sleeping groups of different age and sex groups were recorded. Sleeping groups comprised of at least one adult male and one adult female were recorded only before and during the mating season. Male–male associations in nest boxes were high before and during the mating season as well, and declined drastically afterward. During the nursing period, sometimes 1–3 adult females with young from one to two litters shared a nest box. After the nursing period, aggregations composed of males and young were recorded. An analysis that included both live trapping and nest box use data revealed extensive intra- and intersexual home range overlaps, suggesting that woodland dormice might have a promiscuous mating system (Madikiza *et al.* 2011). Besides nest boxes, radio-tracked woodland dormice utilised natural cavities in trees, especially *Combretum*

caffrum, trunks and branches as their main sleeping sites (Lamani 2011). Higher sleeping site fidelity was observed during the hibernation period in winter (June–August) compared to the mating season (October–November). Females used more natural sites in winter than nest boxes and nest box use increased during the mating season. Males generally used more sleeping sites than females and exhibited lower sleeping site fidelity than females during the mating season (Lamani 2011). Because the data on sleeping site associations were based on nest box occupation, it is unclear whether the observed patterns reflect what would have been observed in natural sleeping sites – with dormice possibly associating more or less often than usual in artificial sites, depending on the attractiveness of such a resource. In addition, because dormice behaviour could only be studied when they used nest boxes, only a subset of the possible sleeping site locations was obtained for each of the marked animals.

In the current study, I expanded on my previous findings and used radio-tracking to study the demographic and seasonal patterns of sleeping site associations of woodland dormice in both natural and artificial sleeping sites. I focussed on the frequency of associations (vs. sleeping alone) and sexual/age categories of associations, which has not been previously studied. Based on prior field observations (see above), I predicted that: 1) adult females would show a higher frequency of sleeping associations than adult males, and this throughout the year; 2) woodland dormice would exhibit high frequency of sleeping associations during winter for thermoregulatory benefits; 3) male–male and 4) male–female sleeping associations would only occur during the mating season (spring); and 5) juveniles would only form sleeping associations with adult females.

Materials and methods

Study area

This study was conducted in the Andries Vosloo Kudu Nature Reserve (E 26.675430, S 33.126846; altitude: 300 m a.s.l.), part of the Great Fish River Reserve complex, East Cape Province, South Africa. The study site (6 ha) was located in a dry riverine *Combretum* forest dominated by stands of African bush willow *Combretum caffrum*. This tree species is prone to rotting from within, resulting in numerous holes and hollows which provide potential nesting sites for arboreal animals (K. Madikiza pers. obs.). The riverine forest is fed by an underground water table which forms a narrow belt (<100 m wide) along the riverbeds and supports several other tree species, including *Olea europaea* ssp. *africana*, *Ziziphus mucronata*, *Maytenus heterophylla* and *Rhus* spp. On both sides of the riverbed, the study

area is bordered by relatively large expanses of bush clump karroid thicket, a semi-open habitat composed of *Rhus* spp. and *Scutia myrtina* bush clumps and a karroid herbaceous layer.

The study site was divided into two sections by a road which passed through the forest: the north-western part (2.5 ha) and the south-eastern part (3 ha) (Figure 1). The north-western part contained 80 wooden nest boxes that were installed sequentially between 2003 and 2010 for studies of the population biology, nest box use and resting site ecology of woodland dormice (Madikiza 2010; Lamani 2011**).** Nest boxes were set randomly and spaced irregularly in the 2.5-ha section of the riverine forest.

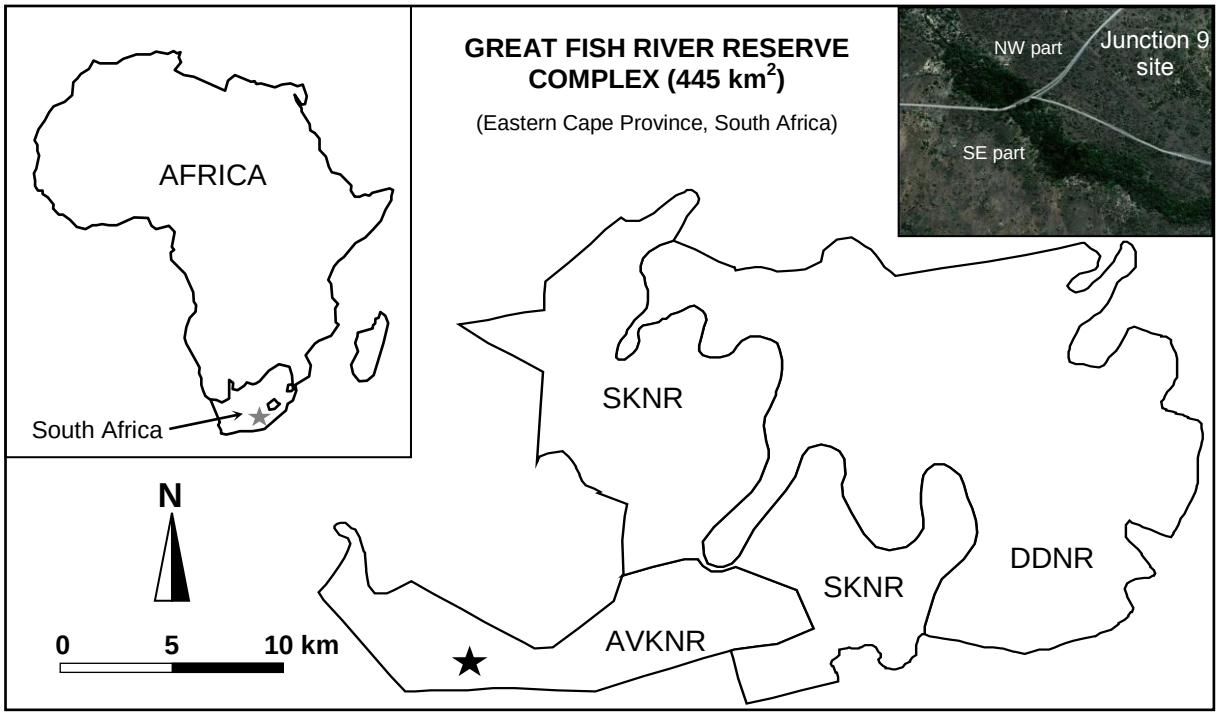


Figure 1. Map showing the location (small grey-shaded star in the upper left-hand side inset) and the structure of the Great Fish River Reserve Complex. The location of the "Junction 9" study site is indicated by a large black star. The upper right-hand side inset shows an aerial view of the 6-ha study area – a riverine *Combretum* forest of ca. 100 m wide and 600 m long. The north-western (NW) part that contained 80 nest boxes is separated from the south-eastern part (without nest boxes) by a gravel dirt road. African woodland dormice *Graphiurus murinus* can move freely between both parts. AVKNR: Andries Vosloo Kudu Nature Reserve; SKNR: Sam Knott Nature Reserve; DDGR: Double Drift Game Reserve.

Nest boxes were constructed of pine wood, approximately 2 cm thick, with internal dimensions (B × L × H) of 11.5 × 13 × 12 cm. Nails were fixed on trees and nest boxes were hung on nails by a wire sling, with the entrance hole facing the tree trunk, so as to be more accessible to small mammals climbing the tree or branch. This design was also intended to

deter birds from entering by obstructing their direct line of flight to the entrance hole (Morris *et al.* 1990). Two transverse spacing bars, above and below the entrance hole, held the box about 2.5 cm clear of the tree to which it was attached, allowing dormice to access the nest boxes easily. The south-eastern part, on the other hand, did not contain any artificial nest boxes and dormice could only sleep in natural sites (i.e. inside tree branches and trunks, or exceptionally in burrows). Except for the possible, and unpredictable, influence of nest boxes on sleeping site association patterns, I had no reason to predict any potential additional effects as the habitat was similar in both parts.

Live trapping and age and sex determination

I trapped woodland dormice using Sherman folding aluminium traps (H. B. Sherman Traps, Tallahassee, Florida, USA) (B × H × L: 8 × 9 × 23 cm). Traps were baited with a mixture of rolled oats and sunflower oil and set randomly in trees and on logs during late afternoons. To reduce mortality during cold months, cotton wool was placed inside the traps. Trapping sessions were carried out over three consecutive nights.

I transferred trapped woodland dormice into a plastic bag and weighed them to the nearest gram using a Pesola spring balance (Pesola, Baar, Switzerland). Dormice were classed as pups (1–15 g in spring and summer), juveniles (16–25 g in summer) or adults (generally >25 g throughout the year), following Madikiza (2010). I sexed adults by visually inspecting the ano-genital distance (much shorter in females) and determining the presence or absence of descended testes (during the mating season). The sex of juveniles could not always be established with certainty, and therefore juveniles were regarded as a single group in this study. Dormice first captured as pups or juveniles were considered as adults once they had reached their first spring (1st September) and became members of the reproductive cohort. The sex of these individuals would then be confirmed or determined if they were re-trapped as adults. The reproductive status was recorded as follows: males – scrotal (testes descended into the scrotal sac) or non-scrotal (testes in abdominal cavity); females – vaginal orifice perforated or imperforated.

Based on the high trapping effort and recapture success (nearly 100%), and the fact that adult woodland dormice are highly mobile and “trap-happy”, I estimated that 90% of the resident adult dormice in my study population could be marked and monitored during the study period (K. Madikiza unpubl. data). An unknown but possibly substantial number of juveniles were probably predated upon, died of other natural causes or dispersed before they could be trapped.

Radio-collaring and sleeping site determination

I collected data on sleeping associations from June 2010 to December 2012. Trapped adults (*n* = 55) and juveniles (*n* = 21) weighing at least 23 g, were equipped with radio-collars (Model BD-2C, Holohil, Ontario, Canada) that had a battery life span of 6 to 9 weeks. Because this constraint permitted tracking individuals over a single season of the annual cycle, I recaptured as many individuals as possible, replaced their collars, and tracked them during additional seasons. Individuals were recaptured and collars removed at the end of the study. In all cases, collars weighed (1.15 to 1.9 g) less than 6% of an individual dormouse's body mass, ensuring that the collar did not interfere with the routine behaviour of dormice (K. Madikiza pers. obs.). I could track only juveniles from mid-summer onwards, as prior to that period, they were too small/light to be fitted with radio-collars. I radio-tracked dormice during the day (generally between 8:00 and 17:00), when they were inactive (resting and sleeping), enabling me to establish the location of their sleeping sites. I located dormice by a combination of triangulation and homing techniques (Mech & Barber 2002) using a R-1000 telemetry receiver (Communication Specialists, California, USA) and a hand-held rubber duck R-14 'H' type antenna (Telonics, Mesa, Arizona, USA). I then accurately (±10 cm) determined the position of sleeping sites by moving the receiver equipped with a rubber duck pocket antenna along the trunk or the branch of the tree. For each sleeping site, I recorded the following parameters: date, time, and the GPS co-ordinates. I marked all sleeping sites with a colour tag around the branch and established lists of individual sleeping sites. I located each individual dormouse 3–7 days per week. Tracking of dormice took place during the hibernating period (winter: June–August), main mating period (spring: September–November), nursing period (summer: December–February) and post-breeding period (autumn: March–May), following the findings of Madikiza (2010). Due to technical (transmitter battery life) and manpower limitations, I could not monitor individual dormice in all seasons (see Appendix 1 for individual data).

Data analysis

I calculated the percentage of sleeping associations as the number of locations during which a focal (i.e. specific or target) radio-collared dormouse was found sharing a natural sleeping site or a nest box with at least another radio-collared individual, divided by the total number of locations for the focal individual, multiplied by 100. Repeated associations between the same individuals were regarded as independent events (information on the strength of dyadic sleeping associations is provided in Chapter 3). In order to obtain reliable information on the

percentage of sleeping associations per individual, radio-collared animals for which fewer than 8 locations (n = 7) were obtained during the study period were omitted from analyses.

Overall, I recorded 21 types of associations involving adult males (M), adult females (F) and juveniles (J) during the study. These were further combined into five broad categories as follows: adult males (MM tot = MM and MMM), adult females (FF tot = FF, FFF), adult males with adult females (MF tot = MF, MFF, MFFF, MMF and MMFF), adults with juveniles (FJ/MJ tot = FJ, FJJ, FJJJ, MJ and MJJ), and juveniles (JJ tot = JJ and JJJ). As indicated earlier, juveniles were considered as a unit and not by sex because of difficulties in sexing them.

All statistical analyses were conducted with IBM SPSS Statistics 24.0 (SPSS Inc.). Unless stated otherwise data are reported as median ± interquartile range (or range). In a first step, I carried out univariate analyses to investigate age, sexual and seasonal variations in the number of locations and associations. Because data were not normally distributed (Kolmogorov-Smirnov test, $p < 0.05$), I compared the number of daily sleeping site locations for adult male, adult female and juvenile dormice with a non-parametric Kruskall-Wallis test. Differences between observed distributions of sleeping associations (sleeping alone vs. sharing; number of individuals forming sleeping associations) and expected homogenous distributions were investigated with a chi-square test of homogeneity. Comparisons between the proportions of sleeping associations occurring in nest boxes and natural sleeping sites, as well as between those for males and females, were analysed with Fisher's exact test. Potential differences in seasonal distributions of sleeping associations between different categories of dormice (e.g. male vs female) were investigated with a chi-square test of independence. A chi-square goodness-of-fit test was used to test whether specific observed seasonal distributions of sleeping associations (e.g. male–male vs female–female) differed from an expected distribution.

In a second step, to investigate the influence of age and sex (combined category with adult males, adult females and juveniles), season, and type of sleeping sites on the occurrence of dormouse sleeping associations (dependent binary variable "sleeping association": 0 = no association; 1 = sleeping together), generalized linear mixed models (GzLMMs) were generated, using a binomial distribution and a logit link function (Norušis, 2008). Because a varying number of repeated measures of the same individuals were collected during the study, animal identity was entered in the models as a random factor. Alternate models were ranked based on differences in values of Akaike's Information Criterion corrected for small sample size (ΔAIC_c). Only the main (first order) effects were considered in the analyses.

Results

Tracking period and number of locations

Locations were obtained for a total of 76 different radio-collared dormice (Appendix 1), but only 68 animals for which at least 8 locations were collected; these were 21 adult males, 26 adult females, and 21 juveniles (Appendix 1). Ten of the juveniles transitioned to adulthood during the study period and were later considered part of the adult cohort. Overall, 3193 locations were made (70.1% in natural sleeping sites, 29.9% in nest boxes), with fewer data for summer compared to the other seasons (Table 1). Radio-collared individual dormice were located on an average of 47 days (median = 36; range 8–174), with no significant difference between males (39; 8–165), females (43; 9–174) and juveniles (25; 9–114) (Kruskal-Wallis test: H = 2.52, $df = 2$, $p = 0.280$).

Table 1. Seasonal and yearly distribution of African woodland dormouse *Graphiurus murinus* sleeping site locations during the study period.

Season (Months)	**Year**			**Total**
	2010	2011	2012	
Spring (September–November)	586	430	235	**1250**
Summer (December–February)	0*	24	166	**190**
Autumn (March–May)	0*	701	316	**1017**
Winter (June–August)	357	222	158	**736**
Total	**943**	**1377**	**873**	**3193**

*No data were obtained during these two seasons because the study started in June only (Winter).

Percentage of associations and temporal/sexual variation

Throughout the study period, radio-tracked dormice were found sharing a sleeping site (and therefore a nest) with at least another radio-collared individual in 26.4% of the cases (n = 842), occurring alone in 73.6% of the locations (n = 2351). This proportion differed significantly from a 50:50 distribution (Chi-square test of homogeneity: $\chi^2 = 713.15$, df = 1, $p < 0.001$). Sleeping associations took place significantly more often in nest boxes (41.7% associations and 57.3% alone; n = 956) than in natural sleeping sites (19.8% associations and 80.2% alone; n = 2237) (Fisher's exact test: $p < 0.001$). The percentage of sleeping associations was lower in summer (15 of 190 = 7.9%) and peaked in autumn (328 of 1017 = 32.3%). Similarly, high values were observed in spring (324 of 1250 = 25.9%) and winter

(175 of 736 = 23.8%). Throughout the year, adult females (409 of 1663 = 24.6%) showed a slightly but significantly higher percentage of associations than adult males (217 of 1039 = 20.9%) (Fisher's exact test: p = 0.028; Figure 2). The seasonal association distributions differed significantly between males and females (chi-square test of independence: χ^2 = 18.40, df = 3, $p < 0.001$; Figure 1): males shared sleeping sites more than expected by chance in spring (χ^2 = 15.85, df = 1, $p < 0.001$) and less than expected in winter (χ^2 = 11.07, df = 1, $p < 0.001$), whereas the opposite pattern was observed in adult females. Adults of both sexes shared sleeping sites with other dormice at similar percentages in summer (χ^2 = 0.06, df = 1, p = 0.801) and autumn (χ^2 = 2.42, df = 1, p = 0.119). Juveniles associated with other juveniles or adults more during autumn than in summer or winter (Figure 2). It is however important to highlight that sample size was particularly small for juveniles in summer (n = 33 locations) as opposed to autumn (n = 269) and winter (n = 185).

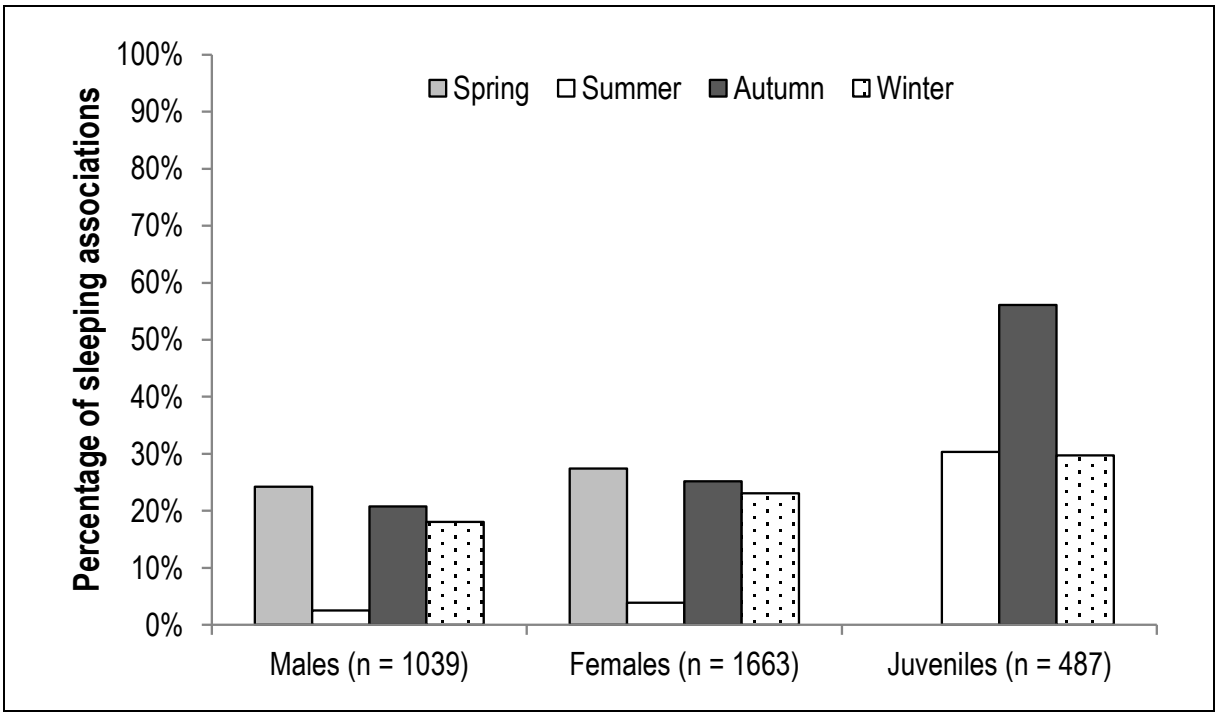


Figure 2. Seasonal variation in the percentage of times that male, female and juvenile radio-tracked woodland dormice *Graphiurus murinus* were found sharing a nest with other radio-monitored individuals from June 2010 to December 2012 (n = 3193 locations). The number of locations for males, females and juveniles are given in parentheses. There were no juveniles in the population in spring.

Types of associations

A total of 390 sleeping associations involving on average 2.18 (± 0.46) individual dormice were observed throughout the study period. A similar number of associations took place in nest boxes (n = 209) and natural sleeping sites (n = 182). Only pooled data are considered hereafter, as the focus of the analyses is on sexual, age and seasonal variations. Only two dormice slept together in most cases (84.9%), while associations of three (12.1%) or four individuals (3.1%) were rarely recorded. These results differed significantly from a homogeneous distribution (Chi-square test of homogeneity: χ^2 = 470.88, df = 2, p < 0.001). Seasonal variation in the percentages for the five main broad categories of sleeping associations is presented in Figure 3. Overall, 73.1% of these associations comprised females, and 46.9% males. Male–female (33.6%) and female–female (28.5%) total associations were common. Adult–juvenile (16.9%) and juvenile–juvenile (14.9%) total associations were also observed frequently, while male–male total associations were rare (6.2%). Adult–juvenile associations comprised of adult females in 65.2% of cases and adult males in 42.4% of the cases (these percentages do not add up to 100% because some associations were made up of three or four animals; hence for a specific association both an adult male and an adult female could be present).

Female–female seasonal distribution of sleeping associations differed significantly from that of male–male (Chi-square test of independence: χ^2 = 19.03, df = 3, p < 0.001) and male–female groups (χ^2 = 14.43, df = 3, p = 0.002; Figure 3). No difference, however, was observed between male–male and male–female seasonal distributions of associations (χ^2 = 7.75, df = 3, p = 0.051; Figure 3). Male–male associations were observed significantly more often than expected during spring (with 92% of all male–male associations taking place during this season), and less often than expected in autumn and winter (Chi-square goodness-of-fit test: χ^2 = 27.77, df = 3, p < 0.001; Figure 3). Female–female associations were more frequent than expected in winter and less frequent than expected in autumn (χ^2 = 11.26, df = 3, p = 0.010; Figure 3). Male–female associations were higher than expected in spring (mating season; 63% of all male–female associations) and lower than expected in autumn (24%) and winter (12%) (χ^2 = 31.99, df = 3, p < 0.001; Figure 3). The seasonal distributions of adult–juvenile (χ^2 = 3.95, df = 2, p = 0.138) and juvenile–juvenile (χ^2 = 3.494, df = 2, p = 0.174) associations did not vary significantly between summer and winter (Figure 3).

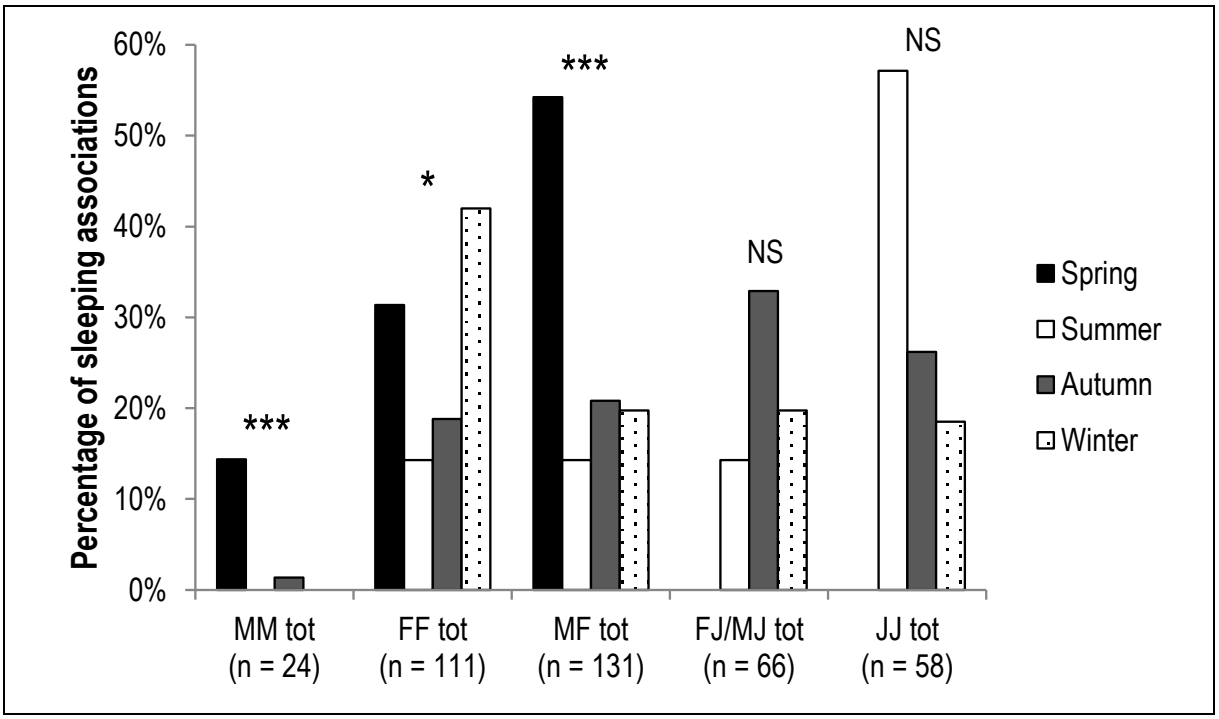


Figure 3. Seasonal variation in the percentages of sleeping associations (n = 390; the sum of percentages for each season is equal to 100%) between adult males (MM tot), adult females (FF tot), adult males with adult females (MF tot), adults with juveniles (FJ/MJ tot), and juvenile dormice (JJ tot) from June 2010 to December 2012. The number of associations for each broad category is given in parentheses. There were no juveniles in the population during spring; very few juveniles were large enough to be fitted with radio-collars during summer, hence explaining the low percentages of sleeping associations observed. Seasonal patterns that differed significantly from an expected distribution based on the yearly percentage (chi-square goodness-of-fit test) are indicated. Tests ran for the FJ/MJ tot and JJ tot categories excluded the spring season. * = $p < 0.05$; *** = $p < 0.001$; NS = non-significant.

Multivariate analyses

The results of the GzLMM analyses indicated that sex and age (combined category), season, and type of sleeping sites significantly affected sleeping associations of woodland dormice (Table 2). Further analyses indicated that the model which only included sex and age as predictor variable had a better explanatory power than the full multivariate model (Table 3). For sex and age, the parameter estimates of the full model suggest that juveniles were significantly more associated with dormice of any sex and age than females (reference category), whereas the occurrence of sleeping associations in males and females was similar (Table 4). Seasonally, sleeping associations occurred more often in autumn and less often in summer as compared to winter (reference category), but results observed in winter and spring were similar. Finally, these analyses confirmed that sleeping associations occurred more often in nest boxes than in natural nests (reference category).

Table 2. Effects of sex and age (combined category: adult males, adult females, juveniles), season (spring, summer, autumn, winter) and type (nest box vs natural site) of sleeping sites on woodland dormouse sleeping associations (n = 3,189 valid diurnal locations included) according to the results of a GzLMM procedure. Significant effects ($p < 0.05$) are indicated in bold.

Parameters	**F**	**df_1**	**df_2**	***p***
Sex & Age	12.727	2	3182	**< 0.001**
Season	15.381	3	3182	**< 0.001**
Type	124.747	1	3182	**< 0.001**

Table 3. List of alternate fitted GzLMM models in which single or multiple independent variables better explained the binary values of the response variable (sleeping associations) than intercept-only models. The models are ranked according to ascending ΔAIC_c values. AIC_c = Akaike's Information Criterion corrected for small sample size.

Variables	**F**	**df_1**	**df_2**	***P***	**AIC_c**	**ΔAIC_c**
Sex & Age	24.219	2	3186	< 0.001	15020.203	0.000
Season	15.396	3	3189	< 0.001	15104.800	84.597
Type	140.690	1	3181	< 0.001	15204.543	184.340
Sex & Age, Season	18.358	5	3183	< 0.001	15138.810	118.607
Sex & Age, Type	55.483	3	3185	< 0.001	15204.090	183.887
Season, Type	47.373	4	3188	< 0.001	15375.680	355.477
Type, Sex & Age, Season	33.830	6	3182	< 0.001	15377.282	357.079

Table 4. Parameter estimates of a GzLMM procedure aiming at testing the effects of sex and age (combined category), season and type of sleeping site on woodland dormouse sleeping associations (n = 3189 valid diurnal locations included). Significant effects ($p < 0.05$) are indicated in bold.

Parameters	**B**	**Std. Error**	**t**	***p***	**Lower**	**Upper**
Intercept	-1.901	0.229	-8.285	**< 0.001**	-2.351	-1.451
Juveniles	1.157	0.270	4.293	**< 0.001**	0.629	1.686
Males	-0.137	0.298	-0.459	0.646	-0.720	0.447
Females	0*	–	–	–	–	–
Spring	-0.020	0.144	-0.137	0.891	-0.301	0.262
Summer	-1.884	0.339	-5.561	**< 0.001**	-2.548	-0.1220
Autumn	0.317	0.140	2.256	**0.024**	0.041	0.592
Winter	0*	–	–	–	–	–
Nest box	1.522	0.136	11.169	**< 0.001**	1.255	1.789
Natural sleeping site	0*	–	–	–	–	–

*Reference categories.

Discussion

I investigated the demographic and seasonal patterns of sleeping site associations (i.e. nest sharing) in a free-living population of woodland dormice. I predicted that adult females would show a higher frequency of sleeping associations than adult males, and this throughout the year. This prediction was true as female intra-sexual association levels were higher than those of males, and were apparent throughout the year, with the exception of summer. My results are in agreement with previous nest box monitoring studies whereby females were recorded occupying artificial nestboxes with other females across all seasons, and the number of times females were recorded with other females was reported to be higher than those of males (Madikiza 2010).

The surprisingly low occurrence of intra-sexual association in females during summer could hint at the possibility that reproductive females are more territorial during this period. Such tendencies would allow females to defend territories and thus potentially reduce the chances of infanticide of unweaned offspring. In the edible dormouse *Glis Glis*, nursing females have been observed to kill pups of communally nesting females (Pilastro *et al.* 1996). Yet, occurrences of sleeping site sharing by females during the breeding season were recorded in my study even though these occasions were low in comparison with other seasons, indicating tolerance between some females. Previous studies on the same population have revealed that breeding females shared nest boxes during summer and female aggregation in nest boxes were frequently high during the core breeding season than in any other season, and in most cases female aggregations were in the company of young (Madikiza 2010). In addition, trapping data revealed that females that shared nests also showed an extensive overlap of home ranges in comparison to other females that rarely shared nests, suggesting that there is no spatial segregation, and possibly these could be related females (e.g. sisters, mothers and daughter?) associating with kin (Madikiza *et al.* 2011). Pilastro *et al.* (1996) showed that female edible dormice *Glis Glis* that communally nested and nursed were closely related individuals, specifically (mother and daughter pairs). Taken together, my results firstly suggest that there exists some level of intra-sexual tolerance between female woodland dormice throughout the year. Secondly, these sleeping associations in female woodland dormice do not seem to be driven by thermoregulatory gain alone, as females sleeping associations occurred throughout all seasons, but could be linked to alloparental care. Similarly, in the natural populations, several species of dormice, for example the edible dormouse (Pilastro 1992; Marin & Pilastro 1994; Sevianu & David 2012), garden dormouse

Eliomys quercinus (Viñals *et al.* 2017) as well as anectdotal evidence in the forest dormouse *Dryomys niteluda* (Juskaitis & Kertuka 2016), showed that breeding females also share natural or artificial sleeping sites with other females and communally nursed their young. Therefore, the summer sleeping association patterns need to be interpreted with caution, because it is plausible that my results are more likely due to a small sample size of radio-tracked females during summer in comparison to all the other seasons.

In support of the social thermoregulation prediction, woodland dormice indeed exhibited high occurrences of sleeping associations during winter, revealing associations composed of different ages and sexes. The high levels of association in winter indicate a tolerance in all cohorts, which could be driven by thermoregulatory needs. Low temperatures pose a thermal challenge to the heterothermic small mammals, such as *Graphiurus* (Mzilikazi *et al.* 2012). Sharing nests with conspecifics might lead to energy savings (Ebensperger 2001; Scantlebury *et al.* 2006), indicating the benefits of huddling.

In accordance with my third prediction, male–male associations were indeed highest during spring (i.e. mating season) and were notably infrequent throughout the study period as compared to other types of associations. Similar occurrences were noted in the fat dormice *Glis glis,* in which males shared nest boxes in groups of 8-10 individuals during the mating season (Fietz *et al.* 2010; Koppmann-Rumpf *et al.* 2012; Sievanu & David 2012). In these studies, male-male associations in nests were explained through energetic and physiological demands (high testosterone levels leading to high energy costs), although the causal mechanisms need scrutiny, given the role of testosterone in aggression.

My data primarily of high male intra-sexual associations, almost exclusively recorded during the mating season, indicate that males form ephemeral associations, and may not necessarily defend territories during this period. It is therefore plausible that even at a time when males presumably have high testosterone levels (usually associated with aggression), they are still able to associate and be tolerant of one another. I suggest that males 1) tolerate and form coalitions and cooperate with each other (i.e. neighbouring males) in order to increase breeding opportunities (i.e. with receptive females) through joint mate attraction and nest guarding, as has been recorded in chimpanzees *Pan troglodytes* (Watts 1998) and 2) after natal dispersal, males may still maintain close or overlapping home ranges with brothers or kin, thus displaying "parallel dispersal" – which occurs when kin related or familiar males immigrate together, and form groups with, related or familiar individuals (van Hooff 2000; Schoof *et al.* 2009). Empirical evidence of parallel dispersal has been shown in the white-faced capuchin monkeys *Cebus capucinus* (Schoof & Jack 2014).

I further predicted that male–female sleeping associations would only occur during the mating season (spring). Indeed, intersexual association levels were higher during spring, consistent with the mating season of woodland dormice in this population (Madikiza 2010). There are two plausible explanations for these associations, all from a male reproductive strategy's perspective. 1) Since female woodland dormice are seasonal breeders displaying a short but unpredictable receptive period, it is advantageous for males to roam and stay in close proximity to receptive females during this window period (Madikiza *et al.* 2011), thus increasing the chance to locate and possibly mate with a receptive female. Therefore, finding females at their sleeping sites increases the chance of locating them than random (chance) encounters. This type of reproductive strategy by males has been described for grey mouse lemurs *Microcebus murinus* (Radespiel 2000). 2) Once localization of females by males occurs, mate guarding would be possible, ensuring that fertilization is successful. Mate guarding has been observed in fork-marked lemurs *Phaner furcifer* (Schulke 2002). Such strategies allow for direct access, control and defence of these receptive females.

Observations of male–female associations during autumn and winter (non-breeding seasons) in my study were unanticipated. A parsimonious explanation for such tolerance could again be linked to the reproductive strategy of males, whereby males increase their probabilities of finding females during the next mating season by developing social ties (familiarity) with females. Such social ties have been described for male grey mouse lemurs *Microcebus murinus* (Radespiel 2000), and reddish-gray mouse lemur *Microcebus griseorufus* (Génin 2008). Another possible explanation could be that, since autumn is a pre-hibernation period, tolerance for all age classes and sexes in sleeping sites during this period could facilitate advantageous behaviours such as social thermoregulation in winter. Under such circumstances, I predict that individuals that once shared sleeping sites during the pre-hibernation period are more likely to associate again during the hibernation period due to social familiarity. In a captive population of southern flying squirrels *Glaucomys volans*, familiarity was one of the factors contributing to nest sharing in winter (Thorington & Weigl 2011).

My final prediction was that juveniles would form sleeping associations only with adult females. This prediction was supported. Juvenile association with adult females could be due to unweaned offspring dependency on parents, and hence the high frequency of association during the breeding period. However, female–juvenile (mother–offspring?) associations was evident also in the hibernation season, during a time when juveniles are expected to have been weaned and become independent from mother. This first suggests a high degree of tolerance

between *G. murinus* mothers and offspring, potentially leading to philopatry and the formation of kin groups (Solomon 2003), particularly when insulated sleeping sites become a limiting factor. Tolerance of weaned offspring by parents has been documented in the striped mouse *Rhabdomys pumilio*, leading to natal philopatry and group-living (Schradin & Pillay 2003). Secondly, my results could potentially reveal that parental (mother and father?) and possibly alloparental care (mother and aunts?) could be involved in keeping juveniles warm. If so, then juveniles gain thermoregulatory advantages by remaining with adults which have accumulated enough body fat prior to winter (McNab 1983).

High frequency of sleeping association between juvenile–juvenile could be the results of pooled first and second litters, since female woodland dormice exhibit post-partum oestrus (Madikiza 2010). This again reveals tolerance between siblings, which allows for formation of early social bonds leading to group formation, if it persists into adulthood. During trapping studies by Madikiza (2010), two juveniles were sometime caught in the same trap, suggesting that they foraged together.

In conclusion, I investigated the sleeping association patterns in a natural population of woodland dormice. I found that sleeping groups are not coincidental, and occurred both in nest boxes and natural sleeping sites. Sleeping associations were significantly more frequent in artificial sleeping sites, but patterns of associations were similar in both types of sleeping sites. Sleeping associations varied by sex and age seasonally. It seems that female associations are driven by not only thermoregulatory benefits but also by allo-parental gains, and might in fact be kin based. Tolerance between parents and offspring as well as between siblings or littermates suggests natal philopatry, but whether this could lead to group formation requires further tests. Male associations seem to be thermoregulatory based and possibly also related to their mating strategies.

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Appendix 1. List of the 76 African woodland dormice *Graphiurus murinus* that were radio-tracked between June 2010 and December 2012. The "/" indicates that some individuals were tracked both as juveniles and adults. Selected? = individuals with ≥8 locations (Yes) or <8 locations (No).

Animal code	Sex/Age	Start date	End date	No. locations	Selected?
B1	Female	12.07.2010	25.11.2010	59	Yes
B10	Female	02.07.2010	04.04.2011	88	Yes
B11F	Female	14.03.2011	05.05.2011	45	Yes
B11M	Male	13.03.2011	13.05.2011	51	Yes
B13	Female	13.04.2011	25.04.2011	12	Yes
B14	Female	14.03.2011	21.04.2011	32	Yes
B15	Male	13.03.2011	22.05.2011	61	Yes
B17	Female	03.10.2011	28.07.2012	62	Yes
B2	Male	12.06.2010	25.11.2010	97	Yes
B20	Female	12.06.2010	24.11.2010	86	Yes
B21	Male	03.10.2010	25.11.2010	48	Yes
B22	Female	03.10.2010	11.12.2011	144	Yes
B23	Male	02.10.2010	25.11.2010	50	Yes
B24	Female	12.06.2010	25.11.2010	89	Yes
B25	Female	15.06.2010	01.09.2011	174	Yes
B26	Male	03.10.2010	28.03.2011	39	Yes
B27	Male	03.10.2010	25.11.2010	48	Yes
B28	Male	03.10.2010	03.07.2012	165	Yes
B3	Female	15.06.2010	23.11.2010	89	Yes
B31	Male	28.01.2012	17.12.2012	31	Yes
B4	Female	14.03.2011	01.05.2011	42	Yes
B51	Male	23.07.2011	29.11.2011	23	Yes
B7	Female	12.06.2010	13.03.2011	26	Yes
B8	Female	13.07.2010	31.10.2010	43	Yes
B9	Female	02.07.2010	18.05.2011	129	Yes
G0	Juvenile	28.04.2012	17.06.2012	23	Yes
G11	Male	26.04.2012	04.05.2012	8	Yes
G12	Juvenile/Female	05.02.2012	17.12.2012	34	Yes
G13	Juvenile/Male	05.02.2012	14.05.2012	9	Yes
G14	Juvenile/Female	05.02.2012	02.12.2012	22	Yes
G15	Juvenile	05.02.2012	29.10.2012	77	Yes
G16	Juvenile/Male	05.02.2012	14.10.2012	25	Yes
G17	Juvenile	05.02.2012	23.06.2012	18	Yes
G2	Juvenile	20.02.2012	17.06.2012	26	Yes
G20	Male	21.02.2012	02.12.2012	28	Yes
G21	Male	24.09.2012	29.10.2012	19	Yes
G23	Female	07.10.2012	29.10.2012	12	Yes
G24	Female	14.10.2012	29.10.2012	5	No
G26	Female	28.09.2012	04.10.2012	4	No
G40	Female	27.09.2012	29.10.2012	18	Yes
G41	Male	24.09.2012	28.10.2012	12	Yes
G42	Male	28.09.2012	30.09.2012	3	No
G43	Female	28.09.2012	14.11.2012	19	Yes
G45	Male	14.10.2012	29.10.2012	16	No
G46	Male	29.10.2012	14.11.2012	4	No
G5	Juvenile	26.04.2012	23.06.2012	31	Yes
G6	Juvenile	29.04.2012	09.05.2012	9	Yes
G60	Female	24.09.2012	14.10.2012	14	Yes
G61	Male	28.09.2012	14.10.2012	13	Yes
G8	Female	27.09.2012	04.10.2012	5	No
G9	Juvenile	05.02.2012	02.08.2012	49	Yes
W41	Juvenile	23.03.2011	07.05.2011	11	Yes
W42	Juvenile	23.03.2011	13.08.2011	39	Yes
W43	Juvenile/Female	03.05.2011	09.11.2011	23	Yes
W44	Female	08.11.2011	03.07.2012	83	Yes
W45	Juvenile	01.08.2011	13.08.2011	12	Yes
W46	Juvenile	03.05.2011	21.05.2011	17	Yes
W52	Juvenile/Female	01.04.2011	02.12.2012	121	Yes
W59	Male	28.04.2011	28.10.2011	47	Yes
W61	Juvenile/Sex undetermined	21.03.2011	19.10.2011	43	Yes
W62	Juvenile/Male	21.03.2011	15.06.2012	95	Yes
W64	Male	14.10.2011	19.10.2011	5	No
W65	Male	29.10.2011	03.07.2012	89	Yes
W66	Male	30.10.2011	02.11.2011	4	No
W7	Male	25.08.2011	30.01.2012	54	Yes
W71	Female	18.10.2011	01.11.2011	9	Yes
W72	Juvenile/Female	21.04.2011	01.09.2011	24	Yes
W73	Juvenile/Female	30.07.2011	30.11.2011	63	Yes
W74	Female	23.11.2011	20.04.2012	33	Yes
W76	Male	24.10.2011	11.12.2011	37	Yes
W77	Male	30.10.2011	11.12.2011	34	Yes
W78	Female	31.10.2011	09.04.2012	42	Yes
W79	Female	24.11.2011	13.03.2012	17	Yes
W80	Female	29.01.2012	21.02.2012	15	Yes
W81	Male	30.01.2012	16.03.2012	27	Yes
W82	Female	05.02.2012	17.06.2012	54	Yes

CHAPTER THREE
Social Network Structure of the African Woodland Dormouse *Graphiurus murinus*

Abstract

The social structure of a specific animal population is determined by the spatio-temporal patterns of relationships between individuals. Here, I investigated the social structure of a free-living population of African woodland dormice *Graphiurus murinus* using association indices from, and social network analysis of, dyadic sleeping associations. Woodland dormice are heterothermic arboreal rodents that exhibit communal breeding and extensive intra- and intersexual home range overlaps, and are hypothesised to have a promiscuous mating system. I therefore predicted that 1) the dyadic association index (AI; defined as the number of sleeping associations between two focal animals observed during a common monitoring period, divided by the number of simultaneous daily locations, converted to percentage) would be higher in female–female (FF) than in male–female (MF) and male–male (MM) dyads; 2) the number of opposite-sex sleeping partners should be similar in both males and females and increase with the duration of the monitoring period; and 3) at least some juveniles should associate with more than one adult female. Between June 2010 and December 2012, the locations of 28 adult males, 31 adult females, and 21 juveniles were recorded, using both radio-tracking and use of up to 80 artificial nest boxes. A total of 3238 individual locations (average = 40/individual) were collected. Sixty-eight (85%) of the 80 dormice formed sleeping associations. A total of 496 sleeping associations between 112 dyads and involving 68 individual dormice were recorded. The average AI was 15.05%. As predicted, FF dyads (17.31%) had a significantly higher AI than MF (11.72%) and MM dyads (7.33%). AI was significantly negatively correlated with the number of simultaneous locations in MF dyads, but not in FF dyads, hence indicating that FF dyads are temporally more stable than MF dyads. As expected, males (median = 1.00; range 0–6) and females (median = 1.00; range 0–3) had a similar number of adult opposite-sex sleeping partners, and this number increased monotonically with the number of locations and the monitoring period. Social network analysis revealed a complex web (density = 5%; median degree ± interquartile range = 3.00 ± 4.00) of relatively even associations (edges) between adult males and females,

with no significant intersexual difference in the five network metrics studied. The presence of duos and trios of females involved in dyadic associations, and the fact that juveniles formed dyadic associations with up to three different females, is consistent with prior observations of communal nesting and possible allo-parental care in this species. In conclusion, using social network analysis, my study demonstrated the number of partners by sex and age, and the strength and regularity of individual dyadic associations in woodland dormice. Sleeping associations mirrored the social tendencies of the species as well as the strong affinity between certain individuals. These affinities are sex specific relating to the need to huddle on the one hand and their putative promiscuous mating strategies on the other hand.

Keywords: Social relationships, sleeping associations, association index, partner index, nest sharing

Introduction

The social structure of a specific animal population can be defined as the different types of relationships between individuals of that population which exist in time and space (Hinde 1976). The patterns of these relationships are a direct consequence of individual social interactions and the environment inhabited (Krause *et al.* 2007). However, social interactions in populations are known to be non-random, creating individual differences in interactions (Krause *et al.* 2007). In particular, individuals in a population might be selective with which individual they associate more than others. For example, juvenile lemon sharks (*Negaprion brevirostris*) associate highly with individuals of similar body length (Guttridge *et al.* 2009). Some individuals might show higher sociability than others (e.g. guppies (*Poecilia reticulate*) (Croft *et al.* 2009), leading to more inter-individual connections or contacts (such as spatial and temporal overlaps).

Social structures can change in space and time due to ecological, life history characteristics and physiological factors (Croft *et al.* 2009). Ecological factors can alter movement, temporal associations and space use by individuals in a particular environment, eventually affecting the extent of social relationships that take place between individuals in a population. Ecological factors, such as resource availability (i.e. presence, abundance and distribution of resources, e.g. food and nesting sites), can affect the nature of interactions between individuals, thus influencing the spacing patterns of conspecifics (Eifler 1996; Foster *et al.* 2012). In addition, coupled with ecological factors, life history characteristics, such as

age, sex, reproductive status and genetic relatedness may also singly or in combination affect the type of interactions between individuals, thus shaping the overall social structure of the population (Hinde 1976; Silk 2007; Whitehead 2008). Age can modify social interactions between individuals, whereby younger individuals may actively or passively associate with adults, acquiring skills, food and/or protection (Durant 2000; Bourjade *et al.* 2008; Cockburn *et al.* 2008). Within sexes, competition for mates can lead to different spacing and reproductive strategies (Emlen & Oring 1977). The reproductive state of individuals may affect associations, when, for example, breeding females interact with one another in order to reduce energetic demands associated with lactation. Genetic relatedness may lead to associations between kin (i.e. kin selection; Kapsalis & Berman 1996). Furthermore, the physiology of a species coupled with the environment in which individuals exist can dictate the type of social interactions and social relationships that form. For example, the thermoregulatory strategies (such as huddling) utilised by heterothermic species will affect the type and intensity of interactions that take place between individuals, the overall space use and the activity patterns within a population (Pretzlaff *et al.* 2010). For example individuals may form aggregations with certain other individuals when ambient temperatures are not favourable, as shown for big brown bat *Eptesicus fuscus* (Lausen & Barclay 2003), or be selective on the type of sleeping sites used (based on insulator capabilities), as shown for Bechstein's bat *Myotis bechsteinii* (Kerth *et al.* 2001).

In the past, sociality was often measured through associations (i.e. the number of individuals in close spatial proximity), but this metric only provided a single facet of the social structure (Wey *et al.* 2008) This rendered it difficult to develop an all-inclusive model of sociality which would address which individuals interact, as well as why those individuals interact and how often these interactions take place. In other words, a comprehensive understanding of the social interactions and the patterns of social relationships that exist at different levels (between individuals, within groups and at population scale), and of the drivers (causes and consequences) that shape these patterns are required to fully understand sociality. To account for these various characteristics of social systems, Wilson (1975) proposed the use of social networks in the study of sociality. Social networks reveal how individuals in a population interact with one another (i.e. how their behaviour affects other individuals' behaviour), as well as how groups of individuals are inter-connected, thus providing a holistic and quantifiable information on social relationship at all levels within social groups (Wasserman & Faust 1994; Wey *et al.* 2008; Whitehead 2008; Sih *et al.* 2009).

For small, nocturnal, cryptic species such as dormice (Madikiza 2010), detection of direct interactions between individuals is challenging. To overcome such challenges, one can use associations instead of interactions (e.g. behaviour) as measure of sociality (Klaich *et al.* 2011). According to Smolker *et al.* (1992), associations in space and time are a necessity for social interaction to develop. Associations are defined as the proximity of individuals in time and space (Whitehead 2008). These associations can be measured through the use of association indices, whereby the proportion of time two individuals spend in contact is assessed in order to quantify relationships between dyads of individuals (Cairns & Schwager 1987). For instance, bat studies have used the nature and quality of associations in order to elucidate the social interaction and social structure of different populations (Kerth & Konig 1999; Vonhof *et al.* 2004). Indeed, social structure can be reflected in space-use patterns (Lusseau *et al.* 2006; Wolf *et al.* 2007; Mourier *et al.* 2012) and information on space use can provide insights into social structure not available from patterns of association alone (Leu *et al.* 2010, 2011).

Understanding the social structure of dormice (family Gliridae) using social network analysis is of particular interest because social grouping is very common in members of this rodent family, both geographically within species as well as species within genera. Some form of grouping has been recorded in the edible dormouse *Glis glis* (Pilastro 1992; Marin & Pilastro 1994; Scinski & Borowski 2008; Fietz *et al.* 2010; Koppmann-Ruf *et al.* 2012; Sevianu & David 2012), common dormouse *Muscardinus avellanarius* (Likhachev 1966; Morris *et al.* 1990; Bright & Morris 1996; Juškaitis 1997), garden dormouse *Eliomys quercinus* (Viñals *et al.* 2017), forest dormouse *Dryomys nitedulla* (Juškaitis & Keturka 2016), Japanese dormouse *Glirulus japonicus* (Kawamichi *et al.* 2000; Shibata *et al.* 2004), African spectacled dormouse *Graphiurus ocularis* (Van Hensbergen & Channing 1990) and African woodland dormouse *Graphiurus murinus* (Kingdon 1974; Madikiza 2010; Madikiza *et al.* 2011; Madikiza & Do Linh San, in prep.),. However, for most Gliridae, and more specifically in the case of woodland dormice, there is no quantifiable information on the nature of these interactions as well as on the causes or drivers of these associations leading to the species social structure.

Woodland dormice are nocturnal, insectivorous and frugivorous rodents that use torpor and hibernation during winter. Some adult females have overlapping home ranges and share sleeping sites – tree holes and artificial nest boxes – and 2–3 females may communally nest and co-nest with young (Madikiza *et al.* 2010; Lamani 2011). A nest box monitoring study showed that males form groups during the mating season, which dissociate afterwards

(Chapter 2). During the hibernation season, mixed sex and age groups (male, female and juveniles) of huddling individuals have been recorded in nests (Madikiza 2010; Chapter 2).

The aim of the current study was to investigate the social structure of free-living woodland dormice using dyadic sleeping associations (i.e. association indices) of individual of different sex and age, and to interpret the patterns of these relationships using social network analysis. Considering that this species is believed to adopt a promiscuous mating system (with asynchronous breeding and clumped distribution of females; Madikiza *et al.* 2011) and that females are at least sometimes nest communally during the breeding season (Madikiza & Do Linh San, in prep.), I made three predictions. 1) The dyadic association index (AI; defined as the number of sleeping associations between two focal animals observed during a common monitoring period, divided by the number of simultaneous daily locations, converted to percentage) should be higher in female–female than in male–female and male–male dyads. Indeed, whereas females will potentially associate during the breeding season over a relatively long period, males are only expected to briefly associate with females for mating. 2) The number of adult opposite-sex sleeping partners should be similar in both males and females and increase with the duration of the monitoring period (and/or number of locations), as adult individuals are expected to have several sexual partners (more of these will be detected with time) and associate with new ones over time. 3) If dormice sometimes nest communally during the breeding season, at least some juveniles should associate with more than one adult female.

Materials and methods

Study area

This research was carried out between June 2010 and December 2012 in the Great Fish River Reserve complex, and more precisely in the Andries Vosloo Kudu Nature Reserve (E 26.675430, S 33.126846; altitude: 300 m a.s.l.). The study site (*ca* 6 ha) was located in a dry riverine *Combretum* forest dominated by stands of African bush willow *Combretum caffrum*. This tree species is prone to rotting from the inside, resulting in numerous holes and hollows which provide suitable nesting sites for a wide range of arboreal animals (Lamani 2011; Gebe 2014; K. Madikiza pers. obs. 2004–2012; E. Do Linh San pers. comm.). The riverine forest is fed by an underground water table which forms a narrow belt (<100 m wide) along the riverbeds and supports several other tree species, including *Olea europaea* ssp. *africana*, *Ziziphus mucronata*, *Maytenus heterophylla* and *Rhus* spp. On both sides of the riverbed, the

study area is bordered by relatively large expanses of bush clump karroid thicket, a semi-open habitat composed of *Rhus* spp. and *Scutia myrtina* bush clumps and a karroid herbaceous layer.

The study site is divided by a gravel dirt road into two sections: the north-western part and the south-eastern part (Figure 1). The north-western part contained 80 wooden nest boxes that were installed sequentially between 2003 and 2010 for studies on the population biology, nest box use and resting site ecology of woodland dormice (Madikiza 2010; Lamani 2011). In contrast, the south-eastern part (3.5 ha; B × L: 100 × 350 m) of the study site did not contain any artificial nest boxes and dormice could only build nests in natural sites – inside tree branches and trunks, or exceptionally in burrows (Lamani 2011; K. Madikiza & E. Do Linh San unpubl. data).

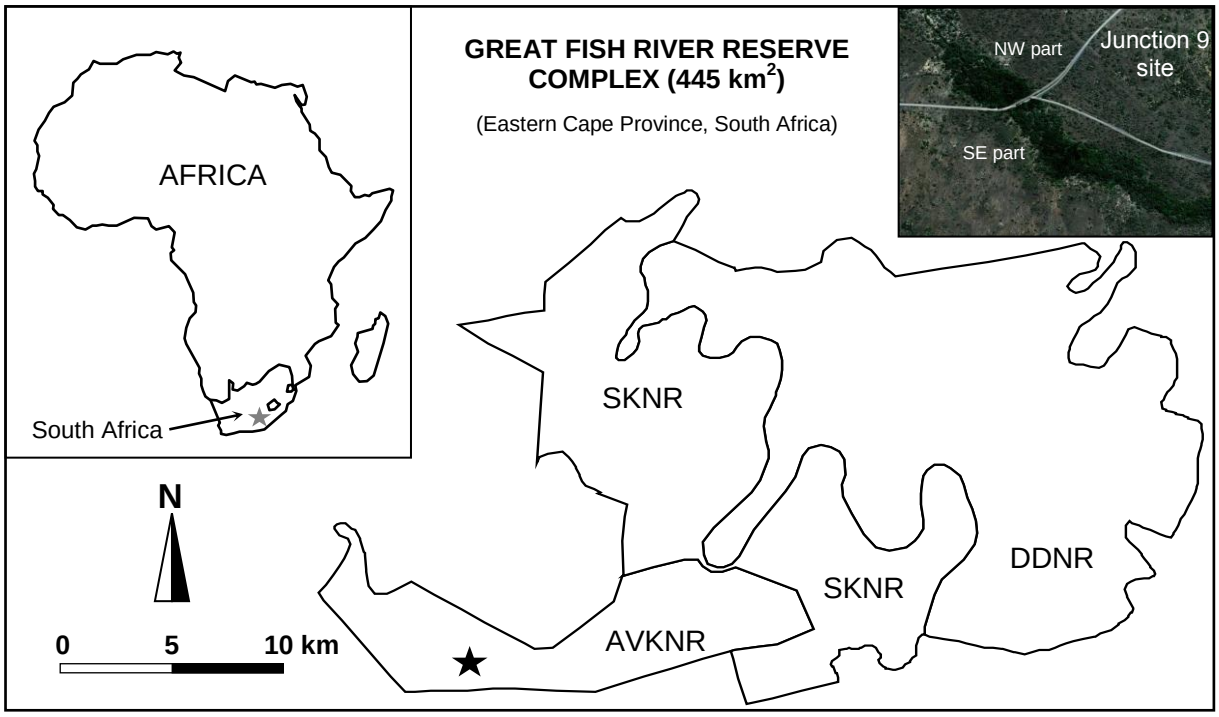


Figure 1. Map showing the location (small grey-shaded star in the upper left-hand side inset) and the structure of the Great Fish River Reserve Complex. The location of the "Junction 9" study site is indicated by a large black star. The upper right-hand side inset shows an aerial view of the 6-ha study area – a riverine *Combretum* forest of ca. 100 m wide and 600 m long. The north-western (NW) part that contained 80 nest boxes is separated from the south-eastern part (without nest boxes) by a gravel dirt road. African woodland dormice *Graphiurus murinus* can move freely between both parts. AVKNR: Andries Vosloo Kudu Nature Reserve; SKNR: Sam Knott Nature Reserve; DDGR: Double Drift Game Reserve.

Nest boxes were made out of timber wood, approximately 2 cm thick, with internal dimensions (B × L × H) of 11.5 × 13 × 12 cm. They were set randomly and spaced irregularly in a 2.5-ha section of the riverine forest (B × L: 100 × 250 m) and were hung on trees with a nail and a wire sling. In order for the entrance hole to be more accessible to small mammals

climbing the tree or branch, the nest box entrances faced the tree trunk. Following Morris *et al.* (1990), this design was also intended to deter birds from entering by obstructing their direct line of flight to the entrance hole. Indeed, no single bird was found nesting in nest boxes during their deployment. Two transverse spacing bars, above and below the entrance hole, held the box about 2.5 cm clear of the tree to which it was attached, allowing dormice to access the nest boxes easily.

Marking of animals and age and sex determination

In order to individually mark woodland dormice, I used two trapping protocols. First, I caught dormice in nest boxes during seasonal or *ad hoc* checks performed throughout the study period. Second, I trapped dormice once per month or at least once per season using 165 (north-western part) or 200–350 (south-eastern part) Sherman folding aluminium traps (H. B. Sherman Traps, Tallahassee, Florida, USA; B × H × L: 8 × 9 × 23 cm). I baited traps with a mixture of rolled oats and sunflower oil and set them randomly in trees and on logs. To avoid fatalities during cold months, I placed a roll of cotton wool inside the traps and insulated traps with a cotton cloth and wrapped with sail, waterproof material.

Trapping took place during independent sessions that lasted for 3–5 consecutive days. I checked traps twice per day, early morning and late afternoon, essentially to release the odd diurnal rodent (essentially striped mice *Rhabdomys* sp.) caught and make the trap available for the night trapping. I removed dormice from nest boxes with thick protecting gloves and placed in a pre-weighed Ziploc® bag. Animals caught with traps were directly dropped into the bag. Dormice were then weighed to the nearest gram using a Pesola spring balance (Pesola, Baar, Switzerland). I classed them as young (0–15 g in spring and summer), juveniles (15–25 g in summer) or adults (generally >25g throughout the year), following Madikiza (2010). I then briefly anaesthetized each animal with diethyl ether, marked it by perforating one or both ears with single digit spikes attached to forceps and then rubbed the holes with a permanent tattoo-ink (black, green or white). I sexed adults by visually measuring the distance (much shorter in females) between the anal and genital apertures. I recorded the reproductive status as follows: females – vaginal orifice perforate or imperforate; males – scrotal (testes descended into the scrotal sac) or non-scrotal (testes in the abdominal cavity). I could not always determine the sex of young (unweaned) and juvenile (weaned) dormice with certainty, and therefore these were not differentiated by sex in this study. I regarded dormice first captured as young or juveniles as adults once they had reached their first spring

(September) and became part of the reproductive cohort. I would then confirm or determine the sex of these individuals when they were re-trapped as adults.

Radio-collaring, nest box checks and sleeping site location

I established the location of dormice sleeping sites by means of radio-tracking in both parts of the study site, as well as through nest box checks in the north-western section. Both methods were used during the hibernating period (winter: June–August), main mating period (spring: September–November), nursing period (summer: December–February) and post-breeding period (autumn: March–May) following Madikiza (2010).

I equipped adults (n = 52) as well juveniles (n = 19) weighing ≥23 g with radio-collars (Model BD-2C, Holohil, Ontario, Canada). The weight of collars ranged from 1.15 to 1.9 g and was <6% of the animals' body mass, thereby ensuring that the collar did not interfere with dormice routine behaviour. I did not radio-track any juvenile during spring, as they were too small to be fitted with radio-collars. The radio-collars used in my study had a battery life of 6–9 weeks, which only allowed radio-tracking of individuals over a single season, I recaptured as many individuals as possible, replaced their collar, and tracked them during additional seasons. Individuals were recaptured and collars removed at the end of the study. I determined the location of dormice sleeping sites during the day, generally between 1 h after sunrise and 1 h before sunset, when dormice were inactive. I located sleeping sites by a combination of the triangulation and homing techniques (Mech & Barber 2002) using a R-1000 telemetry receiver (Communication Specialists, California, USA) and a hand-held rubber duck R-14 'H' type antenna (Telonics, Mesa, Arizona, USA). I then accurately (±10 cm) determined the position of resting sites by moving the receiver fitted with a rubber duck pocket antenna along the trunk or the branch of the tree. I could confirm the accuracy of this technique on some occasions when a dormouse or typical dormouse nesting material (old man's beard lichen *Usnea barbata*; Lamani 2011; K. Madikiza pers. obs. 2004–2012) could be seen through a crack, and/or the animal could be heard vocalising. For this reason, I was also able to confidently evaluate when two or more radio-tracked dormice were sharing the same sleeping site (nest). For each sleeping site, I recorded the date, time, height above ground, type (trunk, branch, burrow) and the GPS co-ordinates. Sleeping sites were marked with a colour tag and lists of individual sleeping sites established and continuously updated. Dormice were radio-tracked 3–7 days per week for single or multiple periods of 6–9 weeks.

In addition to using radio-telemetry, I determined the sleeping locations of non-collared dormice by checking nest boxes monthly when capturing and radio-collaring individuals, as

well as on almost all the radio-tracking days, when walking through the north-western section to locate collared individuals. In the latter case, only a haphazard and therefore variable subset of the 80 nest boxes would be checked, depending on the daily distribution of sleeping sites in that area.

Data recorded

For each marked (hereafter called "focal") dormouse, I recorded the following parameters: 1) the monitoring period (number of days between the last record – being a location or a capture – and the date of marking); 2) the number of radio-tracking periods; 3) the duration of individual radio-tracking periods (number of days between the first and the last location); 4) the total number of locations – either radio-locations or visual observations in nest boxes – obtained during the monitoring period; and 5) the number of sleeping partners (Appendix 1).

I defined the number of sleeping partners as the total number of different dormice a focal dormouse shared a sleeping site with during the monitoring period. Because it was not possible to determine whether some non-collared individuals were sharing a natural sleeping site with collared individuals, the data on the number of sleeping partners per focal dormouse presented in this study should be viewed as a subset of the total potential associations in the study site. Also, I considered an individual as being a sleeping partner irrespective of whether it had shared a sleeping site with the focal individual on a single day or on numerous instances. In order to compare the number of sleeping partners between animals with differing numbers of locations (and therefore differing monitoring periods), I created a "partner index", defined as the number of sleeping partners divided by the number of locations for a focal animal. This index can theoretically vary between 0 (when the focal animal does not have a sleeping partner) and ∞ (when the focal animal is found with an infinite number of partners). However, in most cases, the partner index is expected to be much smaller than 1 (value which would be obtained when the focal animal is found sharing a sleeping site with a new partner at each new location).

Considering that social networks are constructed based on the strength of relationships between pairs of individuals (e.g. Whitehead 2008; Patriquin *et al.* 2010; Makagon *et al.* 2012; Johnson *et al.* 2013; Eifler *et al.* 2016), I recorded all dyadic sleeping associations that could be determined within the limitations of the methods used (see above). A dyadic sleeping association was defined as the sharing of a sleeping site by two focal dormice on the same day, either by locating two radio-collared animals in the same natural sleeping site, or by observing two dormice – collared or not – in the same nest box (i.e. artificial nest box). In

addition, I also recorded instances when three or four dormice (excluding mothers and unweaned young) shared the same sleeping site (see Chapter 2). In such cases, three or six dyadic interactions, respectively, were considered. I could establish the absence of a dyadic association on a specific day based on three mutually exclusive situations: 1) the two animals (collared or not) were located and/or observed in different resting sites (natural or artificial); 2) one radio-collared animal was located in a natural resting site and the other radio-collared animal could not be found (radio tracking signal not audible) or located precisely (signal heard further away) on that day; 3) one animal was found in a nest box (alone or with other dormice) and the other individual could not be found or located on that day. For situations 2) and 3) to be taken into consideration, the animal which could not be found had to be known to be present in the study area on previous days (which would not necessarily be the case for immigrating dormice or "floaters") and to be both alive and reside in the study site on subsequent days. I considered six types of dyadic associations in this study: male–male (MM), female–female (FF), male–female (MF), male–juvenile (MJ), female–juvenile (FJ), and juvenile–juvenile (JJ). I generated an association index (AI) for all dormouse dyads that were found sharing a sleeping site on at least one occasion. I defined the AI as the number of sleeping associations between the two focal animals observed during a common monitoring period, divided by the number of simultaneous daily locations, converted to percentage. A simultaneous daily location corresponded to any daily record for which it could be indisputably established that both focal individuals were either sharing a sleeping site or sleeping in separate locations at the time of data collection.

Social network analyses

To describe woodland dormice network of sleeping associations, each focal individual was treated as a node and dyads of sleeping partners were connected by an edge. I generated social network diagrams and used social network analysis to respectively visualise and explore statistically the network of relationships and detect possible clusters or independent subgroups of focal individuals – called "components" (i.e. a set of nodes that are interconnected but not connected to the rest of the network). For this purpose, I imported data on dyadic sleeping associations ("network edge list"; see Appendix 2) into NodeXL 1.0.1.350 for Microsoft® Excel® (https://nodexl.codeplex.com).

In a first step, I used the association index defined above to represent the thickness of the edges, while I used the partner index to calibrate the size of the nodes (called "vertices" in NodeXL) representing each focal individual. To obtain a general overview of associations in

the population, I included all dormice monitored between June 2010 and December 2012 and involved in dyadic sleeping associations in a single network diagram. Next, to avoid possible biases linked to small sample size, all dormouse dyads for which less than 8 simultaneous daily locations were obtained during the study were discarded and a series of more specific network diagrams generated for: (1) associations for the period June 2010 to May 2011; (2) associations for the period June 2011 to December 2012; (3) male–female associations; (4) male–male associations; (5) female–female associations; (6) male–juvenile associations; (7) female–juvenile associations; and (8) juvenile–juvenile associations. I generated diagrams for (2) and (3) because they correspond to a better temporal overlap in the monitoring of the corresponding individuals and therefore provide a more representative depiction of associations of the overall social network during each period. Due to small sample sizes, dyadic associations were considered collectively, and not by seasons, during each of these two main periods. Some associations which overlapped both periods listed in (2) and (3) were included in each network diagram. For these associations, the edge thickness is proportional to the association index during the whole monitoring period, and not specifically periods listed in (2) and (3). I generated diagrams (4)–(9) in order to gain better insights into the associations of specific categories of individuals.

In a final step, I calculated a series of metrics to characterize the overall social network as well as the separate networks for the periods 2010–2011 and 2011–2012. The metrics of interest are described in Table 1. In order to identify which focal individuals played a preponderant role in the social networks during the two separate periods, I redrew diagrams (2) and (3) and used centrality metrics (eigenvector, betweenness and closeness) and clustering coefficients to calibrate the size of the nodes.

Table 1. The definition of metrics used to describe and compare social networks in African woodland dormice *Graphiurus murinus* (Sources: Aldhous 2012; Eifler *et al.* 2016).

Metrics	Definition
Density	The proportion of all possible edges (i.e. connections between all pairs of nodes) present in the network. This metric may vary from 0–100%.
Degree	A count of the number of connections for each node (equivalent to the number of dyadic sleeping partners for each dormouse).
Eigenvector centrality	Metric that accounts not only for the node's own degree, but also the degrees of the nodes to which it connects.
Betweenness centrality	This metric reveals how important each node is in providing a "bridge" between different parts of the network. It highlights the nodes that, if removed, would cause the corresponding network to fall part.
Closeness centrality	This is a measure of how close each node is, on average, to all of the other nodes in a network. It highlights the nodes that connect to the others through a lower number of edges.
Clustering coefficient	The proportion of an individual's associates which are themselves associated.

Statistical analyses

All statistical analyses were conducted with IBM SPSS Statistics 24.0 (SPSS Inc.). Because data were not normally distributed (Kolmogorov-Smirnov test, $p < 0.05$), non-parametric tests were used and measures of central tendency and dispersion provided for compared groups (sex, age classes and monitoring periods) are median ± interquartile range. Comparisons between sexes and between the two monitoring periods were carried out with the Mann-Whitney test, whereas potential differences between sex and age classes (males, females, juveniles) and between categories of dyadic sleeping associations (MM, FF, MF, MJ, FJ, JJ) were evaluated with the Kruskal-Wallis test. Potential monotonic (increasing or decreasing) correlations between two variables were investigated with Spearman's rank correlation test.

Results

Sampling

A total of 80 individually marked (or focal) dormice were monitored over an average timespan of 134 days (range 2–640), including 28 adult males, 31 adult females, and 21 juveniles (Appendix 1). Ten of the 21 focal juveniles transitioned to adulthood and were therefore subsequently regarded as belonging to the adult cohort. Based on the high trapping effort and recapture success, and the fact that adult woodland dormice are highly mobile and "trap-happy", I estimated that around 90% of the resident adult dormice population in my study site could be marked and monitored during the study period (K. Madikiza unpubl. data). An unknown but possibly substantial number of juveniles were probably predated upon, died of other natural causes or dispersed before they could be trapped. A large majority (n = 71, 89%) of the marked dormice were radio-tracked, and this during an average of 1.58 (range 1–5) tracking periods spanning over a mean sum of 65 days (range 5–253). Taking nest box checks in addition to radio-tracking data into consideration, a total of 3238 locations were collected, on average 40 per individual (range 2–174; n = 80). The numbers of locations obtained for males (median = 33; range 3–174; n = 31), females (29.5; 2–165; 28) and juveniles (25; 9–121; 21) were similar (Kruskal-Wallis test: H = 0.55, df = 2, p = 0.759). On average, a location was collected for each dormouse every 3.3 monitoring days.

Sleeping associations and sleeping partners

Sixty-eight (85%) of the 80 marked dormice formed sleeping associations during their respective monitoring periods. Solitary sleepers (median ± interquartile range: 10.5 ± 19.0) were characterised by significantly fewer locations than associating individuals (34.0 ± 43.0; Mann-Whitney test: U = 629, $p = 0.003$).

The number of different sleeping partners per individual ranged from 0 to 15, with an average of 2.79. This value increased to 3.10 when individuals with less than 8 locations (i.e. likely unrepresentative samples; $n = 12$) were discarded from the analyses. Males and females did not differ in the number of sleeping partners (Table 2). They also did not differ statistically (U = 242.0, $p = 0.48$) in the number of adult opposite-sex partners. The number of adult male and female sleeping partners increased monotonically with the number of locations in both sexes (Spearman rank correlation: $r_s > 0.51$, $p < 0.01$) and the monitoring period ($r_s > 0.39$, $p < 0.05$). Therefore, to compare between dormouse categories and remove the bias generated by differing numbers of locations per individual, the partner index rather than the number of partners was considered. Indeed, in adults, the partner index was not correlated with the number of locations ($r_s = -0.002$, $p = 0.99$) nor the monitoring period ($r_s = -0.005$, $p = 0.97$).

The partner index ranged from 0 to 0.56 ($n = 68$), with an average of 0.084. This average value corresponds to the detection of, or association with, an additional sleeping partner about every 12 locations or 40 days. The partner index did not differ between sexes (males: 0.05 ± 0.00, $n = 21$; females: 0.05 ± 0.00, $n = 26$; U = 223.5, $p = 0.29$), but was significantly greater in juveniles than in adults (juveniles: 0.13 ± 0.17, $n = 21$; adults: 0.05 ± 0.06, $n = 47$; U = 230.5, $p < 0.001$).

Table 2. Number of sleeping partners of all sexes and ages for 47* focal adult woodland dormice located on at least 8 days (mean = 51; max = 174) between June 2010 and December 2012. Values are median (range).

	Sleeping partners' sex and age			
Focal adult dormice	Males	Females	Juveniles	Total
Males ($n = 21$)	1.00 (0–5)	1.00 (0–6)	0.00 (0–4)	2.00 (0–15)
Females ($n = 26$)	1.00 (0–3)	1.00 (0–4)	0.00 (0–4)	2.00 (0–9)
Mann-Whitney test	U = 299.0 $p = 0.56$	U = 576.5 $p = 0.29$	U = 267.0 $p = 0.86$	U = 258.50 $p = 0.75$

*Juveniles were not included as focal animals.

Dyadic sleeping associations and sexual and age differences in association index

A total of 496 dyadic sleeping associations involving 68 individual dormice were recorded during the study period (Appendix 2). These associations were determined based on the simultaneous monitoring of 112 dormouse dyads over an average of 104 days (range 2–435), yielding a mean of 39 (range 2–160) simultaneous locations. The majority of these associations involved only adults (59.8%), while adult–juvenile (21.4%) and juvenile dyads (18.8%) were less common. Discarding pairs of individuals that were located simultaneously on less than 8 different days (n = 12 pairs), the median association index (AI) was 8.33% (range 0.7–100%). The AI was negatively correlated with the monitoring period and/or the number of locations in MF, MJ and JJ dyads, but not in MM, FF and FJ dyads (Table 3). FF dyads (15.95 ± 15.60%) had a significantly higher AI than MF dyads (6.66 ± 11.90%; U = 185.0, p = 0.036) and MM dyads (4.50 ± 7.60%; U = 100.0, p = 0.007), although the number of simultaneous daily locations was similar for these three dyad categories (FF: 43 ± 36; MF: 42 ± 21; MM: 55 ± 40; H = 0.91, df = 2, p = 0.635). No differences were found between all other dyad categories (Figure 2), but there was a tendency for the AI of JJ dyads (11.91 ± 26.20%; U = 184.5, p = 0.065) to be greater than that of MM dyads; yet JJ dyads were located significantly less often than MM dyads (22 ± 34 days; U = 49.0, p = 0.017).

Table 3. Results of Spearman's rank correlation tests between the association index of different categories of sleeping association dyads in woodland dormice and the number of locations and monitoring period. Statistically significant correlations are highlighted in bold. M = male; F = female; J = Juvenile.

Dyad categories →	**MM (n = 10)**	**FF (n = 12)**	**MF (n = 34)**	**MJ (n = 9)**	**FJ (n = 14)**	**JJ (n = 21)**
Number of locations	r_s = -0.29	r_s = 0.39	**r_s = -0.43**	**r_s = -0.743**	r_s = -0.52	**r_s = -0.59**
	p = 0.421	p = 0.205	**p = 0.011**	**p = 0.022**	p = 0.056	**p = 0.005**
Monitoring period	r_s = -0.59	r_s = 0.28	r_s = -0.28	**r_s = -0.902**	r_s = -0.45	**r_s = -0.48**
	p = 0.072	p = 0.388	p = 0.106	**p = 0.001**	p = 0.103	**p = 0.027**

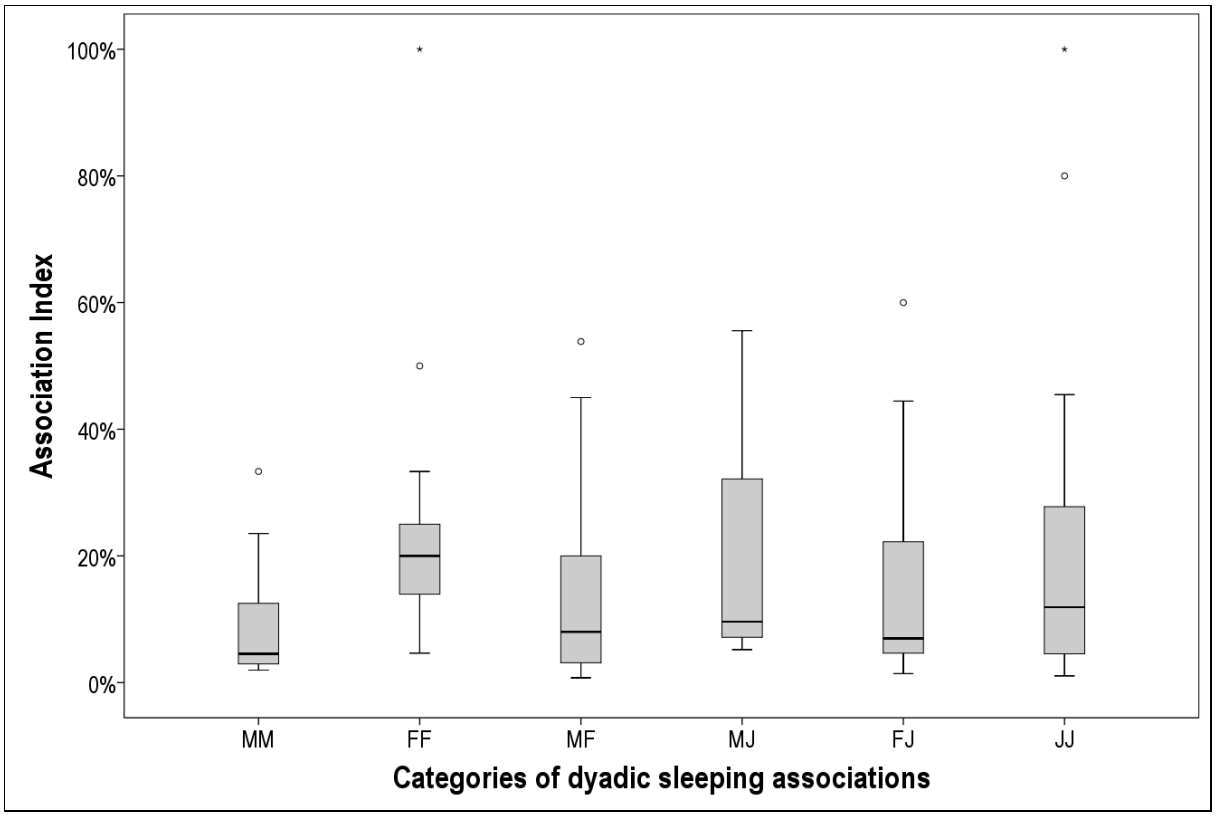


Figure 2. Differences or similarities in the association index (AI) between dyads composed of either adult male (M), adult female (F) or juvenile (J) woodland dormice. The thick horizontal lines represent the medians, the lower and upper hinges of the boxes represent the 1st (Q_1) and 3rd quartiles (Q_3), and the length of the boxes correspond to the interquartile ranges (IQR). The whiskers delimitate the ranges that contain all data points comprised within $Q_1 - 1.5 \times IQR$ and $Q_3 + 1.5 \times IQR$. The dots and stars represent outliers and extreme values.

Social network analysis

General characteristics

Figure 3 represents the social network of dormice marked and monitored during the study period, and involved at least once in a dyadic sleeping association (n = 68). The overall density of associations was *ca* 5% (Table 4). Other metrics are presented in Table 4. The diagram reveals a complex web of relatively even associations (edges) between most dyads. However, discarding dyads for which less than 8 simultaneous locations were collected, and separating the dataset into two periods (2010–2011: Figure 4; 2011–2012: Figure 5), provides information with better temporal synchronicity and therefore less bias.

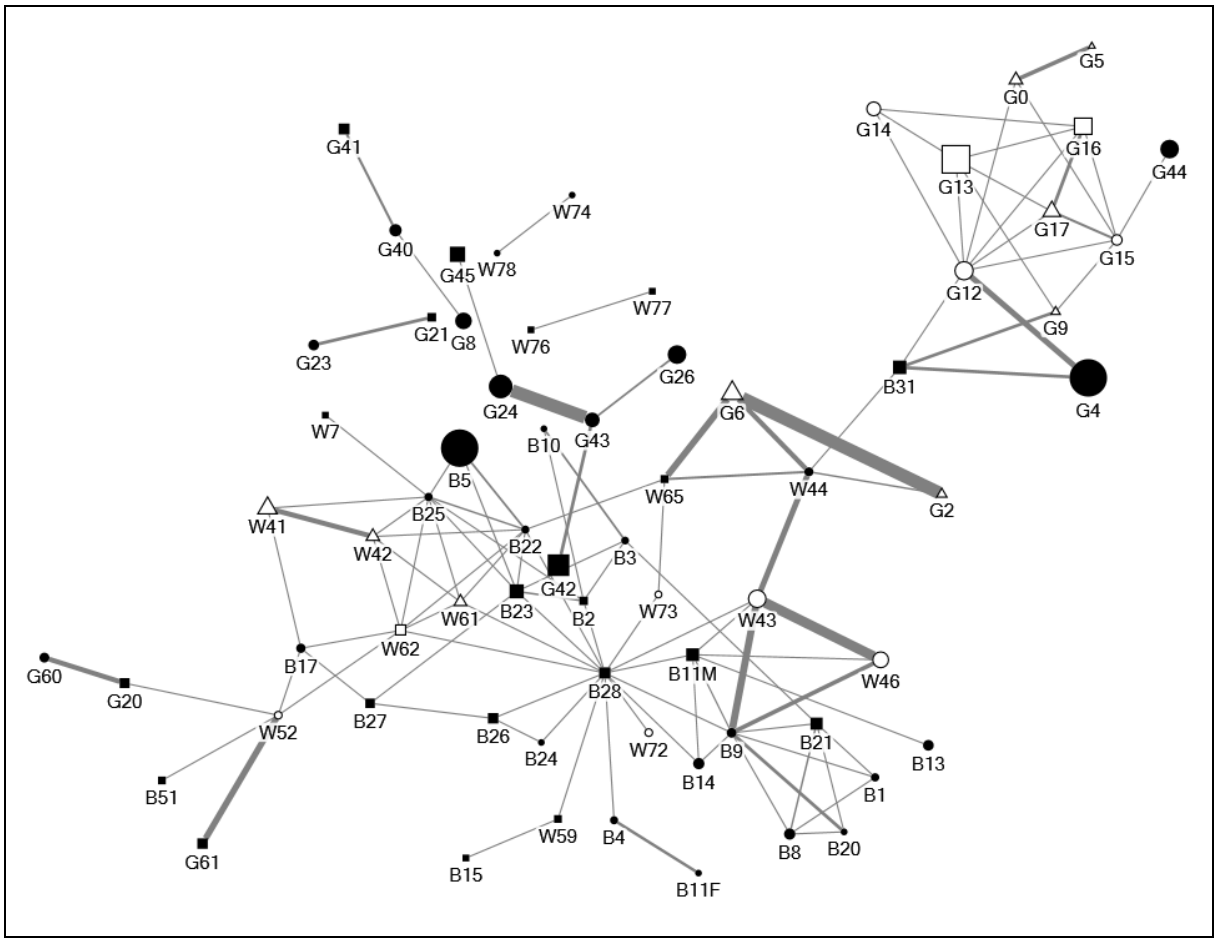


Figure 3. Overall social network diagram showing the dyadic sleeping associations (edges) between 68 woodland dormice (nodes) monitored and located between June 2010 and December 2012 (see list of dyads in Appendix 2). The letters and numbers correspond to the dormice identification codes. The size of the nodes is proportional to the partner index (a measure of the number of partners weighted based on the number of locations collected), while the thickness of the edges is proportional to the association index. ■: males; ●: females; □: juvenile males also tracked as adults; ○: juvenile females also tracked as adults; △: juveniles of either sex.

Most large nodes (e.g. for individuals B5, G4, G24 or G42) and some thick edges (e.g. G24–G43) present in Figure 3 no longer appear in the new outputs , which shows and confirms that individuals monitored for short periods often have biased and disproportionate partner and association indices. The outputs of Figures 4 and 5 are provided in the next sub-section, below. Thick edges, and therefore high association indices, not related to small sample sizes are mostly observed between juvenile–juvenile dyads (e.g. W41–W42, W43–W46 or G2–G6) or female–juvenile dyads (e.g. B9–W43, B9–W46 or G4–G12) (Figures 3–5).

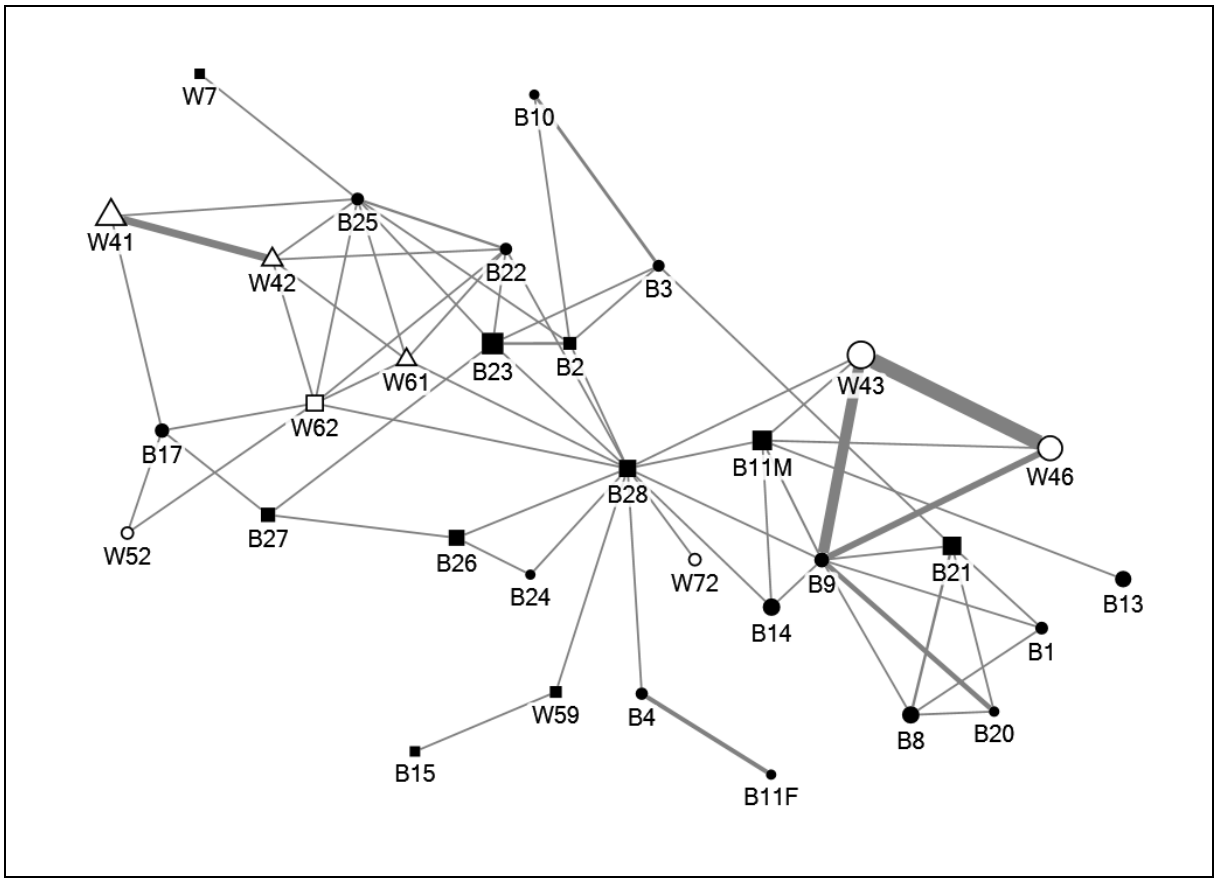


Figure 4. Social network diagram showing the dyadic sleeping associations (edges) between all woodland dormice (nodes) monitored and located between June 2010 and May 2011 (see list of dyads in Appendix 2). Dyads with less than 8 simultaneous locations were discarded. The letters and numbers correspond to the dormice identification codes. The size of the nodes is proportional to the partner index, while the thickness of the edges is proportional to the association index. ■: males; ●: females; □: juvenile males also tracked as adults; ○: juvenile females also tracked as adults; △: juveniles of either sex.

Comparison between the two monitoring periods

The social network diagrams for the two periods first differ visually. In 2010–2011 (Figure 4), most individuals were monitored in the north-western part of the study area. Possibly all adults in the population were marked and monitored, but only very few juveniles could be radio-tracked. The network appears very dense, with some males (B28, B11M, B21, B23) and females (B9, B22, B25) clearly having a greater number of partners than other same-sex individuals (Figure 4). In 2011–2012 (Figure 5), the monitoring was conducted equally in the north-western and south-eastern parts, more juveniles were equipped with radio-collars, and an estimated 20% of marked individuals could not be monitored, or not monitored for long enough. The network is less dense (Figure 5), with some clusters and isolated dyads (MM, FF, and MF). A cluster of juvenile dormice (which then transitioned to adulthood) is present on the left-hand side, while a cluster of two females (B22, B25) and three juveniles (W42, W61, W62) can be detected in the middle (Figure 5).

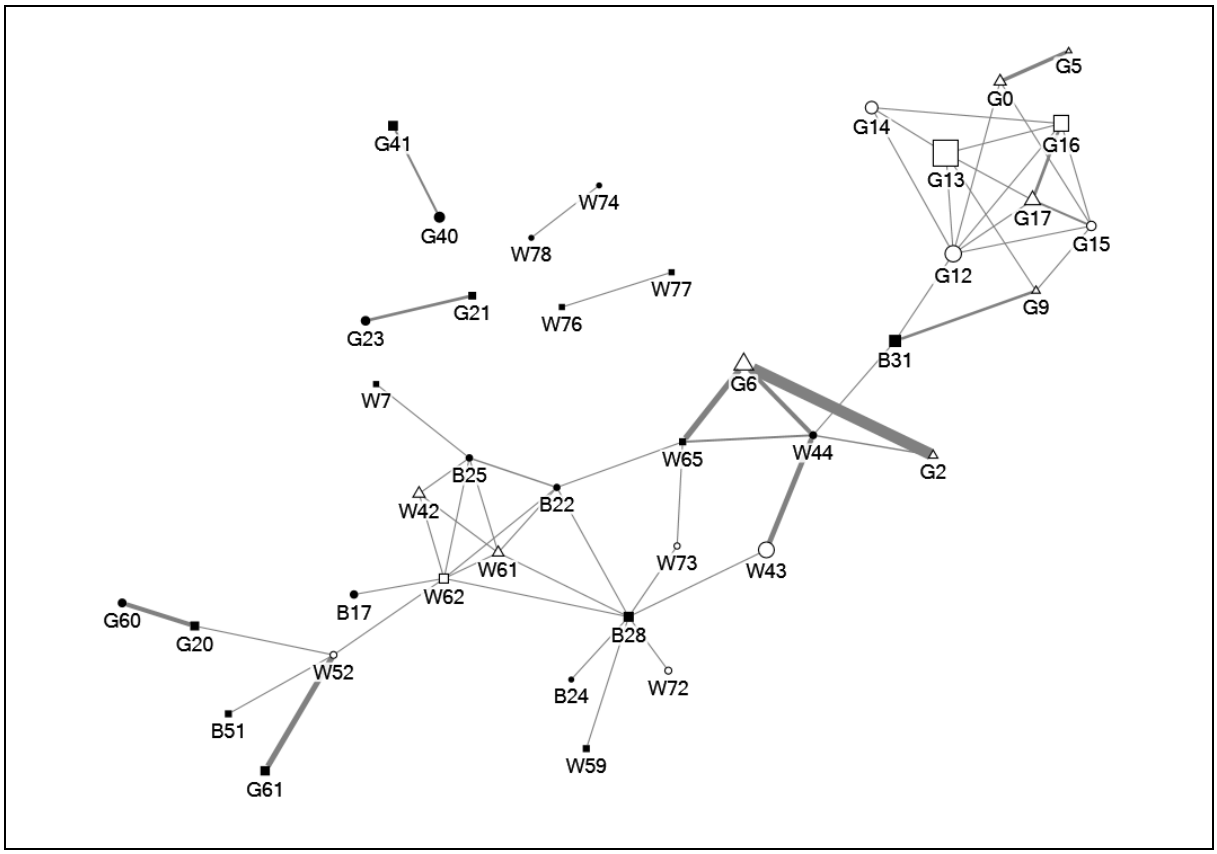


Figure 5. Social network diagram showing the dyadic sleeping associations (edges) between all woodland dormice (nodes) monitored and located between June 2011 and December 2012 (see list of dyads in Appendix 2). Dyads with less than 8 simultaneous locations were discarded. The letters and numbers correspond to the dormice identification codes. The size of the nodes is proportional to the partner index, while the thickness of the edges is proportional to the association index. ■: males; ●: females; □: juvenile males also tracked as adults; ○: juvenile females also tracked as adults; △: juveniles of either sex.

Statistically, the network density reached nearly 13% in 2010–2011 compared to 7% in 2011–2012 (Table 4). As a result, with exception of the eigenvector centrality, all network metrics were significantly larger during the first monitoring period (Table 4). In contrast, no differences were found between male and female metrics – density not considered – in both the overall and separate social networks (Mann-Whitney tests, $p > 0.05$ in all cases).

Table 4. Metrics calculated to describe and compare social networks in woodland dormice. Metrics for the 2010–2011 and 2011–2012 networks were compared with a Mann-Whitney (MW) test. Some individuals were tracked during both periods. Except for density (%), data are provided as median ± interquartile range. Significant results are indicated in bold. *n* = number of individuals in each social network.

Metrics	**Overall network for 2010–2012 (*n* = 68)**	**2010–2011 network (*n* = 32)**	**2011–2012 network (*n* = 40)**	**MW test (2010–2011 vs 2011-2012)**
Density	4.92%	12.90%	7.18%	-
Degree	3.00 ± 4.00	3.00 ± 3.00	2.00 ± 4.00	**U = 458.0, *p* = 0.035**
Eigenvector centrality	0.005 ± 0.019	0.023 ± 0.031	0.014 ± 0.045	U = 595.0, *p* = 0.593
Betweenness centrality	1.42 ± 52.00	7.38 ± 30.00	0.13 ± 32.59	**U = 317.5, *p* < 0.001**
Closeness centrality	0.005 ± 0.002	0.013 ± 0.003	0.008 ± 0.004	**U = 460.0, *p* = 0.041**
Clustering coefficient	0.17 ± 0.50	0.37 ± 0.80	0.00 ± 0.48	**U = 410.5, *p* = 0.007**

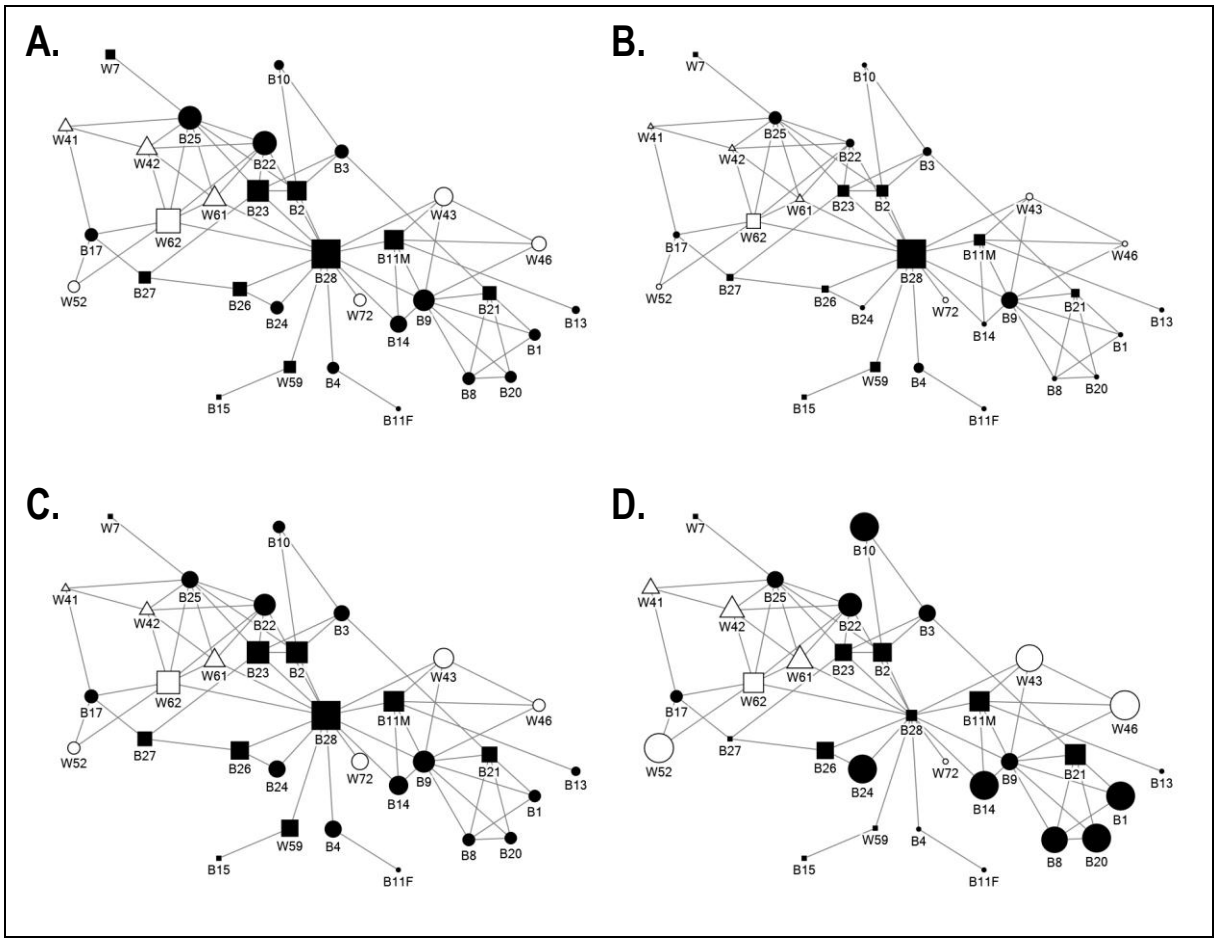


Figure 6. Social network diagram showing the dyadic sleeping associations (edges) between all woodland dormice (nodes) monitored and located between June 2010 and May 2011 (see list of dyads in Appendix 2). Dyads with less than 8 simultaneous locations were discarded. The letters and numbers correspond to the dormice identification codes. The size of the nodes is proportional to the **A.** eigenvector centrality, **B.** betweenness centrality, **C.** closeness centrality, and **D.** clustering coefficient (see definitions in Table 1). ■: males; ●: females; □: juvenile males also tracked as adults; ○: juvenile females also tracked as adults; △: juveniles of either sex.

Using individual network metrics (Appendix 3) to calibrate the size of the nodes provide further insights. For the period 2010–2011, Figures 6A and 6C indicate that a small number of adult males (B28, B23, B11M, B2) and females (B22, B25, B9) were characterized by both a large eigenvector and closeness. Figure 6B demonstrates the pivotal role played by male B28 in the network as a direct or indirect link between all individuals, whereas Figure 6D shows a cluster of closely associated adult females (B1, B8 and B20), juveniles (W43 and W46; W42, W61 and W62) or several relatively isolated individuals.

In 2011–2012, some individuals (B28, B22, B25 and W62, now an adult) continued to be characterized by a large eigenvector; some members (e.g. G12, G13, G14, G15, G16, G17) of a group of interconnected juveniles also had a large eigenvector (Figure 7A). Contrary to what was observed during the previous period (Figure 6B), several males (B31, B28, W62,

W65) and females (W44, G12, W43, W52, B22) played a pivotal role in the network by ensuring connectivity between different parts of the network (Figure 7B). As could be expected, the four isolated dyads (G21–G23, G40–G41, W74–W78, W76–W77) had the larger closeness centrality (Figure 7C). Similarly the two main clusters mentioned earlier – a group of juveniles (G0, G5, G9, G12, G13, G14, G15, G16, G17); and females (B22, B25) and juveniles (W42, W61 and W62) – had the larger clustering coefficients (Figure 7D).

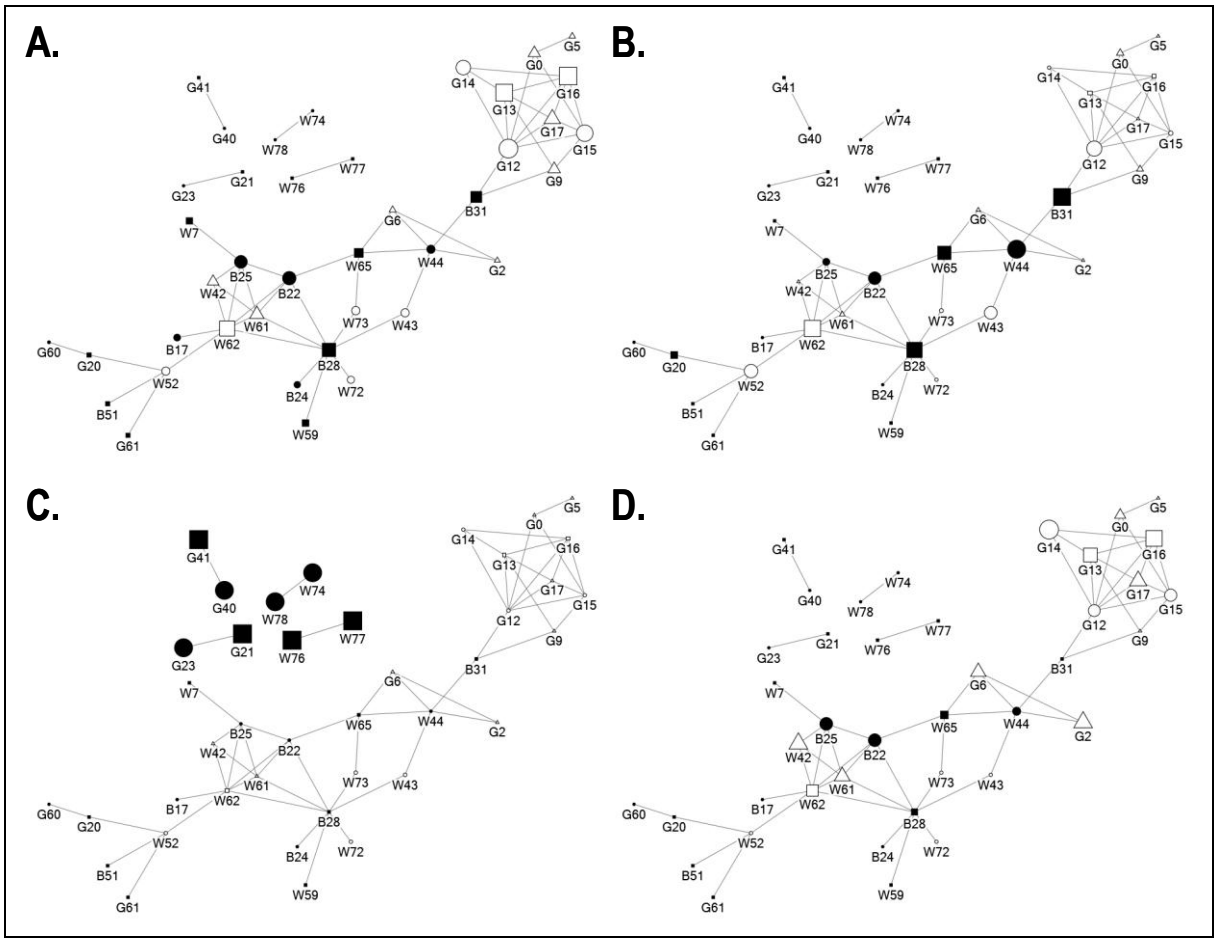


Figure 7. Social network diagram showing the dyadic sleeping associations (edges) between all woodland dormice (nodes) monitored and located between June 2011 and December 2012 (see list of dyads in Appendix 2). Dyads with less than 8 simultaneous locations were discarded. The letters and numbers correspond to the dormice identification codes. The size of the nodes is proportional to the **A.** eigenvector centrality**, B.** betweenness centrality, **C.** closeness centrality, and **D.** clustering coefficient (see definitions in Table 1). ■: males; ●: females; □: juvenile males also tracked as adults; ○: juvenile females also tracked as adults; △: juveniles of either sex.

Intra- and intersexual dyadic associations

I dissected the overall social network to display only subcategories of dyads; this provides further important information on intrasexual, intersexual and age-related associations. The social network diagram of male–female dyads shows that most adult individuals in the population were connected by either a thread or a more complex network (Figure 8). All males and females formed a sleeping association with a least one opposite-sex individual, and sometimes with several individuals at different times. Figure 9B shows that most adult females had one adult female sleeping partner, and that these dyadic associations were isolated and similarly strong (thick edges). In two cases, three females (B1–B8–B9 and B8–B9–B20) formed detectable dyads. A totally different pattern was observed for male–male sleeping associations (Figure 9A). With the exception of B2–B23 and B2–B28, most dyadic associations were weak (as indicated by thinner lines). In addition, most males were involved in two or more dyadic sleeping associations, and they were all interconnected in some way (Figure 9A). The only exception was represented by W76 and W77, two males which were tracked at the south-eastern extremity of the study area.

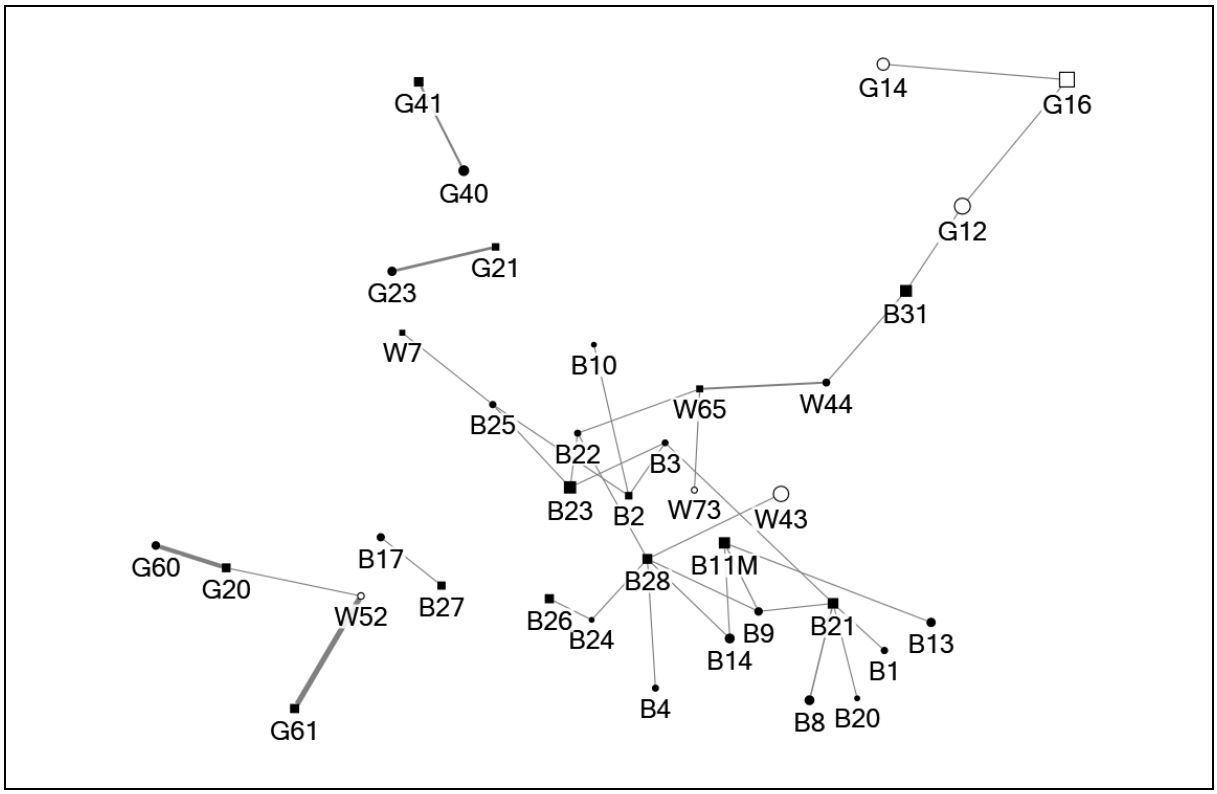


Figure 8. Social network diagram showing the dyadic sleeping associations (edges) between male and female (MF) woodland dormice (nodes) monitored and located between June 2010 and December 2012 (see list of dyads in Appendix 2). Dyads with less than 8 simultaneous locations were discarded. The letters and numbers correspond to the dormice identification codes. The size of the nodes is proportional to the partner index, while the thickness of the edges is proportional to the association index. ■: males; ●: females; □: adult males that were initially tracked as juveniles; ○: adult females that were initially tracked as juveniles.

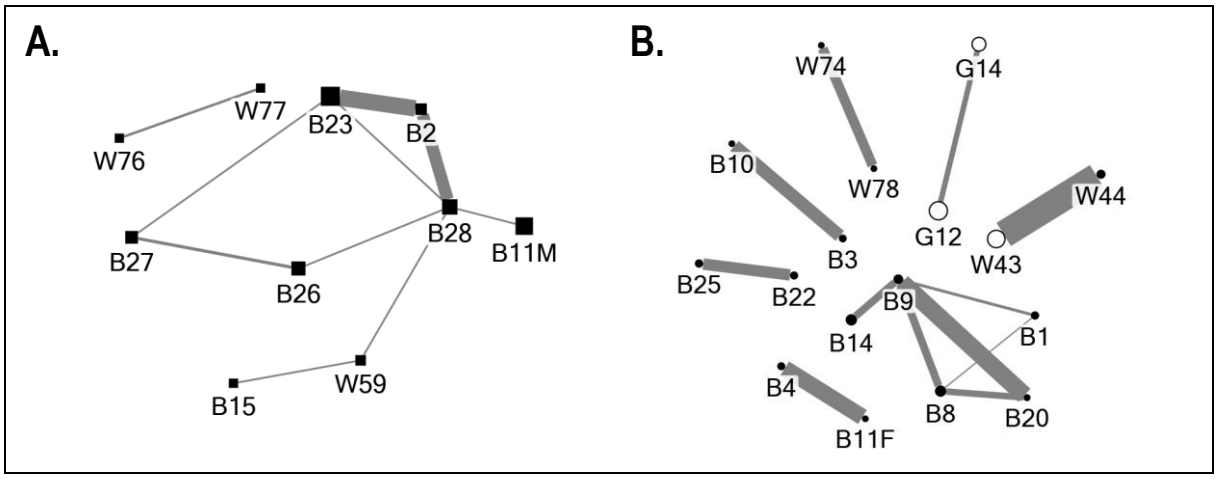


Figure 9. Social network diagram showing the dyadic sleeping associations (edges) between **A.** male (MM) and **B.** female (FF) woodland dormice (nodes) monitored and located between June 2010 and December 2012 (see list of dyads in Appendix 2). Dyads with less than 8 simultaneous locations were discarded. The letters and numbers correspond to the dormice identification codes. The size of the nodes is proportional to the partner index, while the thickness of the edges is proportional to the association index. ■: males; ●: females; □: adult males that were initially tracked as juveniles; ○: adult females that were initially tracked as juveniles.

Male–juvenile and female–juvenile dyadic associations

Adult–juvenile interactions can be considered from the "viewpoint" of either the juveniles or the adults. Figure 9A clearly indicates that juveniles of both sexes (where sex was determined) each engaged in sleeping associations with a single adult male – with the exception of juvenile female G12 which was never found associated with an adult male. On the other hand, juveniles (often of undetermined sex) formed dyadic associations with up to three different females (Figure 10B). Adult females were found to form dyadic associations with between two and three different juveniles; adult males on their own associated with between one and four juveniles (in the last case with young from two different litters). In some cases, these relationships were characterised by very large association indices (i.e. thick lines; e.g. B31–G9, W65–G6, W44–G6–G2, and B9–W43–W46).

Juvenile–juvenile dyadic associations

Some of the dyadic associations between juveniles were exclusive and strong (G2–G6, W43–W46) (Figure 11). Others were strong too (W41–W42, G0–G5, G16–G17), but one or both of the partners were also involved in dyadic associations with other individuals. W42, G2 and G17 were associated with three different juvenile individuals, while G13 had five juvenile sleeping partners during his monitoring period.

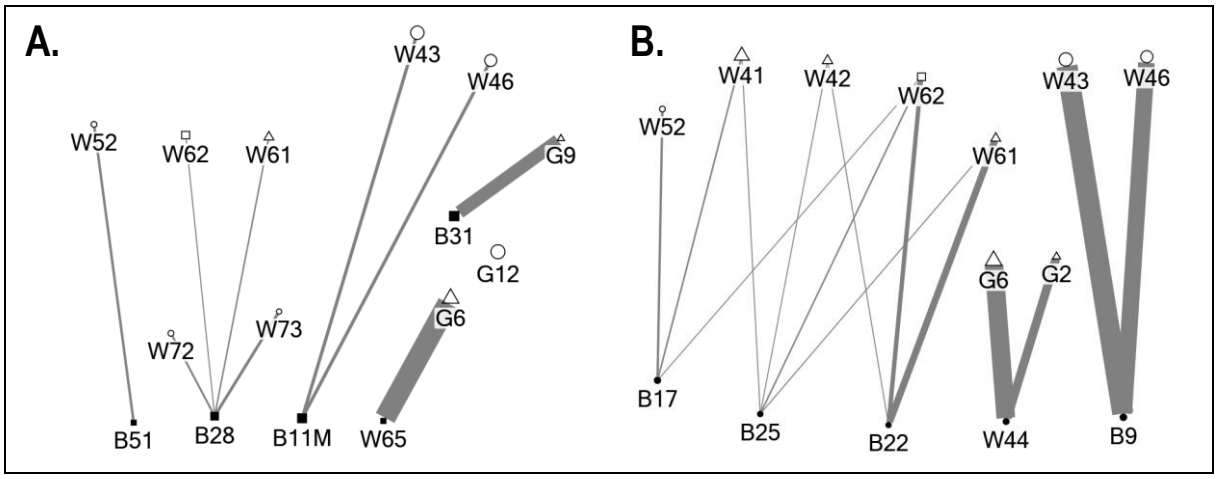


Figure 10. Social network diagram showing the dyadic sleeping associations (edges) between **A.** male and juvenile (MJ) and **B.** female and juvenile (FJ) woodland dormice (nodes) monitored and located between June 2010 and December 2012 (see list of dyads in Appendix 2). Dyads with less than 8 simultaneous locations were discarded. The letters and numbers correspond to the dormice identification codes. The size of the nodes is proportional to the partner index, while the thickness of the edges is proportional to the association index. ■: males; ●: females; □: juvenile males; ○: juvenile females; △: juveniles of either sex.

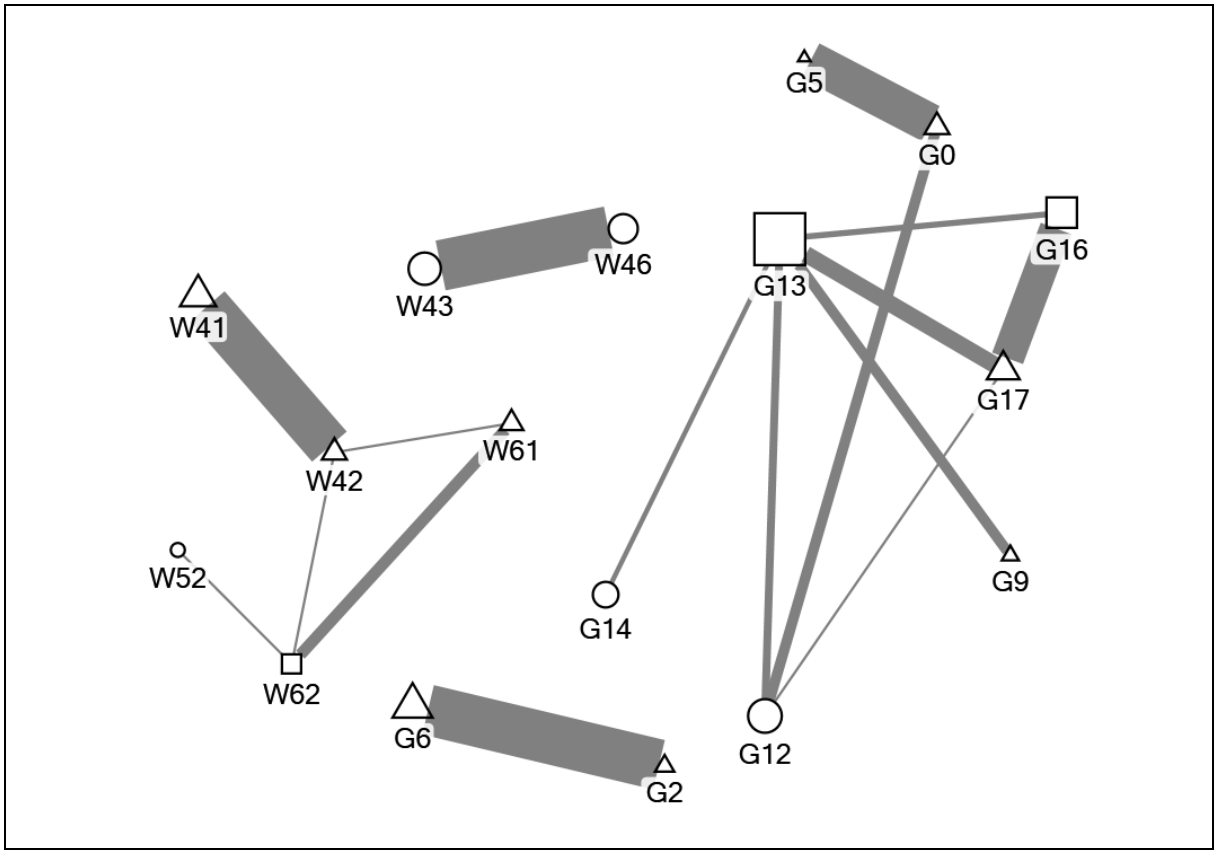


Figure 11. Social network diagram showing the dyadic sleeping associations (edges) between juvenile (JJ) woodland dormice (nodes) monitored and located between June 2010 and December 2012 (see list of dyads in Appendix 2). Dyads with less than 8 simultaneous locations were discarded. The letters and numbers correspond to the dormice identification codes. The size of the nodes is proportional to the partner index, while the thickness of the edges is proportional to the association index. □: juvenile males; ○: juvenile females; △: juveniles of either sex.

Discussion

The social structure and the patterns of dyadic sleeping associations of a free-living population of woodland dormice were investigated using association indices and social network analysis. My results showed that a high proportion of marked dormice (85%) formed sleeping associations during the time they were monitored. In addition, solitary sleepers were observed for significantly shorter periods (with fewer locations) than associating individuals.

Woodland dormice had an average of 3 sleeping partners, with as many as 10–15 different co-sleepers for some individuals. Males and females did not differ in the number of sleeping partners, nor in the number of opposite-sex sleeping partners. It is plausible to link the high number of sleeping partners to the ephemeral nest use by woodland dormice (Lamani 2014). If woodland dormice frequently shift nests, this then increases the probability of meeting potentially new sleeping partners. Nesting partners might be widely dispersed in several trees on any night, thus promoting different associations in the nests. Similar explanations were given in studies of roost switching in Spix's disc-winged bat *Thyroptera tricolor* (Vonhof *et al.* 2004), and for big brown bats *Eptesicus fusccus* (Willis & Brigham 2004).

Another explanation for these patterns could be the sociable nature of the species, as recorded in a laboratory study on sociability (Chapter 5), demonstrating that woodland dormice have an intrinsic motivation to be with conspecifics rather than be alone. Therefore, woodland dormice are more likely to actively seek social partners, thus associating with conspecifics in the population. Under such circumstances, it is then expected that dormice would be predisposed to form novel associations, thus leading to higher number of sleeping partners (connections and contacts) over time. Evidence of active associations has been found in Bechstein's bats *Myotis bechsteinii* sleeping/roosting association patterns (Kerth & König 1999).

I predicted that the association index would be higher in female–female dyads than in male–female or male–male dyads. Indeed, females had strong associations with other females and formed relationships with specific individual females, resulting in non-random associations. The social network diagram of adult females revealed the presence of pairs or trios of potentially communally breeding females. The existence of non-random association in females could be due to genetic relatedness (Kapsalis & Berman 1996) and/or through similar reproductive states, where females may prefer to associate with individuals that have similar reproductive status. This tendency for females to associate with conspecifics with similar

reproductive conditions has been found in Bechstein's bats *Myotis bechsteinii* (Kerth & König 1999) and big brown bat *Eptesicus fuscus* (Willis & Brigham 2004). Formation of strong associations in females might increase energetic benefits and could lead to cooperative behaviours (Willis & Brigham 2004; Garroway & Broders 2007, 2008). Even though direct observations of cooperative behaviours were not recorded during radio-tracking, evidence of cooperative nest building and social huddling in females were documented in another study (Chapter 6). In support, communal nesting by female woodland dormice have been reported from previous work on nest-box use on the same population (Madikiza *et al.* 2012) and also in the edible dormouse *Glis glis* (Pilastro 1992; Marin & Pilastro 1994; Sevianu & David 2012), as well as in the forest dormouse *Dryomys nitedula* (Juskaitis & Kertuka 2016).

Male–male association in woodland dormice showed ephemeral and weak relationships in their association patterns. The social network diagram of males revealed that most males were involved in two or more dyadic sleeping associations, and all males but two were interconnected in some way. The short-term nature of these relationships could suggest that: 1) males dissociate from their male partners after a certain period; and 2) that neighbouring males can casually meet but not share territories. The recorded casual acquaintances in males may be explained by the mating strategies of the species, where males form coalitions with other males during competitive or aggressive periods (e.g. chimpanzees *Pan troglodytes*; Watts 1998). However, the strength and the robust nature of these coalitions may depend highly on relatedness, familiarity and mutual tolerance and social status (Olson & Blumstein 2009). In a review, Schoof *et al.* (2009) also mentioned that strong association relationships occur among males because of increased exposure, familiarity and likelihood of meeting that individual. In concurrent laboratory studies (Chapter 6), male dormice were sociable with familiar individuals, showing less aggression and sharing space with them. In addition, the recorded male–male associations in the current study may have social benefits such as huddling with other males. If male woodland dormice form related or familiar associations, cooperative behaviours such as social huddling and mate searching are expected to take place when ambient temperatures are low and when mating season commences. Taken together, formation of male–male relationships indicate social tolerance which could lead to male aggregations.

The mating system of woodland dormouse is hypothesised to be promiscuous (Madikiza *et al.* 2012). In such a system, males and females mate randomly with any number of partners (Clutton-Brock 1989). Based on this putative mating system, I predicted that the number of opposite sex sleeping partners would increase with the duration of the monitoring period in

both males and females, because adults are expected to have several partners, as observed in the sleeping site patterns of promiscuous mating species such as the gray mouse lemurs *Microcebus murinus* (Radespiel 2001) and golden brown mouse lemur *Microcebus ravelobensis* (Weidt *et al.* 2004). Indeed, the number of opposite-sex sleeping partners increased with the duration of the monitoring period in both male and female woodland dormice. Male–female dyadic association consisted of a high number of partners or dyadic relationships. This means that woodland dormice form random and ephemeral associations with opposite-sex conspecifics. Males are indeed only expected to briefly associate with females in order to assess their reproductive state.

The strong and exclusive dyadic associations of juveniles, possibly indicated that juveniles maintained social relationships with specific individuals. These are likely to be relationships between first and second littermates that grow up together, forming strong social relationships, thus allowing for formation of early social bonds. Dyadic association of adults with juveniles (female–juvenile and male-juvenile) indicated that adults and juveniles form strong relationships and is similar to previous field observations that juveniles can be found in nests with two or more females (Madikiza & Do Linh San, in prep.). Male-juvenile associations indicated that males co-slept with a number of juveniles. These associations could function as huddling groups and possibly to reduce predation risk.

In conclusion, using social network analysis, my study firstly demonstrated the number of partners by sex and age, and the strength and regularity of individual dyadic associations in woodland dormice. My findings indicate regular female-female and juvenile-juvenile associaions, which could indicate kin groups. While transient male-male groups indicate a thermoregulatory and/or mating advantages enjoyed reciprocally.The strength and regularity of associations between certain individuals suggests recognition of individuals and potentially exclusive grouping. Therefore sleeping associations mirrored the social tendencies of the species as well as the strong affinity between certain individuals. These affinities are sex specific relating to the need to huddle on the one hand and their putative promiscuous mating strategies on the other hand. Future studies should consider assessing the genetic relationships of sleeping partners and the frequency of kin vs non-kin groups.

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Appendix 1. List of the 80 African woodland dormice *Graphiurus murinus* that were monitored during the period June 2010 to December 2012. The "/" indicates that some individuals were monitored both as juveniles and adults. M = adult male; F = adult female; J = Juvenile; ? = sex undetermined; MD = monitoring days (period); TP = number of tracking periods; TD = number of tracking days; No. locations = number of sleeping locations; Selected? = animals with ≥8 locations (Yes) or <8 locations (No); %M = percentage of days of the monitoring period during which sleeping locations were collected; Partner? = whether or not the monitored dormouse had at least one sleeping partner during its monitoring period; A = number of adult sleeping partners; M = number of adult male sleeping partners; F = number of adult female sleeping partners; OS = number of opposite-sex adult sleeping partners; J = number of juvenile sleeping partners; No. partners = total number of partners; Partner index = number of partners divided by the number of locations.

Code	Age/ Sex	First Record	Last Record	MD	Radio-tracked?	TP	TD	No. locations	Selected?	%M	Partner?	A	M	F	OS	J	No. partners	Partner Index
B1	F	12.07.2010	25.11.2010	137	Yes	2	88	59	Yes	43	Yes	3	1	2	1	0	3	0.05
B10	F	02.07.2010	04.04.2011	277	Yes	3	123	88	Yes	32	Yes	2	1	1	1	0	2	0.02
B11F	F	14.03.2011	05.05.2011	53	Yes	1	54	45	Yes	85	Yes	1	0	1	0	0	1	0.02
B11M	M	13.03.2011	13.05.2011	62	Yes	1	62	51	Yes	82	Yes	3	1	3	3	2	6	0.12
B13	F	13.04.2011	25.04.2011	13	Yes	1	13	12	Yes	92	Yes	1	1	0	1	0	1	0.08
B14	F	14.03.2011	21.04.2011	39	Yes	1	39	32	Yes	82	Yes	1	1	0	1	0	3	0.09
B15	M	13.03.2011	22.05.2011	71	Yes	1	71	61	Yes	86	Yes	1	1	0	0	0	1	0.02
B17	F	03.10.2011	28.07.2012	300	Yes	2	67	62	Yes	21	Yes	2	1	1	1	2	4	0.06
B2	M	12.06.2010	25.11.2010	167	Yes	2	125	97	Yes	58	Yes	5	3	2	2	0	5	0.05
B20	F	12.06.2010	24.11.2010	166	Yes	2	116	86	Yes	52	Yes	3	1	2	1	0	3	0.03
B21	M	03.10.2010	25.11.2010	54	Yes	1	54	48	Yes	89	Yes	0	0	5	5	0	5	0.10
B22	F	03.10.2010	11.12.2011	435	Yes	3	160	144	Yes	33	Yes	4	3	1	3	3	7	0.05
B23	M	02.10.2010	25.11.2010	55	Yes	1	55	50	Yes	91	Yes	7	3	4	4	0	7	0.14
B24	F	12.06.2010	25.11.2010	167	Yes	2	117	89	Yes	53	Yes	2	2	0	2	0	2	0.02
B25	F	15.06.2010	01.09.2011	444	Yes	4	224	174	Yes	39	Yes	5	3	2	3	4	9	0.05
B26	M	03.10.2010	28.03.2011	177	Yes	1	15	39	Yes	22	Yes	3	2	1	1	0	3	0.08
B27	M	03.10.2010	25.11.2010	54	Yes	1	54	48	Yes	89	Yes	3	2	1	1	0	3	0.06
B28	M	03.10.2010	03.07.2012	640	Yes	4	191	165	Yes	26	Yes	11	5	6	6	4	15	0.09
B3	F	15.06.2010	23.11.2010	162	Yes	2	112	89	Yes	55	Yes	3	3	1	3	0	4	0.04
B31	M	28.01.2012	17.12.2012	325	Yes	2	95	31	Yes	10	Yes	3	1	2	2	1	4	0.13
B4	F	14.03.2011	01.05.2011	49	Yes	1	50	42	Yes	86	Yes	2	1	1	1	0	2	0.05
B5	F	04.10.2010	07.10.2010	4	No	0	0	3	No	75	Yes	3	1	2	1	0	3	1.00
B51	M	23.07.2011	29.11.2011	130	Yes	1	40	23	Yes	18	Yes	1	0	1	1	1	1	0.04
B7	F	12.06.2010	13.03.2011	275	Yes	2	29	26	Yes	9	No	0	0	0	0	0	0	0.00
B8	F	13.07.2010	31.10.2010	111	Yes	2	62	43	Yes	39	Yes	4	1	3	1	0	4	0.09
B9	F	02.07.2010	18.05.2011	321	Yes	3	165	129	Yes	40	Yes	7	3	4	3	2	9	0.07
G0	J	28.04.2012	17.06.2012	51	Yes	1	55	23	Yes	45	Yes	0	0	0		3	3	0.13
G11	M	26.04.2012	04.05.2012	9	Yes	1	14	8	Yes	89	No	0	0	0	0	0	0	0.00
G12	J/F	05.02.2012	17.12.2012	317	Yes	1	53	34	Yes	11	Yes	4	3	1		4	8	0.24

Appendix 1. Continued.

Code	Age/ Sex	First Record	Last Record	MD	Radio-tracked?	TP	TD	No locations	Selected?	%M	Partner?	A	M	F	OS	J	No partners	Partner Index
G13	J/M	05.02.2012	14.05.2012	100	No	0	0	9	Yes	9	Yes	0	0	0		5	5	0.56
G14	J/F	05.02.2012	02.12.2012	302	Yes	1	54	22	Yes	7	Yes	2	1	1		1	3	0.14
G15	J/F	05.02.2012	29.10.2012	268	Yes	3	171	77	Yes	29	Yes	1	0	1		5	6	0.08
G16	J/M	05.02.2012	14.10.2012	253	Yes	1	23	25	Yes	10	Yes	2	0	2		3	5	0.20
G17	J	05.02.2012	23.06.2012	140	Yes	1	38	18	Yes	13	Yes	0	0	0		4	4	0.22
G2	J	20.02.2012	17.06.2012	119	Yes	1	57	26	Yes	22	Yes	1	0	1		1	2	0.08
G20	M	21.02.2012	02.12.2012	286	Yes	1	68	28	Yes	10	Yes	1	0	1	1	0	2	0.07
G21	M	24.09.2012	29.10.2012	36	No	0	0	19	Yes	53	Yes	1	0	1	1	0	1	0.05
G23	F	07.10.2012	29.10.2012	23	No	0	0	12	Yes	52	Yes	1	1	0	1	0	1	0.08
G24	F	14.10.2012	29.10.2012	16	Yes	1	16	5	No	31	Yes	2	1	1	1	0	2	0.40
G26	F	28.09.2012	04.10.2012	7	Yes	1	7	4	No	57	Yes	1	0	1	0	0	1	0.25
G4	M	05.02.2012	06.02.2012	2	No	0	0	2	No	100	Yes	2	1	1	1	0	2	1.00
G40	F	27.09.2012	29.10.2012	33	Yes	1	33	18	Yes	55	Yes	2	1	1	1	0	2	0.11
G41	M	24.09.2012	28.10.2012	35	Yes	1	38	12	Yes	34	Yes	1	0	1	1	0	1	0.08
G42	M	28.09.2012	30.09.2012	3	Yes	1	6	3	No	100	Yes	1	1	1	1	0	1	0.33
G43	F	28.09.2012	14.11.2012	48	Yes	1	50	19	Yes	40	Yes	3	1	2	1	0	3	0.16
G44	F	28.09.2012	02.12.2012	66	No	0	0	4	No	6	Yes	1	0	1	0	0	1	0.25
G45	M	14.10.2012	29.10.2012	16	No	0	0	6	No	38	Yes	1	0	1	1	0	1	0.17
G46	M	29.10.2012	14.11.2012	17	Yes	1	17	4	No	24	No	0	0	0	0	0	0	0.00
G48	M	12.11.2012	17.12.2012	36	No	0	0	5	No	14	No	0	0	0	0	0	0	0.00
G5	J	26.04.2012	23.06.2012	59	Yes	1	47	31	Yes	53	Yes	0	0	0		1	1	0.03
G6	J	29.04.2012	09.05.2012	11	Yes	1	14	9	Yes	82	Yes	0	0	0		1	3	0.33
G60	F	24.09.2012	14.10.2012	21	Yes	1	19	14	Yes	67	Yes	1	1	0	1	0	1	0.07
G61	M	28.09.2012	14.10.2012	17	Yes	1	23	13	Yes	76	Yes	0	0	1	1	0	1	0.08
G8	F	27.09.2012	04.10.2012	8	Yes	1	8	5	No	63	Yes	1	0	1	0	0	1	0.20
G9	J	05.02.2012	02.08.2012	180	Yes	2	116	49	Yes	27	Yes	1	1	0		2	3	0.06
W41	J	23.03.2011	07.05.2011	46	No	0	0	11	Yes	24	Yes	1	0	2		1	3	0.27
W42	J	23.03.2011	13.08.2011	144	Yes	2	35	39	Yes	27	Yes	2	0	2		3	5	0.13
W43	J/F	03.05.2011	09.11.2011	191	Yes	2	36	23	Yes	12	Yes	4	2	2		1	5	0.22
W44	F	08.11.2011	03.07.2012	239	Yes	3	171	83	Yes	35	Yes	3	2	1	2	2	5	0.06
W45	J	01.08.2011	13.08.2011	13	Yes	1	13	12	Yes	92	No	0	0	0		0	0	0.00
W46	J	03.05.2011	21.05.2011	19	Yes	1	19	17	Yes	89	Yes	2	1	1		1	3	0.18
W52	J/F	01.04.2011	02.12.2012	612	Yes	5	253	121	Yes	20	Yes	4	3	1		1	5	0.04
W59	M	28.04.2011	28.10.2011	184	Yes	3	67	47	Yes	26	Yes	2	2	0	0	0	2	0.04
W61	J/?	21.03.2011	19.10.2011	213	Yes	1	5	43	Yes	20	Yes	3	1	2		2	5	0.12

Appendix 1. Continued.

Code	Age/ Sex	First Record	Last Record	MD	Radio-tracked?	TP	TD	No locations	Selected?	%M	Partner?	A	M	F	OS	J	No partners	Partner Index
W62	J/M	21.03.2011	15.06.2012	453	Yes	1	63	95	Yes	21	Yes	4	1	3		3	7	0.07
W64	M	14.10.2011	19.10.2011	6	Yes	1	7	5	No	83	No	0	0	0	0	0	0	0.00
W65	M	29.10.2011	03.07.2012	249	Yes	3	178	89	Yes	36	Yes	3	0	3	3	1	4	0.04
W66	M	30.10.2011	02.11.2011	4	Yes	1	5	4	No	100	No	0	0	0	0	0	0	0.00
W7	M	25.08.2011	30.01.2012	159	Yes	3	74	54	Yes	34	Yes	1	0	1	1	0	1	0.02
W71	F	18.10.2011	01.11.2011	15	Yes	1	18	9	Yes	60	No	0	0	0	0	0	0	0.00
W72	J/F	21.04.2011	01.09.2011	134	Yes	1	32	24	Yes	18	Yes	1	1	0		0	1	0.04
W73	J/F	30.07.2011	30.11.2011	124	Yes	2	80	63	Yes	51	Yes	2	2	0		0	2	0.03
W74	F	23.11.2011	20.04.2012	150	Yes	1	61	33	Yes	22	Yes	1	0	1	0	0	1	0.03
W76	M	24.10.2011	11.12.2011	49	Yes	1	55	37	Yes	76	Yes	1	1	0	0	0	1	0.03
W77	M	30.10.2011	11.12.2011	43	Yes	1	44	34	Yes	79	Yes	1	1	0	0	0	1	0.03
W78	F	31.10.2011	09.04.2012	162	Yes	2	78	42	Yes	26	Yes	1	0	1	0	0	1	0.02
W79	F	24.11.2011	13.03.2012	111	Yes	1	42	17	Yes	15	No	0	0	0	0	0	0	0.00
W80	F	29.01.2012	21.02.2012	24	Yes	1	25	15	Yes	63	No	0	0	0	0	0	0	0.00
W81	M	30.01.2012	16.03.2012	47	Yes	1	48	27	Yes	57	No	0	0	0	0	0	0	0.00
W82	F	05.02.2012	17.06.2012	134	Yes	2	126	54	Yes	40	No	0	0	0	0	0	0	0.00

Appendix 2. List of the 112 sleeping dyads between 68 woodland dormice which were recorded during the period June 2010 to December 2012. M = adult male; F = adult female; J = Juvenile; SL = simultaneous location; MD = monitoring days (period); Selected? = sleeping dyads with ≥8 simultaneous locations (Yes) or <8 simultaneous locations (No); ST = number of times both partners were found sleeping together; NSL = number of simultaneous locations; ST/NSL = association index; AI = association index expressed as a percentage.

Dyad	Age/Sex	First SL	Last SL	MD	Period	Selected?	ST	NSL	ST/NSL	AI
B11M–B13	MF	13.04.2011	25.04.2011	13	2010/2011	Yes	1	12	0.083	8.33
B11M–B14	MF	14.03.2011	21.04.2011	39	2010/2011	Yes	2	32	0.063	6.25
B11M–B28	MM	13.03.2011	13.05.2011	62	2010/2011	Yes	2	52	0.038	3.85
B11M–W43	MJ	03.05.2011	13.05.2011	11	2010/2011	Yes	1	10	0.100	10.00
B11M–W46	MJ	03.05.2011	13.05.2011	11	2010/2011	Yes	1	10	0.100	10.00
B14–B28	MF	13.03.2011	21.04.2011	40	2010/2011	Yes	2	34	0.059	5.88
B15–W59	MM	28.04.2011	21.05.2011	24	2010/2011	Yes	1	22	0.045	4.55
B17–B27	MF	03.10.2010	25.11.2010	54	2010/2011	Yes	2	40	0.050	5.00
B17–W41	FJ	23.03.2011	07.05.2011	46	2010/2011	Yes	1	16	0.063	6.25
B17–W52	FJ	01.04.2011	19.04.2011	19	2010/2011	Yes	1	13	0.077	7.69
B17–W62	FJ	21.03.2011	28.07.2011	130	Both	Yes	2	43	0.047	4.65
B1–B21	MF	03.10.2010	25.11.2010	54	2010/2011	Yes	8	46	0.174	17.39
B1–B8	FF	13.07.2010	31.10.2010	111	2010/2011	Yes	2	43	0.047	4.65
B1–B9	FF	12.07.2010	25.11.2010	137	2010/2011	Yes	5	65	0.077	7.69
B20–B21	MF	10.10.2010	24.11.2010	46	2010/2011	Yes	1	43	0.023	2.33
B22–B23	MF	02.10.2010	25.11.2010	55	2010/2011	Yes	4	51	0.078	7.84
B22–B25	FF	03.10.2010	01.09.2011	334	Both	Yes	27	120	0.225	22.50
B22–B28	MF	03.10.2010	11.12.2011	435	Both	Yes	10	160	0.063	6.25
B22–W42	FJ	15.03.2011	13.08.2011	152	2010/2011	Yes	1	50	0.020	2.00
B22–W61	FJ	19.03.2011	19.10.2011	215	Both	Yes	13	72	0.181	18.06
B22–W62	FJ	21.03.2011	11.12.2011	266	Both	Yes	15	120	0.125	12.50
B22–W65	MF	16.10.2011	11.12.2011	57	2011/2012	Yes	1	38	0.026	2.63
B23–B25	MF	03.10.2010	23.11.2010	52	2010/2011	Yes	4	49	0.082	8.16
B23–B27	MM	02.10.2010	25.11.2010	55	2010/2011	Yes	1	51	0.020	1.96
B23–B28	MM	02.10.2010	25.11.2010	55	2010/2011	Yes	2	45	0.044	4.44
B24–B26	MF	03.10.2010	25.11.2010	54	2010/2011	Yes	2	34	0.059	5.88
B24–B28	MF	03.10.2010	01.09.2011	334	Both	Yes	1	134	0.007	0.75
B25–W41	FJ	23.03.2011	07.05.2011	46	2010/2011	Yes	1	33	0.030	3.03
B25–W42	FJ	23.03.2011	13.08.2011	144	Both	Yes	1	71	0.014	1.41
B25–W61	FJ	21.03.2011	01.09.2011	165	Both	Yes	4	77	0.052	5.19
B25–W62	FJ	16.03.2011	01.09.2011	170	Both	Yes	5	81	0.062	6.17
B25–W7	MF	25.08.2011	01.09.2011	8	Both	No	1	5	0.200	20.00
B26–B27	MM	03.10.2010	25.11.2010	54	2010/2011	Yes	3	45	0.067	6.67

Appendix 2. Continued.

Dyad	Age/Sex	First SL	Last SL	MD	Period	Selected?	ST	NSL	ST/NSL	AI%
B26–B28	MM	03.10.2010	29.03.2011	178	2010/2011	Yes	1	49	0.020	2.04
B28–W43	MF	03.05.2011	09.11.2011	191	Both	Yes	1	31	0.032	3.23
B28–W59	MM	28.04.2011	28.10.2011	184	Both	Yes	1	50	0.020	2.00
B28–W61	MJ	13.03.2011	19.10.2011	221	Both	Yes	3	49	0.061	6.12
B28–W62	MJ	13.03.2011	11.12.2011	274	Both	Yes	5	96	0.052	5.21
B28–W72	MJ	21.04.2011	01.09.2011	134	Both	Yes	2	28	0.071	7.14
B28–W73	MJ	28.07.2011	30.11.2011	126	2011/2012	Yes	6	65	0.092	9.23
B2–B10	MF	30.06.2010	25.11.2010	149	2010/2011	Yes	11	81	0.136	13.58
B2–B23	MM	02.10.2010	25.11.2010	55	2010/2011	Yes	12	51	0.235	23.53
B2–B25	MF	15.06.2010	25.11.2010	164	2010/2011	Yes	1	97	0.010	1.03
B2–B28	MM	03.10.2010	25.11.2010	54	2010/2011	Yes	9	49	0.184	18.37
B2–B3	MF	15.06.2010	25.11.2010	164	2010/2011	Yes	7	99	0.071	7.07
B31–G12	MF	12.10.2012	17.12.2012	67	2011/2012	Yes	1	52	0.019	1.92
B31–G4	MM	28.01.2012	06.02.2012	10	2011/2012	No	1	3	0.333	33.33
B31–G9	MJ	22.02.2012	30.04.2012	69	2011/2012	Yes	9	28	0.321	32.14
B31–W44	MF	28.01.2012	21.04.2012	85	2011/2012	Yes	1	37	0.027	2.70
B3–B10	FF	02.07.2010	23.11.2010	145	2010/2011	Yes	20	80	0.250	25.00
B3–B21	MF	03.10.2010	25.11.2010	54	2010/2011	Yes	1	50	0.020	2.00
B3–B23	MF	03.10.2010	25.11.2010	54	2010/2011	Yes	1	49	0.020	2.04
B4–B11F	FF	14.03.2011	01.05.2011	49	2010/2011	Yes	13	42	0.310	30.95
B4–B28	MF	14.03.2011	01.05.2011	49	2010/2011	Yes	4	43	0.093	9.30
B51–W52	MJ	24.07.2011	08.12.2011	138	2011/2012	Yes	1	12	0.083	8.33
B5–B22	FF	03.10.2010	07.10.2010	5	2010/2011	No	1	4	0.25	25.00
B5–B23	MF	02.10.2010	07.10.2010	6	2010/2011	No	1	6	0.167	16.67
B5–B25	FF	03.10.2010	07.10.2010	5	2010/2011	No	1	5	0.2	20.00
B8–B20	FF	13.07.2010	31.10.2010	111	2010/2011	Yes	6	43	0.140	13.95
B8–B21	MF	09.10.2010	31.10.2010	23	2010/2011	Yes	5	22	0.227	22.73
B8–B9	FF	13.07.2010	31.10.2010	111	2010/2011	Yes	7	43	0.163	16.28
B9–B11M	MF	13.03.2011	13.05.2011	62	2010/2011	Yes	11	53	0.208	20.75
B9–B14	FF	14.03.2011	21.04.2011	39	2010/2011	Yes	5	32	0.156	15.63
B9–B20	FF	02.07.2010	24.11.2010	146	2010/2011	Yes	24	72	0.333	33.33
B9–B21	MF	09.10.2010	25.11.2010	48	2010/2011	Yes	6	43	0.140	13.95
B9–B28	MF	09.10.2010	18.05.2011	222	2010/2011	Yes	3	102	0.029	2.94
B9–W43	FJ	03.05.2011	13.05.2011	11	2010/2011	Yes	6	10	0.600	60.00
B9–W46	FJ	03.05.2011	18.05.2011	16	2010/2011	Yes	6	15	0.400	40.00
G0–G12	JJ	09.05.2012	06.06.2012	29	2011/2012	Yes	1	8	0.125	12.50

Appendix 2. Continued.

Dyad	Age/Sex	First SL	Last SL	MD	Period	Selected?	ST	NSL	ST/NSL	AI%
G0–G15	JJ	28.04.2012	17.06.2012	51	2011/2012	Yes	1	25	0.040	4.00
G0–G5	JJ	28.04.2012	08.06.2012	42	2011/2012	Yes	11	28	0.393	39.29
G12–G13	JJ	05.02.2012	14.05.2012	100	2011/2012	Yes	1	10	0.100	10.00
G12–G14	FF	05.02.2012	02.12.2012	302	2011/2012	Yes	5	41	0.122	12.20
G12–G15	JJ	05.02.2012	29.10.2012	268	2011/2012	Yes	5	50	0.100	10.00
G12–G16	MF	05.02.2012	14.10.2012	253	2011/2012	Yes	4	32	0.125	12.50
G12–G17	JJ	05.02.2012	23.06.2012	140	2011/2012	Yes	1	22	0.045	4.55
G13–G14	JJ	05.02.2012	14.05.2012	100	2011/2012	Yes	1	14	0.071	7.14
G13–G16	JJ	05.02.2012	04.05.2012	90	2011/2012	Yes	1	12	0.083	8.33
G13–G17	JJ	05.02.2012	14.05.2012	100	2011/2012	Yes	2	11	0.182	18.18
G14–G16	MF	05.02.2012	14.10.2012	253	2011/2012	Yes	2	21	0.095	9.52
G15–G16	JJ	05.02.2012	14.10.2012	253	2011/2012	Yes	5	42	0.119	11.90
G15–G17	JJ	05.02.2012	23.06.2012	140	2011/2012	Yes	10	36	0.278	27.78
G15–G44	FF	21.09.2012	02.12.2012	73	2011/2012	Yes	1	18	0.056	5.56
G16–G17	JJ	05.02.2012	23.06.2012	140	2011/2012	Yes	3	9	0.333	33.33
G20–G60	MF	21.02.2012	14.10.2012	237	2011/2012	Yes	9	20	0.450	45.00
G20–W52	MF	21.02.2012	02.12.2012	286	2011/2012	Yes	1	32	0.031	3.13
G21–G23	MF	07.10.2012	29.10.2012	23	2011/2012	Yes	4	12	0.333	33.33
G24–G43	FF	14.10.2012	21.10.2012	8	2011/2012	No	3	3	1	100.00
G24–G45	MF	14.10.2012	29.10.2012	16	2011/2012	No	1	5	0.2	20.00
G26–G43	FF	28.09.2012	04.10.2012	7	2011/2012	No	1	4	0.250	25.00
G2–G6	JJ	20.02.2012	09.05.2012	80	2011/2012	Yes	9	9	1.000	100.00
G2–W44	FJ	20.02.2012	17.06.2012	119	2011/2012	Yes	6	27	0.222	22.22
G40–G41	MF	27.09.2012	29.10.2012	33	2011/2012	Yes	5	18	0.278	27.78
G42–G43	MF	28.09.2012	30.09.2012	3	2011/2012	No	1	3	0.333	33.33
G4–G12	MJ	05.02.2012	06.02.2012	2	2011/2012	No	1	2	0.5	50.00
G61–W52	MF	28.09.2012	14.10.2012	17	2011/2012	Yes	7	13	0.538	53.85
G6–W44	FJ	29.04.2012	09.05.2012	11	2011/2012	Yes	4	9	0.444	44.44
G6–W65	MJ	29.04.2012	09.05.2012	11	2011/2012	Yes	5	9	0.556	55.56
G8–G40	FF	27.09.2012	04.10.2012	8	2011/2012	No	1	5	0.2	20.00
G9–G13	JJ	05.02.2012	14.05.2012	100	2011/2012	Yes	2	16	0.125	12.50
G9–G15	JJ	05.02.2012	02.08.2012	180	2011/2012	Yes	1	61	0.016	1.64
W41–W42	JJ	23.03.2011	06.05.2011	45	2010/2011	Yes	5	11	0.455	45.45
W42–W61	JJ	21.03.2011	05.08.2011	138	Both	Yes	1	39	0.026	2.56
W42–W62	JJ	21.03.2011	11.08.2011	144	Both	Yes	2	47	0.043	4.26
W43–W44	FF	08.11.2011	09.11.2011	2	2011/2012	No	1	2	0.500	50.00

Appendix 2. Continued.

Dyad	Age/Sex	First SL	Last SL	MD	Period	Selected?	ST	NSL	ST/NSL	AI%
W43–W46	JJ	03.05.2011	13.05.2011	11	2010/2011	Yes	8	10	0.800	80.00
W44–W65	MF	29.10.2011	03.07.2012	249	2011/2012	Yes	24	88	0.273	27.27
W52–W62	JJ	21.03.2011	08.12.2011	263	Both	Yes	1	94	0.011	1.06
W61–W62	JJ	21.03.2011	19.10.2011	213	Both	Yes	8	59	0.136	13.56
W65–W73	MF	29.10.2011	30.11.2011	33	2011/2012	Yes	2	32	0.063	6.25
W74–W78	FF	23.11.2011	09.04.2012	139	2011/2012	Yes	6	30	0.200	20.00
W76–W77	MM	30.10.2011	11.12.2011	43	2011/2012	Yes	2	34	0.059	5.88

Appendix 3. List and values of the five network metrics calculated for the 68 woodland dormice that were monitored during the period June 2010 to December 2012 and for which ≥8 locations were obtained. The "/" indicates that some individuals were monitored both as juveniles and adults. M = adult male; F = adult female; J = Juvenile; ? = sex undetermined. Refer to Table 1 for a definition of the metrics.

Code	Age/ Sex	Radio-tracked?	2010-2011					2011-2012				
			Degree	Eigenvector centrality	Betweenness centrality	Closeness centrality	Clustering coefficient	Degree	Eigenvector centrality	Betweenness centrality	Closeness centrality	Clustering coefficient
B1	F	Yes	3	0.0166	0.0000	0.0110	1.0000	-	-	-	-	-
B10	F	Yes	2	0.0115	0.0000	0.0110	1.0000	-	-	-	-	-
B11F	F	Yes	1	0.0030	0.0000	0.0093	0.0000	-	-	-	-	-
B11M	M	Yes	6	0.0441	37.7500	0.0145	0.4667	-	-	-	-	-
B13	F	Yes	1	0.0077	0.0000	0.0101	0.0000	-	-	-	-	-
B14	F	Yes	3	0.0339	0.0000	0.0139	1.0000	-	-	-	-	-
B15	M	Yes	1	0.0030	0.0000	0.0093	0.0000	-	-	-	-	-
B17	F	Yes	4	0.0209	8.7561	0.0115	0.1667	1	0.0126	0.0000	0.0079	0.0000
B2	M	Yes	5	0.0435	41.8264	0.0152	0.4000	-	-	-	-	-
B20	F	Yes	3	0.0166	0.0000	0.0110	1.0000	-	-	-	-	-
B21	M	Yes	5	0.0225	16.6764	0.0122	0.5000	-	-	-	-	-
B22	F	Yes	6	0.0676	18.5693	0.0154	0.6667	5	0.0496	110.3500	0.0111	0.5000
B23	M	Yes	6	0.0543	41.5097	0.0156	0.3333	-	-	-	-	-
B24	F	Yes	2	0.0209	0.0000	0.0128	1.0000	1	0.0109	0.0000	0.0084	0.0000
B25	F	Yes	8	0.0649	55.8924	0.0128	0.3214	5	0.0449	33.4500	0.0093	0.5000
B26	M	Yes	3	0.0234	8.8000	0.0133	0.3333	-	-	-	-	-
B27	M	Yes	3	0.0171	7.8333	0.0118	0.0000	-	-	-	-	-
B28	M	Yes	14	0.0966	300.7069	0.0200	0.1209	8	0.0491	162.3167	0.0112	0.1071
B3	F	Yes	4	0.0229	19.9597	0.0123	0.3333	-	-	-	-	-
B31	M	Yes	-	-	-	-	-	3	0.0325	198.3333	0.0096	0.0000
B4	F	Yes	2	0.0173	30.0000	0.0128	0.0000	-	-	-	-	-
B5	F	No	-	-	-	-	-	-	-	-	-	-
B51	M	Yes	-	-	-	-	-	1	0.0033	0.0000	0.0067	0.0000
B7	F	Yes	-	-	-	-	-	-	-	-	-	-
B8	F	Yes	4	0.0191	0.3333	0.0111	0.8333	-	-	-	-	-
B9	F	Yes	9	0.0541	96.9069	0.0154	0.3333	-	-	-	-	-
G0	J	Yes	-	-	-	-	-	3	0.0369	30.0000	0.0068	0.3333
G12	J/F	Yes	-	-	-	-	-	7	0.0903	145.0833	0.0083	0.3810
G13	J/M	No	-	-	-	-	-	5	0.0722	2.6667	0.0069	0.5000
G14	J/F	Yes	-	-	-	-	-	3	0.0530	0.0000	0.0068	1.0000
G15	J/F	Yes	-	-	-	-	-	5	0.0687	5.3333	0.0069	0.4000
G16	J/M	Yes	-	-	-	-	-	5	0.0777	1.0833	0.0069	0.7000

Appendix 3. Continued.

Code	Age/ Sex	Radio-tracked?	2010-2011					2011-2012				
			Degree	Eigenvector centrality	Betweenness centrality	Closeness centrality	Clustering coefficient	Degree	Eigenvector centrality	Betweenness centrality	Closeness centrality	Clustering coefficient
G17	J	Yes	-	-	-	-	-	4	0.0682	0.2500	0.0068	0.8333
G2	J	Yes	-	-	-	-	-	2	0.0064	0.0000	0.0083	1.0000
G20	M	Yes	-	-	-	-	-	2	0.0035	30.0000	0.0068	0.0000
G21	M	No	-	-	-	-	-	1	0.0000	0.0000	1.0000	0.0000
G23	F	No	-	-	-	-	-	1	0.0000	0.0000	1.0000	0.0000
G24	F	Yes	-	-	-	-	-	-	-	-	-	-
G26	F	Yes	-	-	-	-	-	-	-	-	-	-
G4	M	No	-	-	-	-	-	-	-	-	-	-
G40	F	Yes	-	-	-	-	-	1	0.0000	0.0000	1.0000	0.0000
G41	M	Yes	-	-	-	-	-	1	0.0000	0.0000	1.0000	0.0000
G42	M	Yes	-	-	-	-	-	-	-	-	-	-
G43	F	Yes	-	-	-	-	-	-	-	-	-	-
G44	F	No	-	-	-	-	-	-	-	-	-	-
G45	M	No	-	-	-	-	-	-	-	-	-	-
G5	J	Yes	-	-	-	-	-	1	0.0081	0.0000	0.0057	0.0000
G6	J	Yes	-	-	-	-	-	3	0.0102	5.5417	0.0093	0.6667
G60	F	Yes	-	-	-	-	-	1	0.0008	0.0000	0.0057	0.0000
G61	M	Yes	-	-	-	-	-	1	0.0033	0.0000	0.0067	0.0000
G8	F	Yes	-	-	-	-	-	-	-	-	-	-
G9	J	Yes	-	-	-	-	-	3	0.0383	23.2500	0.0080	0.0000
W41	J	No	3	0.0234	2.2000	0.0098	0.3333	-	-	-	-	-
W42	J	Yes	5	0.0487	6.4515	0.0118	0.7000	3	0.0341	0.0000	0.0081	1.0000
W43	J/F	Yes	4	0.0380	6.9167	0.0141	0.8333	2	0.0150	100.6500	0.0109	0.0000
W44	F	Yes	-	-	-	-	-	5	0.0188	226.7917	0.0109	0.2000
W46	J	Yes	3	0.0237	0.0000	0.0109	1.0000	-	-	-	-	-
W52	J/F	Yes	2	0.0149	0.0000	0.0109	1.0000	4	0.0148	113.0000	0.0084	0.0000
W59	M	Yes	2	0.0173	30.0000	0.0128	0.0000	1	0.0109	0.0000	0.0084	0.0000
W61	J/?	Yes	5	0.0596	15.6359	0.0147	0.8000	5	0.0520	12.6083	0.0097	0.7000
W62	J/M	Yes	7	0.0649	64.2753	0.0154	0.4286	7	0.0569	167.6083	0.0103	0.3333
W65	M	Yes	-	-	-	-	-	4	0.0208	121.3500	0.0110	0.1667
W7	M	Yes	1	0.0113	0.0000	0.0093	0.0000	1	0.0099	0.0000	0.0072	0.0000
W72	J/F	Yes	1	0.0168	0.0000	0.0125	0.0000	1	0.0109	0.0000	0.0084	0.0000
W73	J/F	Yes	-	-	-	-	-	2	0.0155	3.3333	0.0097	0.0000
W74	F	Yes	-	-	-	-	-	1	0.0000	0.0000	1.0000	0.0000

Appendix 3. Continued.

Code	Age/ Sex	Radio-tracked?	2010-2011					2011-2012				
			Degree	Eigenvector centrality	Betweenness centrality	Closeness centrality	Clustering coefficient	Degree	Eigenvector centrality	Betweenness centrality	Closeness centrality	Clustering coefficient
W76	M	Yes	-	-	-	-	-	1	0.0000	0.0000	1.0000	0.0000
W77	M	Yes	-	-	-	-	-	1	0.0000	0.0000	1.0000	0.0000
W78	F	Yes	-	-	-	-	-	1	0.0000	0.0000	1.0000	0.0000

CHAPTER 4

Adult Social Interactions in the African Woodland Dormouse *Graphiurus murinus*

Abstract

Social interactions are often used to assess the level of sociality in animals. Animals displaying greater tolerance characterise group-living species, whereas less tolerance characterise loose aggregations and solitary living. Here, I assessed the components of the social behaviour in the African woodland dormouse *Graphiurus murinus*, which shows some elements of group-living (i.e. sleeping associations) in nature, particularly between females. I focussed on levels of aggression and amicable behaviours that may lead to repulsion and attraction, in order to gain insight into the causal factors underpinning the social system of woodland dormice. I studied the types and intensity of social interactions during 15-min same-sex dyadic encounters. I predicted that social behaviours would differ between the sexes, consisting of a) higher levels of amicability between females than between males, and b) higher aggression levels between males than between females. Overall, males and females differed significantly in the way they responded to the presence of a same-sex dormouse. Males were more aggressive through both overt (e.g. chasing and biting) and ritualised (e.g. tail wagging and open mouth) aggression and performed more social investigation behaviours than females, while females were more amicable and exhibited more exploration and avoidance behaviours than males. However, behavioural comparisons showed that both sexes displayed less amicable and more ritualised aggression, and females displayed less overt aggression and more social investigation. The duration of the different interactions did not differ between sexes. These findings highlight sex-specific differences in social behaviours, thus indicating different behavioural motivations for forming social groups between sexes. Females have a heightened sociability with unfamiliar females, while males have an aversion for unfamiliar males. Female tolerance of other females may be foundational for group formation to exist, leading to co-operative behaviours, and higher female fitness. Male aversion towards strange males seemingly reduces the possibility of male-male groups in woodland dormice.

Keywords: Agonistic behaviour, amicable behaviour, dyadic encounters, social system, social behaviour

Introduction

Social systems can be categorised by the social behaviours taking place among individual conspecifics (Struhsaker 1969; Kappeler & van Schaik 2002; Schradin *et al.* 2012), which in turn impacts on the spatio-temporal distribution of members of a population. Social systems are not static but vary along the endpoints between solitary (asocial) and group-living (Happold 1976), so that the type and level of social interactions are expected to vary according to the social system. At a population level, the social system mirrors the outcome of social relationships among individuals (Lott 1991). Social systems may fluctuate in time and space, as they are driven by extrinsic (ecological) and intrinsic (genetic) factors (Happold 1976). Therefore, in comparative studies of rodents, the occurrence of aggressive and amicable behaviours between conspecifics is axiomatically linked to a species' social system and is shaped by different ecological conditions (Crowcroft & Rowe 1963; Armitage 1981; Patris *et al.* 2002). Social systems are adaptive because they increase the fitness benefits of individuals (Barash 1989).

Social behaviour is defined as the variety of social interactions among conspecifics that result in relationships of variable forms, duration and function (Blumstein *et al.* 2010). Social behaviours encompass the different types of interactions among conspecifics, in various contexts, and these interactions are used as measures of the social system and degree of sociality within a population (Wilson 1975; Ostfeld 1985). Therefore, social interactions result in specific social systems, by offering insights into cooperation and conflicts between conspecifics.

Group-living and solitary living represent the extremes along a continuum of sociality – which is defined as the presence or absence of social groups within a population. Social interactions within group-living species are characterised by tendencies towards affiliative and co-operative behaviours (particularly in egalitarian groups), with comparatively low levels of agonistic behaviours (Barash 1974; Lacey & Sherman 2007). Individuals are attracted to other group members and behave (e.g. amicable, mutual grooming) in ways that maintain proximity to at least some of them (Wilson 1975; Chapter 3 of this thesis), enabling group cohesion. On the other extreme, solitary species have reduced contact with conspecifics, and apart from mating, defending territories and rearing offspring, individuals

rarely interact with conspecifics (Lacey & Wierczorek 2003). They are either impartial towards one another or are simply repelled, and ignore, attack or avoid conspecifics other than mates or offspring (Lott 1991). As a consequence, the array of social behaviours exhibited by group-living species surpasses that of solitary species. Between these endpoints of social systems, species might display various combinations, levels and timing of attractive or repulsive behaviours, highlighting the dynamic nature of social systems in animals.

The African woodland dormouse (hereafter woodland dormouse) *Graphiurus murinus* is a nocturnal, arboreal rodent of the family Gliridae which is patchily distributed from Ethiopia through much of East Africa to South Africa and Lesotho (Baxter 2008). Because of its wide distribution, this glirid appears to be highly adaptable, capable of exploiting a diverse range of habitats. Throughout its distributional range, however, it is often associated with woodlands (Skinner & Chimimba 2005). The species is described as heterothermic, characterised by huddling, multiple-day torpor bouts, and hibernation in response to low ambient temperatures or food deprivation (Whittington-Jones & Brown 1999) (Mzilikazi *et al.* 2012). Webb & Skinner (1996) Ellison & Skinner (1991).

Very little is known about the social system of *G. murinus*, with conflicting reports across the species range. In South Africa, Ansell (1960) claimed that *G. murinus* is primarily solitary in nature, while in East Africa, Kingdon (1974) found as many as 11 adult *G. murinus* of mixed sex in a single nest at the same time. Woodland dormice shared nests with other individuals during all seasons of the year (Madikiza 2010, Chapter 2 this thesis). Aggregations between males and females were high just before and during the mating season and absent during the rest of the year. Similarly, the frequency of male–male aggregations was very high just before and during the mating season but declined drastically afterwards. Aggregations in artificial nest boxes, as well as in naturally-occurring nests (Chapters 2 & 3) among females were observed both before/during and after the mating season (accompanied by one or several young) (Madikiza 2010). Trapping data on woodland dormice in the same study site revealed further that woodland dormice exhibited extensive home range overlaps with both same-sex and opposite-sex conspecifics, thus suggesting a promiscuous mating system (with both males and females mating with multiple partners), and possibly males searched and aggregated around receptive females during the mating season as a mating strategy (Madikiza *et al.* 2011).

The aim of my current study was to assess components of the social behaviour of same-sex adult dyads of woodland dormice. I particularly focussed on levels of aggression and amicable behaviours that may cause repulsion and attraction using staged dyadic encounters

in captivity. Such knowledge would help better understand or gain insight into underlying causal factors of the spatio-temporal patterns of association observed in free-living dormice to assess its social system. I predicted that social behaviours would differ between the sexes, consisting of a) higher levels of amicability between females than between males, and b) higher aggression levels between males than between females.

Materials and methods

Woodland dormice used in this study were derived from free-living populations within the Eastern Cape Province, South Africa. Sampling took place in five different areas (Fort Hare Farm, Winterberg Agricultural School, Lemoenskraal farm, Le Roux farm, and Great Fish communal land) located near the Great Fish River, where riverine *Combretum* forest strips are present. Forest patches in the 5 farm areas were located at least 15 km apart from each other. Based on radio-tracking data from Madikiza (unpubl. data), the maximum straight-line distance covered by any individual at night varied between 50 m and 1 km depending on the sex and season. Hence, it can be assumed that individuals captured in different sampling areas were not familiar with each other prior to the study.

To minimise impacting on the demography of dormouse subpopulations and to obtain unrelated individuals for breeding purposes, a maximum of 4 males and 4 females were removed from each of the five sampling sites. A total of 28 adult dormice were trapped and removed from the natural areas. These wild caught woodland dormice were then housed in the Milner Park Animal Unit, University of the Witwatersrand, Johannesburg. Prior to experiments, they were maintained under controlled environmental conditions: reversed 12L:12D light–dark cycle (lights on at 19:00), 22–24 °C and 30–60% rH. Dormice were individually housed in metal cages (L × B × H: 0.5 × 0.5 × 1 m). Wood shavings (~3 cm) were provided as bedding. Each individual was provided with a galvanised nest box (L × B × H: 15 × 15 × 15 cm) with a 50-mm entrance hole and ~10 g of paper towel was provided as nesting material. Additional natural material in the form of branches and small logs were placed inside the metal cages for environmental enrichment. Food (Versele hamster muesli; Belgium) and water were provided *ad libitum*. Approximately 10 g of a combination of mealworms, peanuts, boiled egg, fruits and vegetables were given as occasional supplements.

Experimental design

The social interactions of dormice were studied in staged dyadic encounters in a separate room from the colony. Twenty adult woodland dormice were used (10 males and 10 females) in staged dyadic encounters, against same-sex and unfamiliar individuals. Test individuals were marked using coloured plastic cable-tie neckbands for identification during videotaping (following Lötter & Pillay 2012). In order to increase the sample size, I used each individual more than once, but each animal participated only in two encounters, with at least a 3-day interval between each trial, each time with a different, unfamiliar dyadic partner.

The social interactions between male–male (n = 11) and female–female (n = 10) dyads took place in a neutral cage arena following Patris *et al.* (2002). The arenas were galvanised steel tanks (L × B × H: 60 × 30 × 30 cm) with three metal sides and a clear Perspex front to facilitate video recording, and a wire-mesh lid. The floor of the cage was covered with 2 cm of wood shavings. Each tank contained two wooden nest boxes (L × B × H: 15 × 15 × 15 cm) to allow test subjects the possibility to avoid or escape from their "opponent", and also to investigate nest box sharing behaviour within dyads.

Dyads were staged during the dark phase of the reversed light cycle, since dormice are nocturnal. Red light (light intensity = 71 lux) was used for video-taping, and to avoid interfering with the nocturnal activity of the animals. On the day of the experiment, two woodland dormice were removed from their home cages and placed simultaneously on opposite sides of the neutral cage to avoid a resident–intruder paradigm. Dyadic encounters were taped for a period of 20 min. In each encounter, the behaviour of the dyad was video-recorded using a single digital camera (Sony, DCR-SX44) mounted on a tripod stand in-front of the cage above floor level. Between every encounter, the chamber floor and walls were cleaned with disinfectant soap and water, air dried completely, and fresh wood shavings placed on the floor, to reduce carry over odour effects. After the experiments, individuals were returned to their home cages at the Milner Park Animal Unit.

I measured the type, frequency and duration of social behaviours (Table 1) for each dyad. The scoring of the different behaviours took place 5 min after the start of the taping session and was conducted for 15 min thereafter. All social behaviours were scored using the video analysis software Observer 3.0® (Noldus Inc., the Netherlands). Behaviours were scored as either point (frequency) or event (frequency and duration) behaviours. All recorded behaviours were then assigned into one of five possible categories (Table 1). The behavioural categories were established based on previous studies on mice (Patris *et al.* 2002).

Table 1. Behaviours scored during dyadic encounters of same-sex woodland dormice *Graphiurus murinus*. The 15 behavioural components scored were grouped into 5 categories. The numbers in bold and parentheses correspond to those used in Figure 1.

Behavioural categories	Behavioural components
Amicable[a]	**(1)** Sitting together
Ritualised aggression	**(2)** Aggressive vocalisation (loud sharp shrieks, which indicate threat or are followed by ritualised behaviour or fight or attack on the opponent); **(3)** raised tails; **(4)** tail wagging; **(5)** lateral display; **(6)** scent marking through rubbing of rump and cheeks; **(7)** open mouth
Overt aggression	**(8)** Chasing, **(9)** leaping, **(10)** biting and **(11)** wrestling with conspecific in a plummeting ball
Social investigation	**(12)** Approaching, **(13)** naso-nasal sniffing and ano-genital sniffing of opponent
Exploration/avoidance	**(14)** Exploration and **(15)** avoidance: individual explores the arena and sometimes avoids interactions by changing direction when approaching the opponent

[a]Allo-grooming was also considered in the amicable category but was not observed during the staged encounters.

Data analysis

All statistical analyses were conducted with the software IBM SPSS Statistics 22.0 (SPSS Inc.). In all analyses, differences were considered statistically significant at $p \leq 0.05$. As the data set was not normally distributed (Kolmogorov-Smirnov test, $p < 0.05$), potential differences in the duration of behavioural components between sexes and behavioural categories were evaluated with Mann-Whitney and Kruskall-Wallis tests, respectively. Similarly, Mann-Whitney tests were used to assess intersexual variation in the frequency of behavioural components. A chi-square test of independence was used to compare the pooled or total frequencies (combined data) of the different behavioural categories exhibited by all male and female dyads during the 15-min intrasexual encounters.

Results

Female and male behavioural patterns observed during staged dyadic encounters are presented in Figure 1. Both male and female displayed similar behaviours; however, some sex-specific behaviours were recorded, as described below.

Female–female interactions

The majority of female dyads ($n = 7$) displayed amicable behaviours which were preceded by females approaching the nest box of other females, sniffing the dyad partner (social investigation) and eliciting very soft vocalisations and then sitting within 1–5 cm distance

from the dyad partner inside the nest box. Before females engaged in social investigation leading to amicable behaviours, they explored the opposite ends of the arena from where they were released, and hence the frequency of exploration and avoidance behaviours scored were relatively high.

Male–male interactions

Compared to females, as soon as the recording started, male dyads (n = 6) frequently investigated the entire arena and approached and sniffed at the opponent's nest boxes frequently (Figure 1). Soon after approaching the dyad partner, they would elicit sharp squeaky vocalisations (n = 4), tails would be raised and pilo-erected (bushy) , and wagged frequently, and dormice would leap at the opponent, and engage in wrestling behaviour. As soon as the aggressions had stopped, males would approach and scent mark on the opponent's nest box involving both face and rump rubbing.

Intrasexual comparisons

Male and female dyads did not differ in the frequency of any of the behavioural components studied (Mann-Whitney tests: $p > 0.05$ in all cases; Figure 1). However, when these frequencies were pooled into the five main behavioural categories (Table 1), males and females differed significantly in their responses (Chi-square test of independence: $\chi^2 = 41.07$, df = 4, $p < 0.001$; Figure 2). Males were more aggressive (both overt and ritualised) and performed more social investigation behaviours than females, while females were more amicable and exhibited more exploration/avoidance behaviours than males (Figure 2). Other analyses indicated that both sexes were less amicable and exhibited more ritualised aggression than expected by chance (Table 2). Females displayed less overt aggression and more social investigation than expected, while males performed less exploration and avoidance behaviours than expected (Table 2).

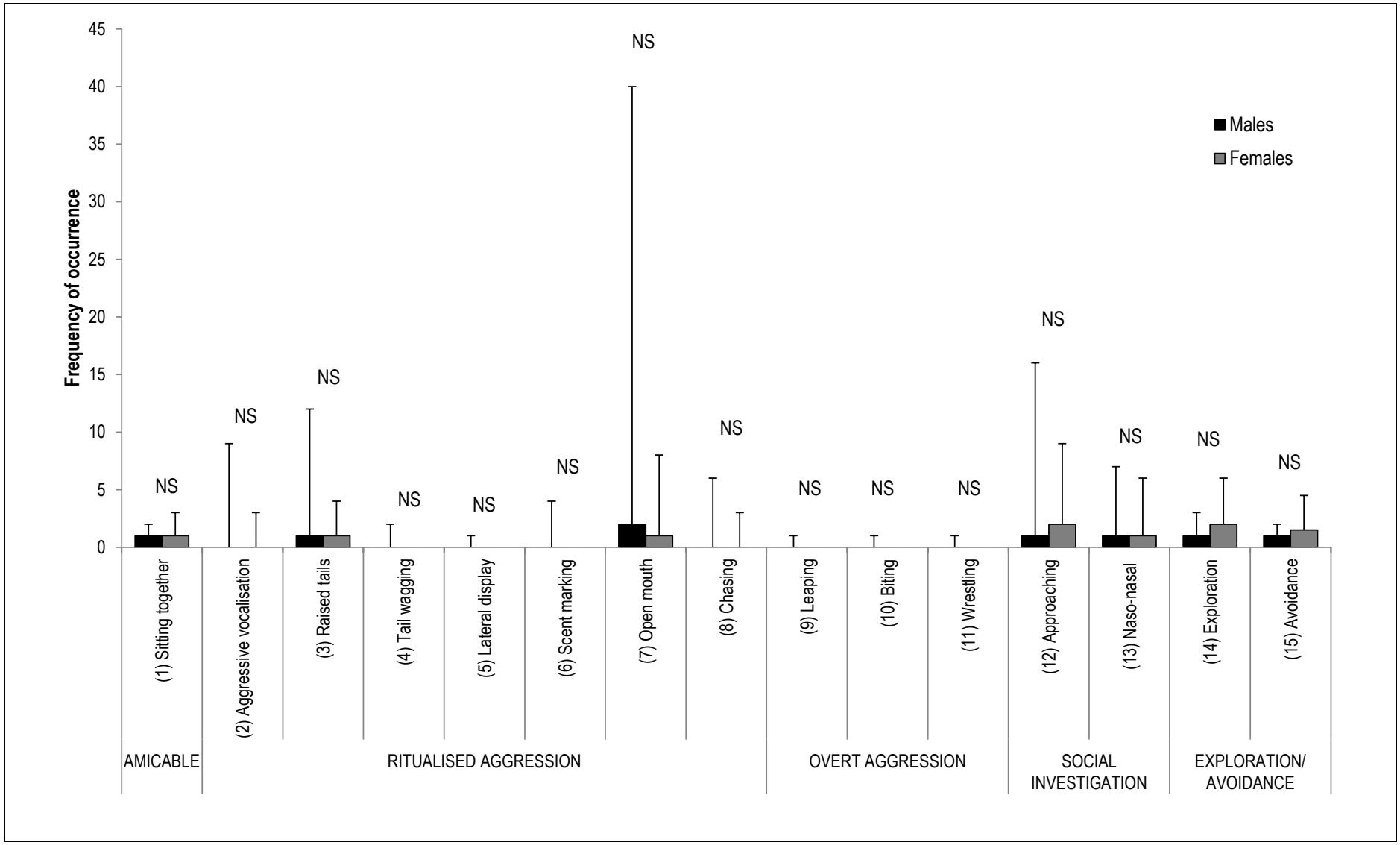


Figure 1. Frequency (median ± interquartile range) of the 15 component behaviours recorded during 15-min male–male (n = 11) and female–female (n = 10) dyadic encounters in African woodland dormice *Graphiurus murinus*. The numbers in parentheses correspond to those used in Table 1.

Table 2. Chi-square tests of homogeneity to investigate whether male (M) and female (F) dormice exhibited specific behaviours more of less than expected according to a theoretical homogeneous distribution. Observed values which are at least 25% larger or smaller than expected values are highlighted in bold.

Categories	Amicable	Ritualised aggression	Overt aggression	Social investigation	Exploration/ avoidance	Chi-square test
M observed	**9**	**242**	112	102	**28**	$\chi^2 = 291.92$, df = 4
M expected	99	99	99	99	99	$p < 0.001$
F observed	**16**	**50**	**26**	**63**	44	$\chi^2 = 35.15$, df = 4
F expected	40	40	40	40	40	$p < 0.001$

For the duration of behaviour data (Table 1), males and females did not differ in any of the five behaviour categories (Mann-Whitney tests: $p > 0.20$ in all four cases; Figure 3), excluding the duration of overt aggression which was scored for frequency only due to its point (rather than bout) occurrence. For the sexes combined, the duration of the four remaining behaviour categories differed significantly (Kruskall-Wallis test: H = 22.53, df = 3, $p < 0.001$). Dormice spent significantly less time involved in ritualized aggression than in any of the other three broad behavioural categories (Mann-Whitney tests: $p < 0.01$ in all three cases); they also spent more time in social investigation than in exploration/avoidance ($p = 0.039$).

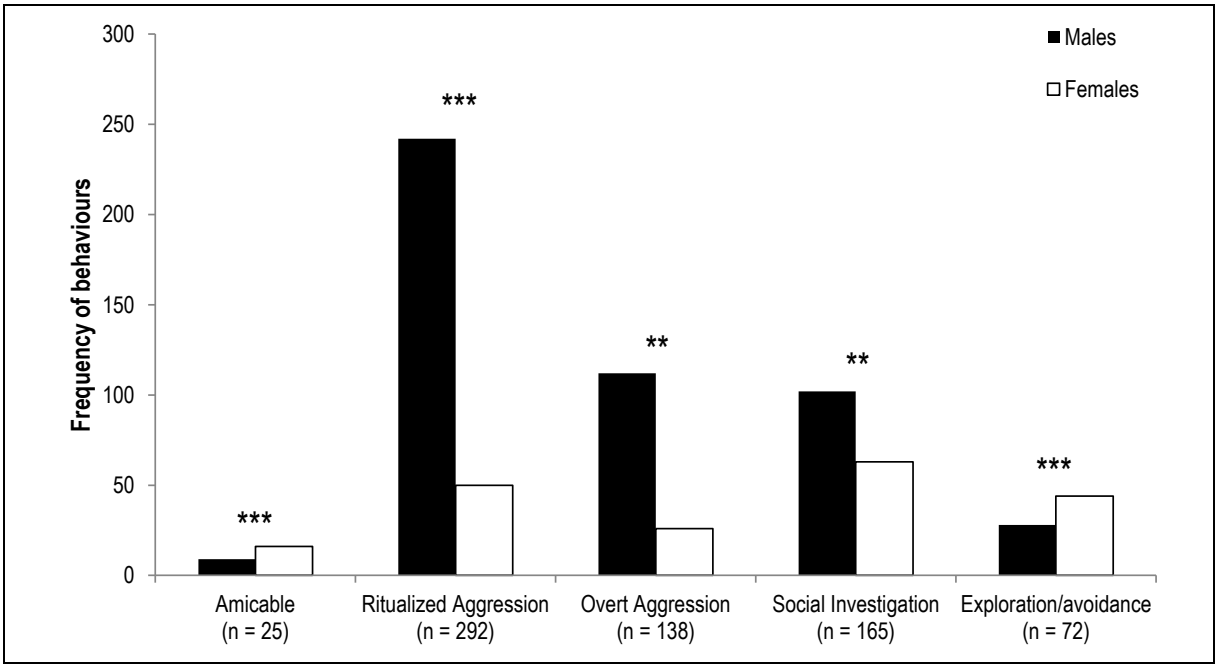


Figure 2. Pooled frequencies of the five behavioural categories recorded during 15-min male–male ($n = 11$) and female–female ($n = 10$) dyadic encounters in woodland dormice. The number of records for each broad category is given in parentheses. Frequencies that differed significantly between males and females (chi-square test of independence) are indicated with ** ($p < 0.01$) or *** ($p < 0.001$).

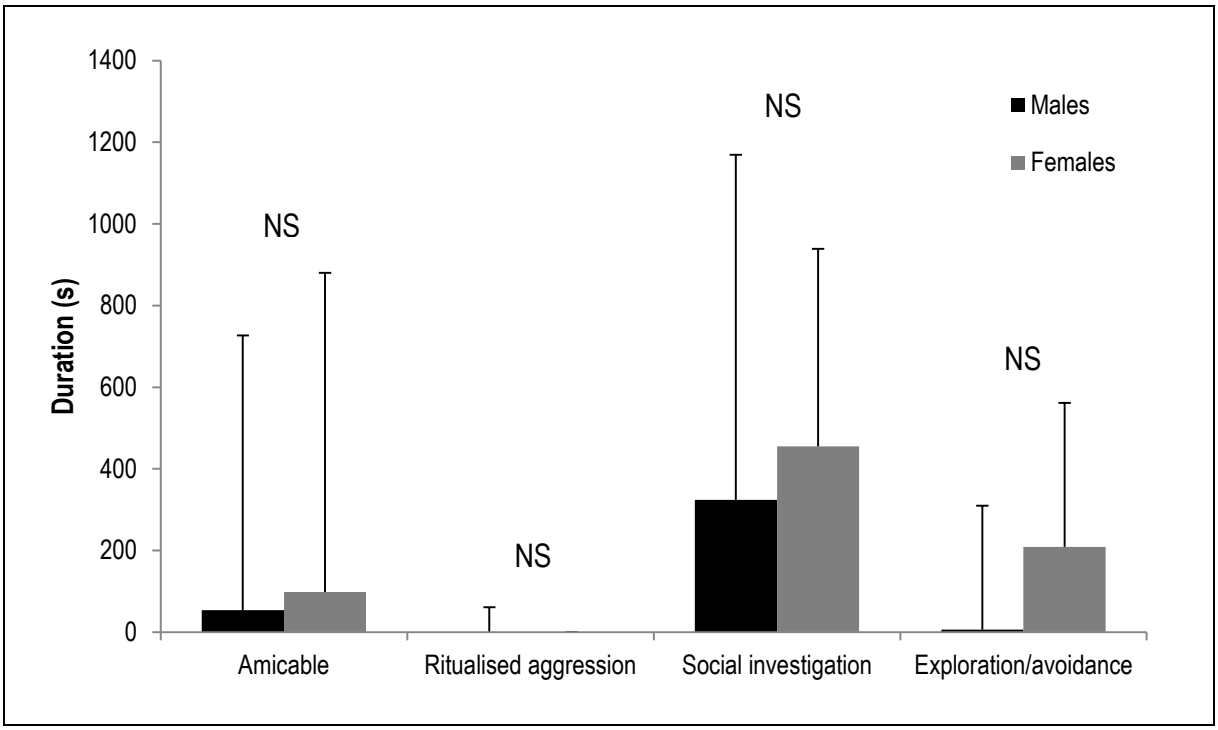


Figure 3. Duration (median ± interquartile range) of the five broad behavioural categories recorded during 15-min male–male (n = 11) and female–female (n = 10) dyadic encounters in woodland dormice. Values did not differ significantly between males and females (Mann-Whitney tests: $p < 0.05$). NS = non-significant.

Discussion

By studying same-sex dyadic encounters of the woodland dormouse in a neutral arena, I was able to assess the elements (i.e. aggression and amicable) of intrasexual social behaviour. Female dormice were intra-sexually more amicable than males. Females participated in amicable/attracting behaviours such as sitting together during their dyadic interactions. Compared to males, females were more tolerant of unfamiliar females, and were behaviourally motivated to be social. Indeed, displaying and seeking tactile contact with strangers could indicate social attraction (Hurst *et al.* 1996). My results are similar to those reported in meadow voles *Microtus pennsylvanicus* where females were more amicable than males in staged encounters (Ferkin & Seamon 1987). It is thus plausible to assume that female woodland dormice are also tolerant of one another in nature, and thus facilitating cohabitation. Pro-social behaviours that show sociable tendencies by approaching conspecifics, followed by tolerance of other individuals, allow for group-living to emerge (reviewed in Soares *et al.* 2010). Indeed, evidence of two or more females were often recorded at the same sleeping sites during the year in my field studies (Chapter 3). Moreover, a nest box monitoring and trapping study revealed that female home ranges overlapped highly

with those of other females, and, on numerous occasions, two or more females were captured in the same nest box (Madikiza 2010).

The motivation to be amicable in females are modulated physiologically, it has been shown that arginine vasopressin and/or oxytocin are involved in the regulation of sociable behaviours such as approach and aversion, cohabitation, pair bonding and affiliation (see review by Lim & Young 2006). For example, female gerbils injected with oxytocin showed an increase in sociability to conspecifics (Razzoli *et al.* 2003), and female Syrian hamsters *Mesocricetus auratus,* injected with oxytocin displayed low aggressive behaviours towards non-aggressive female intruders (Harmon *et al.* 2002). Similarly, infusion of vasopressin in praire voles *Microtus ochragaster* induced social behaviours (Young *et al.* 1999). Therefore, amicability in woodland dormice might also be mediated by oxytocin and/or vasopressin.

The high rates of avoidance behaviours by female dyads, signified by individuals exploring the arena and avoiding direct interactions by changing directions when approaching the unfamiliar female, could suggest that female woodland dormice are cautious as well as amicable. This is reflected by the high rates of amicable behaviours over time. Minimal physical encounters reduces direct aggression and passive behaviours such as minimizing contact or "befriending" to emerge as conflict-resolution strategies for females (Cheney & Seyfarth 1982; Kapusta *et al.* 2007).

Male woodland dormice were intra-sexually less amicable than females. Males engaged in high levels of agonistic/repelling behaviours, displaying both overt and ritualised aggression. It appears that male dormice are not behaviourally motivated to be social upon encounters with strangers. Furthermore, it is plausible to assume that there exists mutual avoidance among males, and that males might be more territorial than females. In fact, no two males were recorded together in traps or in sleeping sites except during winter and breeding season in my field studies (Chapter 2). This further hints at the possibility that male association in natural populations of woodland dormice are rare, and that male–male competition might exist. The high rates of overt and ritualised aggression in male intra-sexual dyads, signified by a combination of aggressive vocalisations, scent marking, body posture (lateral displays, raised tail and tail wagging), chasing and biting, would be associated with territoriality in males, as also reported in the fat dormouse *Glis glis* (Scinksi & Borowski 2008), common dormouse *Muscardinus avellanarius* (Juškaitis 2008) and the striped mouse *Rhabdomys pumilio* (Perrin *et al.* 2001; Schradin 2004). My findings are also in agreement with those of several other studies, stating that intra-sexual aggression is high in males of promiscuous mating species, and may be highly linked to male–male competition for

receptive females (Clutton-Brock & Harvey 1978; Eccard *et al.* 2004). Aggression is normally regulated by the levels of circulating androgens (Wingfield *et al.* 1997); the Challenge Hypothesis (Wingfield *et al.* 1990) proposes that aggression is in direct association to androgen levels, along with the context at which the behaviour takes place (neutral arena in my study).

Ritualized aggression is highly developed in male dormice. My results could firstly be highlighting the different strategies utilised by males as compared to femlaes in agonistic interactions. Secondly, higher levels of ritualised display rather than overt aggression potentially indicates conflict-resolution strategy in male dormice, and might play an important role in defining territories (Ostfeld 1985; Wolff 1985). Since studies by Madikiza *et al.* (2011) revealed that male dormice have overlapping home ranges during the mating season, it is therefore plausible that neighbouring males could encounter each other during this time. Under such circumstances, ritualised aggression can help avoid and lower costly fights and mortality risks (Maynard Smith 1974).

Furthermore, males vocalised in the presence of another male. It appears that vocalisations are emitted during direct (physical) encounters. Such ritualised signals can contribute to the general ritualised aggressive interactions between males. Similar results were recorded in Siberian hamsters *Phodopus sungorus* (Keesom *et al.* 2015).

Males displayed high levels of social investigative behaviours. This could be interpreted firstly as exploration of the unfamiliar area. However, the fact that males and not females investigated the area indicated that males are likely to be territorial and possibly need to evaluate rapidly whether the partner is a familiar (neighbour) or potential rival. It has been suggested that higher investigative and exploratory behaviours could be associated to higher information gathering abilities, risk assessment and ultimately leading to a prompt response to rivals or strangers (Guillette *et al.* 2009; Tebbich *et al.* 2009).

In conclusion, I investigated social behaviours of wild caught woodland dormice under neutral conditions in captivity, and found sex-specific differences in social behaviours. Females had a heightened sociability with other females, while males had an aversion towards other males, displaying ritualised signals of aggression. Such asymmetry between the sexes common in many rodents (Boonstra 1978). Female tolerance for other females may be foundational for group formation to exist, leading to co-operative behaviours, and fitness benefits. My study was conducted in a neutral arena under optimal conditions (e.g. food, shelter) and focussed on the potential intrinsic (motivational) drivers of social behaviours between unfamiliar individuals. Future studies should consider whether familiarity would

facilitate sociality. Another important consideration is to investigate extrinsic drivers of woodland dormice sociality, in particular low ambient temperatures which I hypothesised to drive sleeping site associations in the species (Chapters 2 & 3).

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CHAPTER 5
Sociability and Social Preference in the African Woodland Dormouse *Graphiurus murinus*

Abstract

The degree of sociability (i.e. the motivation to remain in close proximity to conspecifics) is an important component of group-living in animals. I assessed same-sex sociability and social preference in the African woodland dormouse *Graphiurus murinus* (Rodentia, Gliridae) using the protocols in Crawley (2000), in which social attraction for an unfamiliar individual (sociability) and then preference between familiar and unfamiliar individuals were tested. I predicted that: 1) dormice would demonstrate a heightened motivation to be sociable by interacting more often with stimulus dormice than with an empty cage; 2) female woodland dormice would be more sociable than males because they were the associating sex in previous studies; and 3) both sexes would show a preference for previously encountered stimulus dormice (familiar) compared to unfamiliar dormice, and that the strength of this preference would be greater in female than male dormice. I found that both female and male woodland dormice spent significant time sniffing and making contact with conspecifics. Females showed a greater affinity to conspecifics compared to males, which were more aggressive and aggressively vocalized more often than females. During social preference tests, dormice did not spend more time with short-term familiar dormice (i.e. individuals met for the first time during the sociability experiment) than with unfamiliar dormice; however, females sat significantly more often with a familiar than an unfamiliar female, and males aggressively vocalized and displayed aggressive behaviours more often when in the presence of an unfamiliar than a familiar individual. These findings suggest that woodland dormice demonstrated a motivation to affiliate with conspecifics. Furthermore, the motivation to affiliate differed by sex, with females showing a greater affinity for both familiar and unfamiliar woodland dormice, whereas males showed an affinity for familiar males only. Affiliative characteristics are possible drivers of group-living in females, while functioning as a foundation for tolerance in male woodland dormice.

Keywords: Familiarity, *Graphiurus murinus*, sociability, social behaviour, sociality

Introduction

Sociality is a broad term describing how animals live, ranging along a continuum from living alone to forming stable social groups. Sociality can be defined by group size and composition, such as temporary associations, aggregations (e.g. nesting or foraging groups) to relatively stable social units, and the existence of solitary living (Parrish *et al.* 1997; Krause & Ruxton 2002). Individuals of solitary species avoid conspecifics (except during mating and parental care) and may respond to them through aggressive behaviours (Lott 1991). In contrast, group-living individuals engage in comparatively more amicable behaviours that encourage close proximity to at least some conspecifics. For example, solitary species, such as the brown desert mouse *Pseudomys desertor*, are intensely repelled by each other, whereas the northern hopping mouse *Notomys alexis* engages in amicable behaviours with individuals of both sexes, resulting in the formation of groups (Happold 1976).

Group formation may be brought about by a combination of intrinsic drivers, such as kinship, where animals remain in their natal area because of the intrinsic benefits linked to living with relatives (Stacey & Ligon 1991). In group-living rodents, natal philopatry is a main driver of group-living (Solomon 2003). Extrinsic drivers such as food resources and low ambient temperatures may also favour group-living (reviewed in Ebensperger 2001). In Alpine marmots *Marmota marmot*, for example, low ambient temperatures lead to group hibernation (Arnold 1990). Groups may also form when stochastic events, such as a sudden overabundance of resources, result in reduced aggression and increased tolerance among conspecifics, thus permitting aggregations. As an example, in yellow-bellied marmots *Marmota flaviventris*, an improvement in the availability of suitable habitats led to an increase in burrow systems, thus increasing the number of matrilineal groups (Armitage 1988). Ecological constraints such as habitat saturation (high population density) may limit dispersal therefore driving individuals to co-habit (e.g. striped mouse *Rhabdomys pumilio*) (Schradin *et al.* 2010).

Sociability is defined as the motivation to remain in close proximity to conspecifics (Sibbald *et al.* 2006). Understanding the sociability of a species, as well as the nature of social interactions characterising social groups, contribute to an understanding of sociality. The sociability of a species can be measured in different ways. At a group level, it can be expressed through existing synchronised behavioural patterns or social cohesion (Benham 1982; Miller & Woodgush 1991) and/or through proximity between group members (Dudziński *et al.* 1982; Sibbald *et al.* 2005). At an individual level, the motivation to be in

close proximity to conspecifics has been assessed by 1) measuring the motivation of animals to gain access to conspecifics (e.g. calves *Bos taurus*: Holm *et al.* 2002; silver foxes *Alopex lagopus*: Hovland *et al.* 2008), and 2) observations of behavioural responses to isolation, through vocal or locomotory agitation (e.g. in lambs: Ligout *et al.* 2011).

Not all individuals are similarly or instantly attracted to conspecifics, which suggests that some form of selective preference exists by individuals. Social preference demonstrates the sociability of an individual through its interactions with conspecifics. Social preferences are characteristically expressed by pairs of individuals, maintaining close proximity and physical contact (William *et al.* 1992; Insel & Hulihan 1999). Other studies have further emphasised that grouping decisions could be attributed to familiarity between conspecifics which can influence social preferences (reviewed in Holmes 1988). For example, individual meadow voles *Microtus pennsylvanicus* (Ferkin 1988, Ferkin & Rutka 1990; McShea 1990) prefer to associate with familiar conspecifics rather than strangers.

African woodland dormice (hereafter woodland dormice) *Graphiurus murinus* occupy forests in many parts of southern Africa. Although they are solitary foragers, individuals co-habit a single nest (Kingdon 1997; Madikiza 2010). However, the previous studies of nest cohabitation in woodland dormice in nature cannot clearly distinguish whether these aggregations were driven by woodland dormice being attracted to one another intrinsically (e.g. demonstrate sociability), or simply by ecological constraints (e.g. low temperatures, limited number of differing quality of sleeping sites). In other words, it is not known whether woodland dormice are motivated to be social. The aim of my study was to quantify the degree of sociability (i.e. are woodland dormice motivated to associate with conspecifics?) and the social preferences of woodland dormice (i.e. do they prefer familiar to unfamiliar conspecifics?) using Crawley's (2000) three-chambered apparatus and protocol. I predicted that: 1) woodland dormice would demonstrate a heightened motivation to be sociable by interacting more often with stimulus dormice than an empty cage; 2) female woodland dormice would be more sociable than males, because they were the main associating sex in previous studies; and 3) both sexes would show a preference for previously encountered stimulus dormice (familiar) compared to unfamiliar dormice, and that the strength of this preference would be greater in female than male dormice.

Materials and methods

Woodland dormice used in this study were captured in free-living populations within the Eastern Cape Province, South Africa. Sampling took place in 5 different farm and communal areas located at least 15 km apart from each other, near the Great Fish River, where riverine *Combretum* forest strips are present. Based on radio-tracking data from Madikiza (unpubl. data), the maximum straight-line distance covered by any individual at night varied between 50 m and 1 km depending on the sex and season. Hence, it can be assumed that individuals captured in the different sampling areas were not familiar with each other.

To minimise impacting on the demography of dormouse subpopulations and to obtain unrelated individuals, a maximum of 4 males and 4 females were removed from each of the 5 sampling areas. A total of 28 adult dormice were trapped and removed from the natural areas.

Woodland dormice were housed in the Milner Park Animal Unit, University of the Witwatersrand. Prior to experiments, woodland dormice were maintained under partially controlled environmental conditions: reversed 12L:12D light–dark cycle (lights on at 19:00); 22–24 °C and 30–60% rH. Dormice were individually housed in metal cages (L × B × H: 0.5 × 0.5 × 1 m). Wood shavings (~3 cm) were provided as bedding. Each individual was provided with a galvanised nest box (L × B × H: 15 × 15 × 15 cm) with a 5 cm entrance hole, and ~10 g of paper towel was provided as nesting material. Additional natural material in the form of branches and logs were placed inside the metal cages for environmental enrichment. Food (Versele hamster muesli, Belgium) and water were provided *ad libitum*. Approximately 10 g of a combination of mealworms *Tenebrio molitor*, peanuts, boiled eggs, fruits and vegetables were given as occasional supplements.

Experimental design

To test sociability and social preferences, I used a three-chambered apparatus and modified protocol proposed by Crawley (2000), comprising of a social affiliation test and a social preference test. Tests were carried out in a rectangular glass tank (L × B × H: 60 × 30 × 30 cm) with a wire-mesh lid, comprising of three internal chambers separated by two parallel walls made of Plexiglass. The open middle chamber allowed the test dormouse free access to each chamber. The two outer and the central chambers were (L × B × H: 20 × 30 × 30 cm) in size (Figure 1). Square wire-mesh cages (130 × 105 × 95 mm) were placed in each of the two outer chambers; either one cage contained a stimulus mouse and the other was left empty (sociability), or both had a stimulus dormouse (social preference). The wire-mesh cages

allowed for visual and olfactory communication between focal and stimuli dormice, but prevented direct physical interaction. The floor of the cage was covered with 2 cm of sawdust.

Because dormice are nocturnal, tests occurred under red light (light intensity = 71 lux) during the dark phase of the light-dark cycle; red light facilitated video-taping. Prior to experiments, all focal dormice were given 24 h to acclimatise to the experimental three-chambered glass cage (i.e. they could move freely between the three chambers; Figure 1).

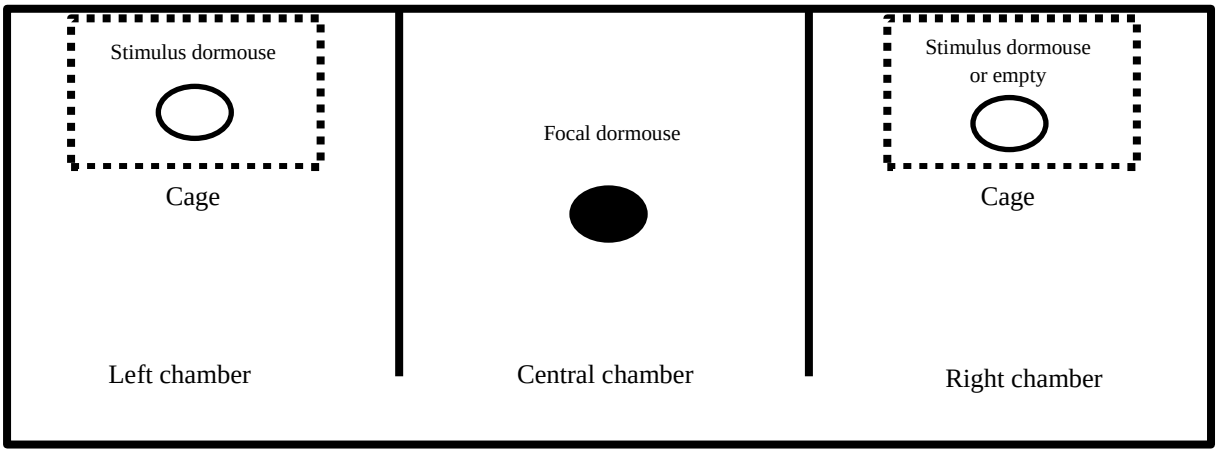


Figure 1. Schematic representation of an aerial view of the experimental glass tank with three internal chambers separated by two parallel walls (solid lines) made of Plexiglass. Focal woodland dormice *Graphiurus murinus* (represented here by the black-filled ellipse in the central chamber) could move freely between the three chambers. The outer chambers contained one square wire-mesh cage (rectangle with dotted line) each which was left empty or in which a stimulus dormouse (white-filled ellipse) was placed.

Sociability test

Prior to experiments, the test dormouse was restricted to the central chamber, by placing plastic barriers on the entrances of the side chambers. A stimulus same-sex adult with which the focal dormouse had never interacted previously (= *unfamiliar individual*) was placed in a wire-mesh box, in a randomly selected (left or right) chamber. An identical empty wire-mesh box was placed in the opposite chamber. At the start of experiments, the plastic barriers were removed and the focal mouse could move freely through all three chambers. The experiment lasted 20 min. This test was run for 10 test males and 10 test females each with a same-sex unfamiliar dormouse.

Social preference test

This experiment followed immediately after the sociability test. The first stimulus dormouse (now called *familiar individual* due to previous short-term contact with the focal dormouse) remained in its wire-mesh cage, and a new unfamiliar same-sex stimulus adult dormouse was placed in a wire-mesh box in the chamber. As before, the test dormouse was restricted to the central chamber, and once experiments commenced, barriers were removed and the test dormouse could move freely through all three chambers. The test lasted 20 min.

Sociability and social preference tests were each video-taped for a period of 20 min, using a digital camcorder (Sony, DCR-SX44) mounted in front of the cage above floor level. Between each complete (sociability + social preference) test, the chamber floor and walls were cleaned with disinfectant soap, air dried to reduce carry-over odour effects of tests subjects and replaced with fresh bedding material.

Behaviours were scored using the video analysis software Observer 3.0 ® (Noldus Inc., the Netherlands), For both tests, I recorded the number of entries into, and the time spent (in seconds) by the focal dormouse in each of the three chambers. I also measured the frequency and duration of behaviours that occurred during each interaction with stimulus dormice (Table 1). The scoring of the different behaviours took place 5 min after the start of the taping session and for 15 min thereafter.

Data analysis

All statistical analyses were conducted with IBM SPSS Statistics 22.0 (SPSS Inc.). Because data were not normally distributed (Kolmogorov-Smirnov test, $p < 0.05$), I used non-parametric Mann-Whitney tests to investigate potential intersexual differences in the number of entries into, and the time spent by, test dormice in the test chambers, as well as the duration of behaviours of the test dormice during sociability and social preference dyadic tests. Wilcoxon matched-pairs signed-ranks tests were used to compare the duration in chambers and behaviours by test dormice in tests with unfamiliar stimulus dormouse vs. empty cage; and unfamiliar vs. familiar stimulus conspecific. Chi-square tests of independence were used to test for potential intersexual differences in the frequencies of behaviours that were recorded for male and female test dormice during the 15-min sociability and social preference tests. Goodness-of-fit tests were performed to compare the frequencies of behaviours exhibited by test dormice in presence of a stimulus dormouse or in an empty chamber (sociability test), as well as in presence of a familiar and an unfamiliar individual (social preference test). Because the occurrences of behaviours were too few, chi-square tests for pooled data (df = 1) were run,

assuming that test individuals would equally choose between both cages (50% of observations in each cage). In order to facilitate data interpretation (i.e. "Do results significantly differ from a 50:50 distribution between choice chambers?"), absolute occurrences were converted to percentages.

Table 1. Behavioural categories and their related behavioural components scored during sociability and social preference tests.

Behavioural categories	Behavioural components
Sociability test	
Attraction	Nose-to-nose contact; sitting next to stimulus dormouse; grooming next to stimulus dormouse's cage
Ritualised aggression	Tail wagging; biting wire of stimulus dormouse's cage
Social investigation/Exploration	Sniffing stimulus dormouse's cage or sniffing empty cage; exploring, approaching stimulus dormouse or empty cage; contact with stimulus dormouse's cage or empty cage
Alone	Sitting next to empty cage
Vocal	Aggressive vocalizations (loud sharp shrieks followed by ritualised behaviour) at stimulus dormouse
Social preference test	
Attraction	Nose-to-nose contact; sitting with any of the stimuli dormice
Ritualised aggression	Tail wagging; biting wire of any of the stimuli dormice cages
Social investigation/Exploration	Sniffing or approaching any of the stimuli dormice; exploring; approaching any of the stimuli dormice; contact with any of the stimuli dormice
Vocal	Aggressive vocalizations (loud sharp shrieks followed by ritualised behaviour) at any stimuli dormouse

Results

Sociability test

Both test male and female woodland dormice entered a similar number of times and spent a similar amount of time in the chamber occupied by an unfamiliar stimulus dormouse compared to the chamber with an empty cage (Table 2). In addition, both sexes spent a similar amount of time sitting next to the stimulus dormouse's cage (median = 57 s; range 0–1384 s) versus next to the empty cage (median = 383 s; range 0–1609 s; Wilcoxon matched-pairs signed-ranks tests: W = -33.00, p = 0.46). Test dormice also approached, groomed or sat equally often next to both types of cages (Table 3). Both sexes, however, sniffed and made contact with the stimulus dormouse's cage significantly more often than with the empty cage; this difference was more pronounced in males than in females (Table 3). Males, but not females, sat more often next to the empty cage than next to the stimulus dormouse's cage.

Table 2. The median number of entries into, and the median duration (seconds) spent in the chamber occupied by a same-sex unfamiliar dormouse vs. an empty chamber, by test male (n = 10) and female (n = 10) African woodland dormice *Graphiurus murinus* during 15-min sociability tests. Ranges are presented in parentheses. Results of Wilcoxon's tests to compare both categories of chambers are provided below the table.

	Number of entries		**Duration in the chamber**	
Chamber	**Males**	**Females**	**Males**	**Females**
Chamber with stimulus dormouse	1.0 (0–5)	2.5 (1–13)	211.0 (0–1200)	67.0 (0–1200)
Chamber with empty cage	1.5 (0–5)	1.5 (0–15)	150.0 (0–1200)	317.0 (0–1065)
Wilcoxon's test → W	9	5	2	3
→ p	0.70	0.74	0.92	0.92

Table 3. Comparisons of specific behavioural components of test male and female woodland dormice in 15-min sociability tests with a same-sex unfamiliar stimulus dormouse vs. an empty cage. Chi-square goodness-of-fit tests (df = 1) for pooled data were run, assuming that test individuals would equally choose between both cages (50% of observations). Absolute occurrence data are provided in parentheses. NS = non-significant with p > 0.27. Bold values indicate significant differences.

Comparisons	**Male vs unfamiliar male** (n = 10)	**Females vs unfamiliar female** (n = 10)
Sitting next to stimulus dormouse's cage	31% (52)	50% (87)
Sitting next to empty cage	**69% (115)**	50% (88)
	$p < 0.001$	NS
	$\chi^2 = 23.77$	$\chi^2 = 0.01$
Sniffing stimulus dormouse's cage	**85% (85)**	**63% (37)**
Sniffing empty cage	15% (15)	37% (22)
	$p < 0.001$	$p < 0.05$
	$\chi^2 = 49.00$	$\chi^2 = 3.81$
Approaching stimulus dormouse	63% (26)	53% (31)
Approaching empty cage	37% (15)	47% (27)
	$p = 0.086$	NS
	$\chi^2 = 2.95$	$\chi^2 = 0.28$
Contact with stimulus dormouse's cage	**81% (57)**	**67% (38)**
Contact with empty cage	19% (13)	33% (19)
	$p < 0.001$	$p < 0.05$
	$\chi^2 = 27.66$	$\chi^2 = 6.33$
Grooming next to stimulus dormouse's cage	-	50% (7)
Grooming next to empty cage	-	50% (7)
	-	NS
	-	$\chi^2 = 0$

Focal male and female dormice did not differ in the time spent exploring, nor in the time spent sitting next to the unfamiliar stimulus dormouse and the empty cage (Mann-Whitney test: p > 0.21 in all cases). However, focal males were significantly more aggressive and vocalized and explored more often than test females (Figure 2). Females, on the other hand, were more attracted to unfamiliar stimuli dormice, but also spent more time alone (i.e. in the empty cage) than males (Figure 2).

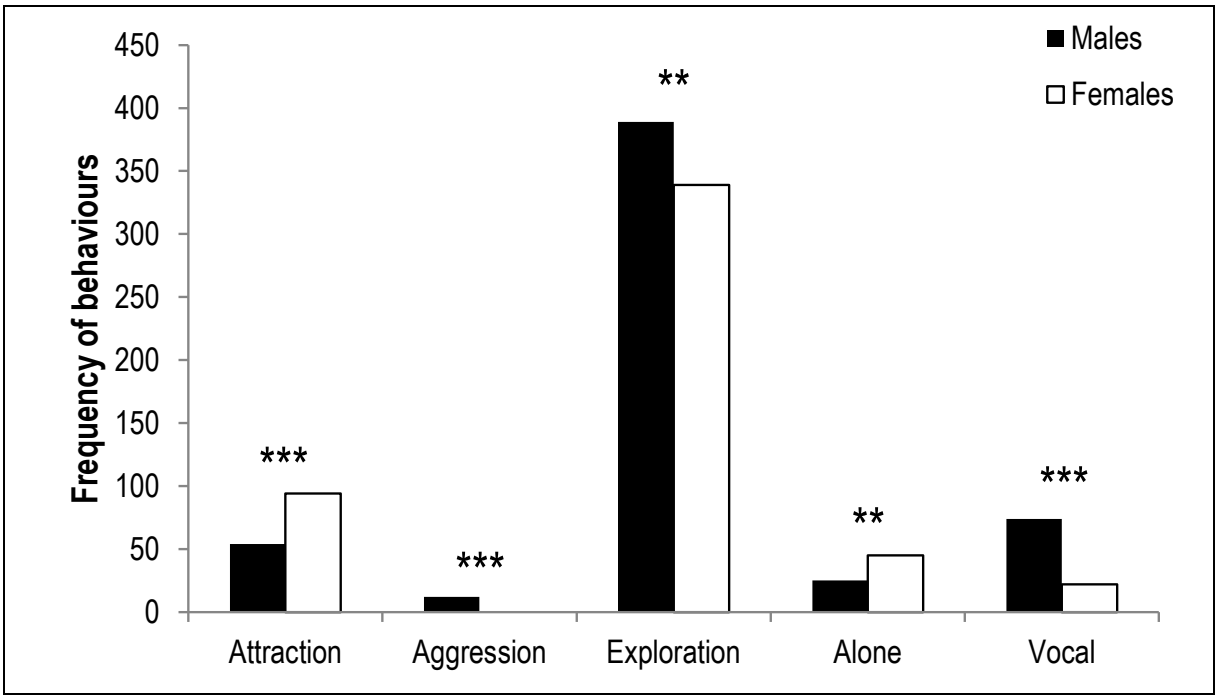


Figure 2. Comparisons of the pooled absolute frequencies of occurrence of broad behavioural categories exhibited by 10 test male and 10 test female woodland dormice in 15-min sociability tests with same-sex unfamiliar stimulus dormice. Behavioural categories that differed significantly (Chi-square test of independence) are indicated with ** ($p < 0.01$) or *** ($p < 0.001$).

Social preference test

Overall, both test male and female woodland dormice did not differ in the number of entries into or the time spent in the chamber occupied by an unfamiliar compared with a familiar individual (Table 4). Also, focal dormice did not spend more time sitting next to familiar dormice (median = 91 s; range 0–608 s) than with unfamiliar dormice (median = 0 s; range 0–463 s) (Wilcoxon matched-pairs signed-ranks tests: W = -38.00, $p = 0.15$).

Focal male dormice aggressively vocalized and displayed tail wagging significantly more often when in presence of an unfamiliar than a familiar individual (Table 5). In addition, focal males sniffed unfamiliar males more often than familiar males (Table 5). Focal females, on the other hand, sat significantly more often next to a familiar female than next to an unfamiliar female (Table 5).

Table 4. The median number of entries into, and the median duration (seconds) spent in, the chamber occupied by a familiar stimulus dormouse vs. a chamber occupied by an unfamiliar stimulus dormouse, by test male (n = 10) and female (n = 10) woodland dormice during 15-min social preference tests. Ranges are presented in parentheses. Results of Wilcoxon's tests to compare both categories of chambers are provided below the table.

	Number of entries		**Duration in the chamber**	
Chamber	**Males**	**Females**	**Males**	**Females**
Familiar stimulus dormouse's chamber	2.0 (0–4)	0.5 (0–11)	170 (0–798)	11.5 (0–1061)
Unfamiliar stimulus dormouse's chamber	1.5 (0–4)	1.0 (0–9)	496 (0–1200)	24.5 (0–910)
Wilcoxon's test → W	-4.00	-4.00	-25	4.00
→ p	0.81	0.84	0.16	0.81

Table 5. The behaviour of test male and female woodland dormice in 15-min social preference tests with one same-sex unfamiliar and one same-sex familiar stimulus dormouse. Chi-square goodness-of-fit test (df = 1) for pooled data were run assuming that test individuals would equally choose between both cages (50% of observations). Absolute occurrence data are provided in parentheses. NS = non-significant with p > 0.10. Bold values indicate significant differences.

Comparisons	**Males** (n = 10)	**Females** (n = 10)
Sitting next to familiar stimulus dormouse's cage	45% (5)	**85% (11)**
Sitting next to unfamiliar stimulus dormouse's cage	55% (6)	15% (2)
	NS	$p < 0.05$
	$\chi^2 = 0.56$	$\chi^2 = 6.23$
Biting wire of familiar stimulus dormouse's cage	0% (0)	0% (0)
Biting wire of unfamiliar stimulus dormouse's cage	100% (1)	100% (3)
	NS	$p = 0.08$
	$\chi^2 = 1.00$	$\chi^2 = 3.00$
Tail wagging at familiar stimulus dormouse	0% (0)	33% (3)
Tail wagging at unfamiliar stimulus dormouse	**100% (7)**	67% (6)
	$p < 0.01$	NS
	$\chi^2 = 7.00$	$\chi^2 = 1.00$
Sniffing familiar stimulus dormouse	29% (9)	62% (8)
Sniffing unfamiliar stimulus dormouse	**71% (22)**	38% (5)
	$p < 0.01$	NS
	$\chi^2 = 10.13$	$\chi^2 = 0.69$
Approaching familiar stimulus dormouse	47% (7)	60% (6)
Approaching unfamiliar stimulus dormouse	53% (8)	40% (4)
	NS	NS
	$\chi^2 = 2.6$	$\chi^2 = 0.40$
Vocalizations at familiar stimulus dormouse	0% (0)	75% (3)
Vocalizations at unfamiliar stimulus dormouse	**100% (12)**	25% (1)
	$p < 0.001$	NS
	$\chi^2 = 13.18$	$\chi^2 = 1.00$

Focal males and females did not differ in the time spent exploring or in the time spent sitting with familiar or with unfamiliar individuals (Mann-Whitney test: $p > 0.43$ in all cases). However, males were more aggressive and vocalized significantly more often than females, while females showed a tendency ($p = 0.06$) to be more attracted to the unfamiliar same-sex stimulus dormouse than males (Figure 3).

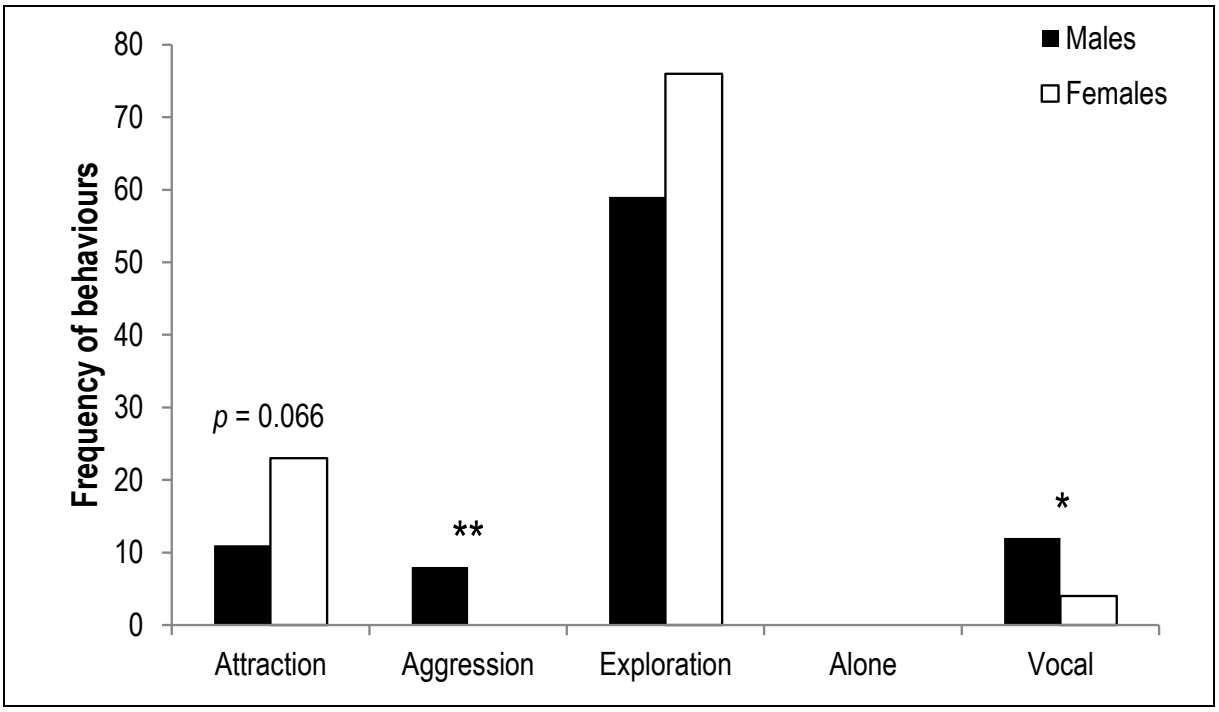


Figure 3. Comparison of the frequency of behaviours exhibited by 10 test male and 10 test female woodland dormice in 15-min social preference tests with both a same-sex unfamiliar stimulus dormouse and a same-sex familiar stimulus dormouse. Behavioural categories that differed significantly (Chi-square test of independence) are indicated with * ($p < 0.05$) or ** ($p < 0.01$).

Discussion

The sociability and social preferences of the woodland dormice were studied in order to ascertain whether they showed a motivation to seek out conspecifics and whether this motivation was modified through familiarity. My first prediction was that woodland dormice would be motivated to be sociable by interacting more often with stimulus dormice as compared to an inanimate object (empty cage). My prediction was supported in the sociability tests. Woodland dormice demonstrated a comparatively high motivation to be sociable with an unfamiliar stimulus dormouse. Both focal male and female woodland dormice spent significantly more time sniffing and in contact with stimulus dormice than with the empty cage. My results indicate that the presence of an unknown conspecific was not perceived as a threat since there was no/little aggression in the species, and that both sexes showed some behavioural affinity towards conspecifics. This motivation to be social was apparent even though woodland dormice did not show differences in the time spent with conspecifics versus inanimate object during the sociability test; affiliative behaviours still made up a larger portion of their behavioural interaction.

My second prediction was that female dormice would be more sociable than males, because they were the main associating sex in previous studies (Chapter 4). Both test female and male dormice showed similarities and differences in behaviours upon encounter of same-sex conspecifics in the sociability test. However, even though there was a demonstration of sociability overall, there were sexual differences in the motivation to be tolerant of strangers. Test females showed a greater affinity and attraction with no display of aggression to unfamiliar females as compared to test males. My results indicate that female woodland dormice are more sociable than males; this is in accordance with my previous chapter on social interactions (Chapter 4) whereby female dormice displayed more amicable behaviours towards conspecifics compared to males. In many species, affiliative tendencies seem to be greater in females than in males (Taylor *et al.* 2000).). In my study, the high degree of intrinsic motivation to be sociable by females, could have been mediated by oxytocin which is known to reduce stress in response to unfamiliar conspecifics. Indeed, empirical evidence shown in goldfish *Carassius auratus*, indicated that administration of oxytocin encouraged sociable approach behaviours, while arginine vasopressin inhibited sociable acts (Thompson & Walton 2004). Other evidence is provided in studies of Mongolian gerbil (*Meriones unguiculatus*) in which artificial injections of oxytocin caused an increase in sociability (Razzoli *et al.* 2003) and reduced aggression to female intruders (Harmon *et al.* 2002).This type of intrinsic tolerance or affiliative tendencies in females could possibly facilitate other behaviours, and have evolutionary advantages such as communal nesting and nursing through which females might benefit from sharing resources, such as nests, and raising young together.

Even though females showed some level of affinity towards unfamiliar dormice, male woodland dormice still displayed more agonistic behaviours and aggressively vocalised more often towards strangers. This indicates that males are less tolerant of male strangers, concurring with previous findings of dyadic interactions (Chapter 4), where males displayed aggression and agonistic behaviours to unfamiliar males. In contrast, in a study of spatial association (Chapter 3), I found that male woodland dormice shared nest sites with other males, and also showed intra-sexual overlapping home ranges in another study (Madikiza *et al.* 2011). The degree of familiarity or kinship among males from the natural population is not known, but at least some form of tolerance or sociable tendency seems to exist in nature. In mammals where males compete for reproduction, males are unlikely to tolerate unfamiliar males (Clutton-Brock & Harvey 1978; Eccard *et al.* 2004).

My third prediction was that both sexes would show a preference for and display more sociable behaviours with a previously encountered stimulus dormouse (familiar) compared to an unfamiliar dormouse, and that the strength of the preference would be greater in females than in males. In support of my prediction, in social preference tests, both tests females and males exhibited different behaviours towards unfamiliar and familiar stimulus dormice. Woodland dormice did not differ in the duration of time spent with familiar or unfamiliar stimulus dormice, yet they aggressively vocalized and displayed agonistic behaviours (such as tail wagging and cage biting) significantly more often when in the presence of an unfamiliar than a previously encountered dormouse. My results suggest that woodland dormice have a tolerance for strangers but this tolerance seems to develop with time, even a short time (20 min) as in my study. Similarly, Scott *et al.* (2005) hypothesised that sociability of a species is highly influenced by the sex of the individual and the level of familiarity, as seen in meadow voles *Microtus pennsylvanicus* (De Jonge 1980; Ferkin 1988) and European free-tailed bats *Tadarida teniotis* (Ancillotto & Russo 2014). These results could further reveal other behavioural aspects of woodland dormice, such as the ability to recognise and distinguish familiar and unfamiliar dormice.

Females showed a similar tolerance for both unfamiliar and familiar individuals, but with a slight preference for familiar individuals. Males had an affinity for familiar individuals and were less tolerant of strangers. Even though males showed greater affinity for familiar dormice by spending more time in the chamber, they were less amicable than females upon encountering of strange dormice, sniffing and displaying more aggressive behaviours, followed by aggressive vocalization more often than females. My results suggest that familiarity is an important factor driving group-living in male woodland dormice. The results also hint at the existence of a form of the "dear enemy phenomenon" (Fisher 1954; Temeles 1994) that is characterised by a tendency to be less aggressive towards familiar individuals than strangers. In nature, male dormice have overlapping home ranges (Madikiza *et al.* 2011) and might be tolerant of established familiar neighbours, as they are most likely to encounter these males frequently (therefore re-enforcing familiarity), and therefore are expected to be less tolerant to unfamiliar males, which might be competitors, as was observed in the thirteen-lined ground squirrel *Spermophilus tridecemlineatus* (Schwagmeyer & Brown 1983; Yahyaoui *et al.* 1995).

In conclusion, my study provided the first tests on the motivation to be social in African woodland dormice. Woodland dormice demonstrated a motivation to associate with unfamiliar conspecifics and a preference for familiar than unfamiliar same-sex individuals.

My data suggested that woodland dormice, particularly females, are motivated to affiliate with conspecifics even in the absence of extrinsic drivers (e.g. low ambient temperatures) that are known to promote sociability and nest cohabitation (Chapter 6; Madikiza 2010). The sexes differ in their motivation to be social, with females showing similar levels of attraction to familiar and unknown females, and males preferring familiar individuals to strangers. Such affiliative characteristics are possible drivers of group-living in female woodland dormice, and may form the foundational basis of spatial tolerance and nest site associations between males.

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CHAPTER 6
Social Huddling in Captive Female African Woodland Dormice *Graphiurus murinus*

Abstract

The social thermoregulation hypothesis states that endothermic species will nest communally to reduce energy expenditure on thermoregulation, hence predicting that the frequency of communal nesting will increase with decreasing ambient temperature (Ta). Here, I tested whether low Ta can lead to nest sharing and social huddling in pairs of unfamiliar female African woodland dormice *Graphiurus murinus*. I predicted that: 1) unfamiliar females would not share nests at high Ta; 2) nest sharing and huddling would occur between unfamiliar females at low Ta; 3) there would be a significant increase in nest temperature of huddling dyads; and 4) huddling pairs formed between unfamiliar individuals at low Ta would persist after Ta is raised and even in a different spatial context. All four predictions were supported. At high Ta, four of the five woodland dormouse dyads used in this study did not share a nest. Under decreasing Ta, nest sharing increased, and all unfamiliar female pairs huddled under cold temperatures. Four dyads did not split up when Ta was increased; this co-habitation continued in large housing cages for 3 months that followed the experiment. My results also demonstrated that huddling significantly warms up the local microclimate inside the nests of huddling dyads, and individuals even transferred and combined nest material (potentially increasing the insulation capability of nests), thus demonstrating cooperative nesting behaviour. These findings suggest that, under natural conditions, thermal challenges during winter may encourage huddling between unfamiliar female woodland dormice, and ultimately lead to the formation of long-term groups.

Keywords: Communal nesting, familiarity, group-living, huddling, social thermoregulation

Introduction

Lee (1994) defined sociality as a "tendency of animals to form groups or to live in groups". Two of the components listed by Hare & Murie (2007) that exemplify sociality are that 1) there exists fundamental ecological and evolutionary factors promoting and maintaining group-living, and 2) the social interactions among group members impart both benefits and costs. With regard to ecological factors, Emlen (1982) proposed the ecological constraint hypothesis, which suggests that grouping in animals might be a consequence of specific environmental conditions. This therefore advocates that animals might be forced to share their space with conspecifics, for example by delayed dispersal, under constraining environmental conditions (e.g. striped mice *Rhabdomys pumilio*: Schradin *et al.* 2011; European badgers *Meles meles*: Rosalino *et al.* 2005).

Alexander (1974) and Lacey (2004) stressed that sociality or group-living only transpires when fitness advantages outweigh costs. One important benefit proposed for sociality in rodents is social thermoregulation. The social thermoregulation hypothesis states that endothermic species will nest communally to reduce energy expenditure for thermoregulation (Canals *et al.* 1989), and predicts that the frequency of communal nesting will increase with decreasing ambient temperature (Ta) (Ebensperger 2001). This hypothesis is supported by communal nesting during winter. For example, in the edible dormouse *Glis glis*, group size is positively correlated with decreasing Ta (Fietz *et al.* 2010). Similar observations were made in several marmot species (Barash 1974; Holmes 1984; Arnold 1988). Furthermore, it has been shown that there is a substantial decrease in energy expenditure among huddling groups (Hayes *et al.* 1992; Ebensperger 2001). Supporting evidence is provided by striped mice (Scantlebury *et al.* 2006; Schradin *et al.* 2006), and Siberian hamsters *Phodopus sungorus* (Jefimow *et al.* 2010).

Although social huddling occurs in kin groups (e.g. Alpine marmots *Marmota marmota* (Arnold 1988); southern flying squirrels *Glaucomys volans* (Thorington & Weigl 2011), social huddling with non-related individuals may exist in some species, such as in deer mice *Peromyscus maniculatus* (Andrews & Belknap 1986) and ice rats *Otomys sloggetti* (Hinze *et al.* 2013). Since there is evidence that even solitary species such as shrews and voles (Webster & Brooks 1981; Hays & Lidicker 2000) engage in social huddling under cold stress, there could therefore exist some form of inter-individual tolerance that develops when animals are under thermal stress. In addition, there are possibly social benefits emerging from, or even promoting, huddling, consequently leading to the development and establishment of long-

term social relationships between individuals post-huddling (Berteaux *et al.* 1996). Familiarity amongst individuals has important impacts on sociality. Indeed, familiarity and tolerance between conspecifics are pre-cursors to sociality and promote group formation, such as in kangaroo rats *Dipodomys ingens* (Ralls 1971; Randall *et al.* 2002; Lovell & Lein 2005).

Dormice (family Gliridae) are heterothermic rodents. Aggregations – i.e. temporary groupings of several individuals in the same nest – are common in several dormouse species (Vietinghoff-Riesch1960; Golodushko & Padutov 1961; Angermann 1963; Pilastro 1992; Juškaitis 1997; Fietz *et al.* 2010; Sievanu & David 2012; Koppmann-Ruf *et al.* 2012; Juškaitis & Kertuka 2016; Viñals *et al.* 2017) and may be linked to thermoregulatory needs. Fietz *et al.* (2010) determined through measurement of oxygen consumption that edible dormouse aggregations reduce energy expenditure. Furthermore, these authors suggested that sexually active males form aggregations during winter in order to counterbalance the high thermoregulatory costs associated with reproductive activity. On the other hand, Pilastro (1992) discussed the possibility that female edible dormouse aggregations may reduce predation risk (e.g. through the dilution effect or increased vigilance) and, importantly, Pilastro *et al.* (1996) confirmed that communal nesting and nursing occurred in these females.

Woodland dormice *Graphiurus murinus* are competent thermoregulators which maintain a body temperature of between 34 °C and 38 °C. This can be achieved by increasing activity and making postural adjustments at low Ta or salivating at high Ta (Whittington-Jones & Brown 1999). Under laboratory conditions, Webb & Skinner (1996) noted that summer-acclimatized dormice used daily torpor spontaneously as an energy-saving mechanism in response to food deprivation. Ellison & Skinner (1991) further described that cold-acclimatized woodland dormice entered hibernation (i.e. prolonged bouts of torpor were observed), characterized by a decrease in both body temperature and body weight. In addition, free-ranging woodland dormice similarly undergo multiple-day torpor bouts of up to 8 days during winter, with body temperature reaching a minimum of 2.5 °C (Mzilikazi *et al.* 2012). Winter aggregations of torpid adult individuals of both sexes were also recorded in artificial nest boxes (Madikiza 2010).

The aim of my study was to test whether thermal challenges lead to nest sharing and social huddling in captive female woodland dormice, and if so, are there possible thermal benefits associated with social huddling. Using pairs of unfamiliar woodland dormice, I predicted that: 1) females would not aggregate at high Ta; 2) nest sharing and huddling would occur between females at low Ta; 3) there would be an increase in nest temperature of

huddling pairs; 4) huddling dyads formed at low Ta would persist after Ta is raised and even in a different spatial context.

Materials and methods

Woodland dormice used in this study were derived from a free-living population in the Eastern Cape Province, South Africa. Sampling took place in five different farm areas located specifically near the Great Fish River, where riverine *Combretum* forest strips are present. Forest patches in the five farmlands were located between 15 and 30 km apart. Based on tracking data, the maximum straight-line distance covered by any individual at night varied between 50 m and 1 km depending on the sex and season (K. Madikiza unpublished data). Hence, it can be assumed that individuals captured in different sampling areas were not familiar with each other.

To minimise impacting on the demography of dormouse subpopulations and to obtain unrelated individuals for behavioural and breeding studies, a maximum of 4 males and 4 females were removed from each of the five sampling sites. A total of 26 adult dormice were trapped and removed from the natural areas.

Prior to experiments, woodland dormice were housed in the Milner Park Animal Unit, University of the Witwatersrand, Johannesburg under partially controlled environmental conditions: reversed 12L:12D light–dark cycle (lights on at 19:00), 22–24 °C and 30–60 % rH. Dormice were individually housed in metal cages (L × B × H: 0.5 × 0.5 × 1 m). Wood shavings (~3 cm) were provided as bedding. Each individual was provided with a galvanised nest box (L × B × H: 15 × 15 × 15 cm) with a 50 mm entrance hole and ~10 g of paper towel was provided as nesting material. Additional natural material in the form of branches and small logs were placed inside the metal cages for environmental enrichment. Food (Versele hamster muesli; Belgium) and water were provided *ad libitum*. Approximately 10 g of a combination of mealworms *Tenebrio molitor*, peanuts, boiled egg, fruits and vegetables were given as occasional supplements.

Experimental design

Experiments on social huddling took place in a conviron at the University of Pretoria under controlled environmental conditions: reversed 12L:12D light–dark cycle (lights on at 19:00); 5–25 °C and 30–60% rH. The experimental set-up comprised of three linearly arranged cages (L × B × H: 46.5 × 31 × 35 cm). Both end cages were connected with PVC pipes (length: 30

cm; diameter: 4.5 cm) to the middle cage. Cages were constructed of galvanised steel on three sides, with a clear Perspex front to facilitate observations, and a wire-mesh lid. Each end cage functioned as the home cage for one individual and contained ~3 cm of wood shavings for bedding, ~10 g of distinctive, colour-coded paper towel as nesting material (i.e. a different colour nesting material for each dyad member) and water bottles. The middle cage contained only a layer of wooden shavings and a food dish. The middle cage thus served as a neutral area separating the two end "home cages".



Figure 1. Picture of the experimental setup showing the three linearly arranged cages connected with PVC pipes. Each end cage functioned as the "home cage" for one individual African woodland dormouse *Graphiurus murinus*, while the middle cage served as a neutral area.

Prior to experiments, 10 female woodland dormice were weighed to the nearest gram using a spring balance, and fur-clipped on the back for individual identification. Each individual was paired with a weight-matched (<5-g difference), unfamiliar dormouse from a different population. Five female–female dyads were thus established. Only female dyads were used in this experiment so as to avoid the confounding effects of sexual behaviour (in male–female dyads) and possible injury or even fatal aggressive interactions between males (see Chapter 4). Individuals were randomly assigned to their experimental "home cages" at least 3 days prior to the start of experiments, so as to allow for familiarisation to their new

environment. Dyads were prohibited from making physical contact by limiting them to their home cage with a removable plastic barrier (i.e. a lid) placed at the end of each interconnecting PVC pipe. This meant that individuals had no access to the neutral cage or their partner's cage prior to the day of experiment. Approximately 10 g of hamster muesli, mealworms, fruits, vegetables and water were provided *ad libitum* in both home cages prior to removal of plastic barriers and thereafter double rations of food were provided in the neutral cage when barriers were removed to reduce territoriality over food.

On the day of experiments, the plastic barriers were removed and dormice were allowed to explore the experimental apparatus. To observe cage occupancy and sharing, the location of each individual (home cage, neutral cage or partner's cage) was recorded once daily for 30 min for all dyads during the light phase of the light–dark cycle between 19:00 and 20:00 for the 34 continuous days of experiments. Nest material transfer was recorded for each dyad by visually observing the combination and the amount of specific colour-coded nest material left in the home cage. Additional colour-appropriate nest material was provided every day in the home cage at the start of each observation.

To test my first prediction, dyads were allowed to interact under stable Ta (~25 °C) for a period of 5 days. Following this, Ta was decreased gradually in 5 °C decrements, from ~25 °C to ~5 °C over a period of 22 days (Days 6–28) in order to test my second prediction. For the third prediction, once the individuals had formed aggregations (huddling pairs), Ta was then increased from ~5 °C to ~25 °C in two 10 °C increments over a period of 3 days (Days 29–32).

To test for possible thermal benefits associated with huddling, nest temperature was monitored for each dyad by inserting one *i*-Button® (Model DS1921G Thermocron, Maxim/Dallas *i*-Buttons Products) inside the centre of each nest. The *i*-Buttons were inserted on the 21st day of experiment, when Ta was at 15 °C, and were programmed to record nest temperature every hour for the remaining days of the experiment. The position of the *i*-Button® was checked daily and repositioned in the nest if it became displaced by the dormice. At the end of the experiment, data from the *i*-Buttons from different nests that were respectively shared by one and two individuals, and from an empty nest that acted as a control throughout the whole monitoring period were retrieved.

To establish whether nest sharing persisted even under different spatial and environmental contexts, after 34 days, dyads were returned to Milner Park Animal Unit, University of the Witwatersrand, Johannesburg, housed under similar spatial and environmental conditions described in experimental Ta experimental protocol (reversed

12L:12D light–dark cycle with lights on at 19:00, Ta~25 °C and 30–60%rH) but in larger metal cages (L × B × H: 0.5 × 0.5 × 1 m), with a similar setup and design described above. Dyads were again observed once daily for 30 min for all dyads during the light phase of the light–dark cycle between 19:00 and 20:00 for a period of 3 months. I recorded whether or not dyads shared nest boxes and consequently shared nesting material.

Data analysis

All statistical analyses were conducted with the software IBM SPSS Statistics 22.0 (SPSS Inc.). The significance level was set at $p < 0.05$ for all analyses. Because data were not normally distributed (Kolmogorov-Smirnov test, $p < 0.05$), a chi-square test for linear trend was used to evaluate variation in the percentage of nest sharing in dyads across the five temperature regimes. I used Mann–Whitney tests to evaluate differences in temperatures between a nest constantly occupied by two dormice, a nest used by one animal and an empty nest.

Results

Dyadic patterns of nest sharing

Females in four out of the five dyads slept separately in different nest boxes during the first 5 days of the experiment, when room Ta was 25 °C. The only exception was the Gm3–Gm5 dyad, which shared nests during all 5 days (Figure 1). When temperature was lowered to 20 °C, a second dyad (Gm10–Gm6; Figure 1) shared a nest from Day 6, and a third dyad followed (Gm7–Gm8; Fig. 5) on Day 8. When I lowered the temperature to 15 °C, a fourth pair (Gm4–Gm9) slept together from Day 21. The last dyad (Gm1–Gm2) only started sleeping in the same nest on Day 27 of the trial, when the temperature was at 5 °C. All five dyads immediately started to sequentially transfer all the nest material to a single home cage as soon as nest sharing occurred. The percentage of nest sharing increased linearly in the five temperature regimes (Chi square test for linear trend: $\chi^2 = 6.49$, df = 1, $p = 0.011$), indicating that female woodland dormice increased associations during colder temperatures.

Four of the five dyads that cohabited during the temperature experiments continued to share a nest when the Ta was increased to 15 °C and 25 °C. When placed in larger cages after the experiment, these four dyads immediately transferred the entire nest material to a single home cage which they then shared. Nest sharing was observed during the 3 months of subsequent monitoring and dyads often ate together. The remaining dyad (Gm3–Gm5) was

excluded from the data set of temperature increase because one animal escaped repeatedly. As a precautionary measure, these two animals were placed in separate cages after the experiment.

Variation of temperature inside the nest

As predicted, nest temperature increased significantly ($p < 0.001$) when the nest was used by one or two dormice, and this at all five temperature regimes (Table 1). Nest temperature was higher when two dormice cohabited than when one dormouse nested alone. This difference was highly significant at the lower temperature regimes, and smaller and/or non-significant at 20–25 °C (Table 1).

Table 1. Median temperature differences (°C) between a nest shared by two individuals, a nest used by one dormouse and an empty nest at five different ambient temperature (Ta) regimes. Statistically significant differences in nest temperatures (Mann–Whitney U tests) are indicated (***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$; NS: not significant).

Comparisons	**Median temperature difference**				
Ta	*25 °C*	*20 °C*	*15 °C*	*10 °C*	*5 °C*
2 individuals vs. 1 individual	+2.5*	+1.25^{NS}	+3***	+7.25***	-[a]
2 individuals vs. Empty	+4***	+3.5***	+5.5***	+10.75***	+7.0***
1 individual vs. Empty	+2.5***	+2.25***	+2.5***	+3.5***	-[a]

[a]No temperature data could be obtained for a single individual nest at 5 °C because all dormouse dyads shared a nest.

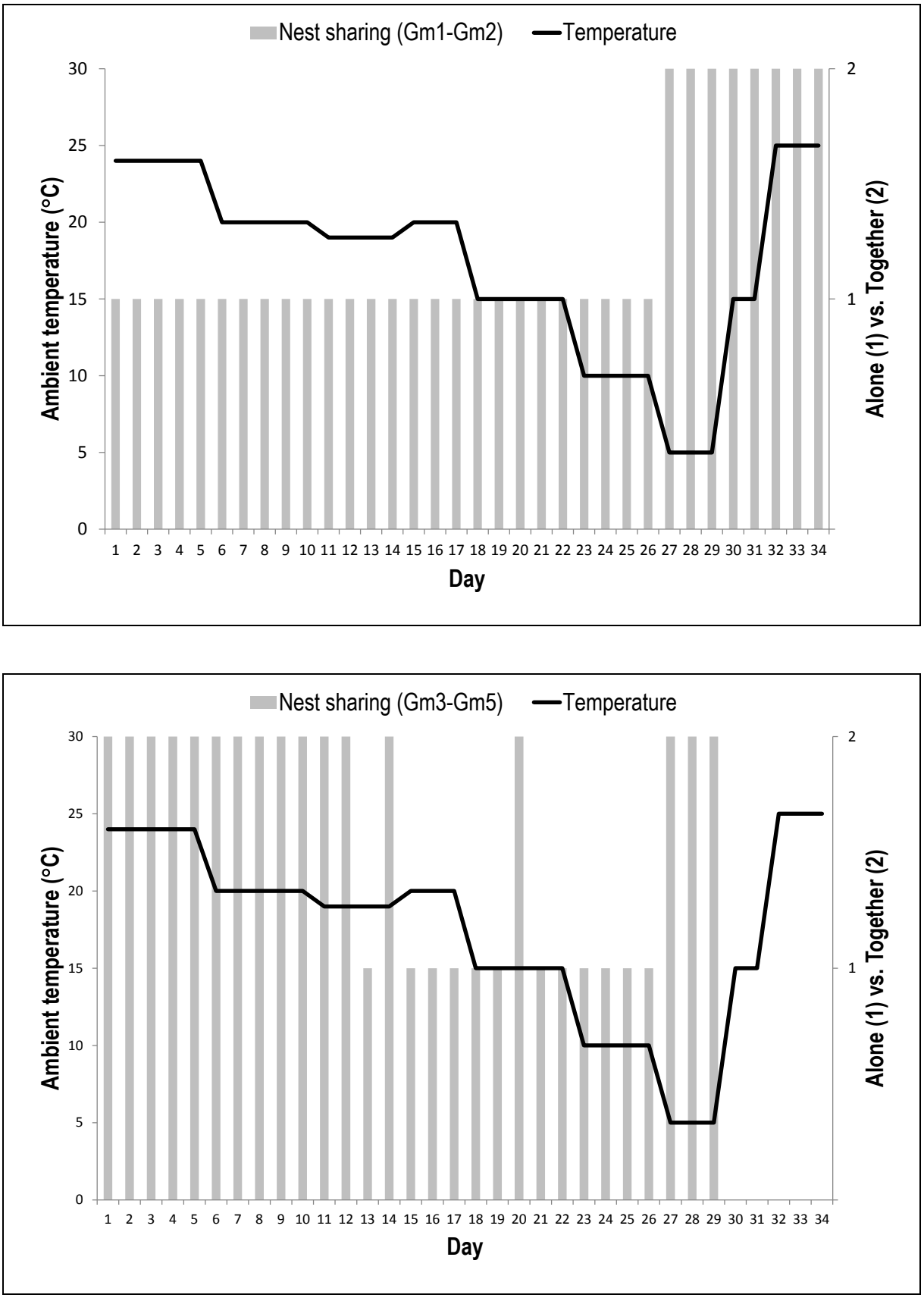
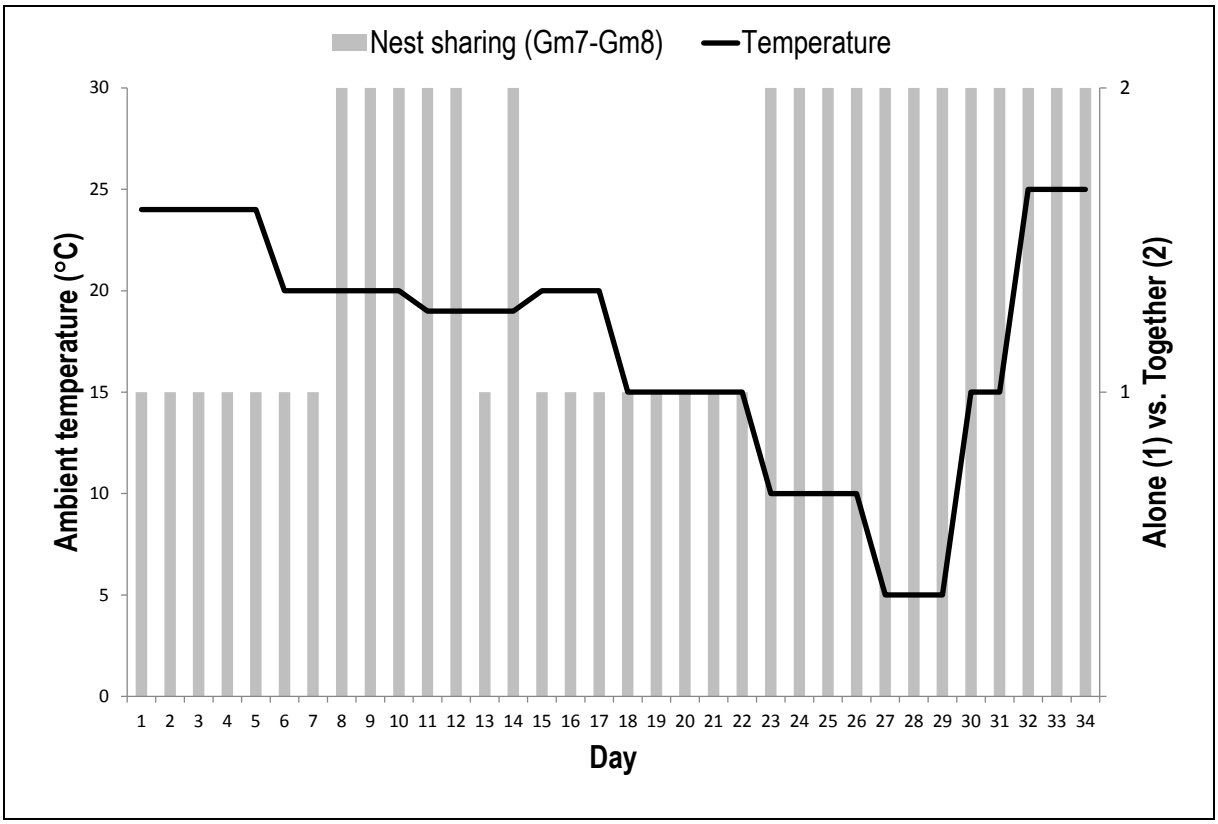


Figure 2. Patterns of nest sharing (i.e. nesting alone vs. nesting together) for five female woodland dormouse dyads (indicated with GM initials and identity numbers at the top of each figure panel) during the 34 days of experiments. No data could be collected for the last 5 days (Days 30–34) for Gm3–Gm5 (see text for explanations).



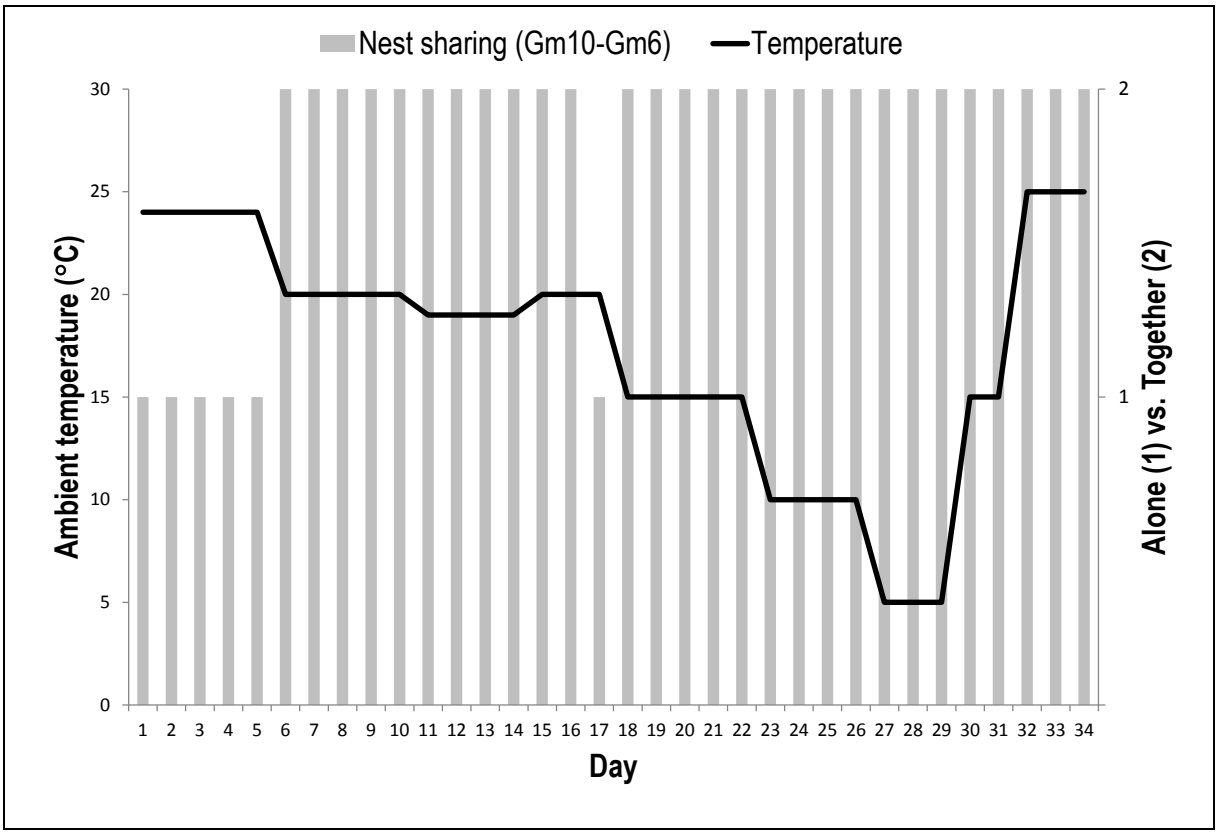


Figure 2. Continued.

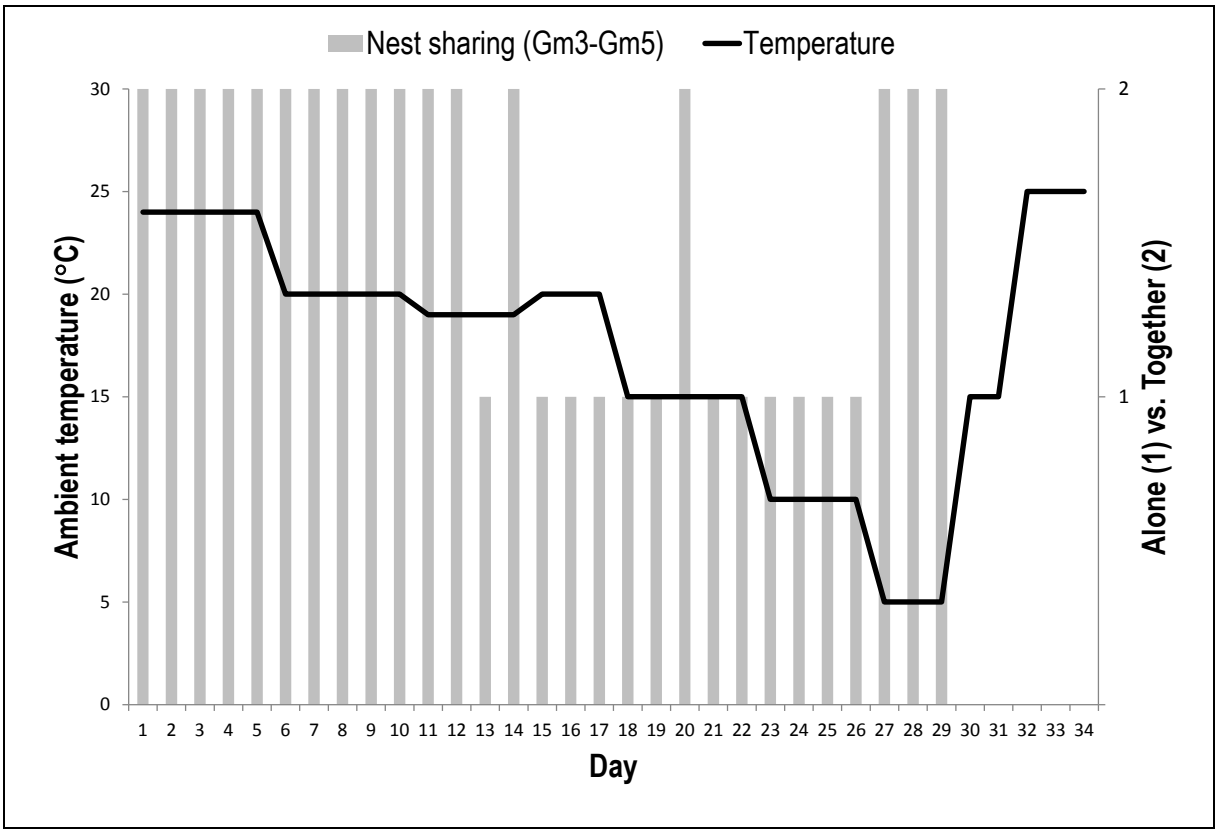


Figure 2. Continued.

Nest material transfer

Nest material transfer to one of the two nests of the female dyads occurred for the first time on Days 18 and 19 for the first three (Gm3–Gm5, Gm10–Gm6, Gm7–Gm8) and four dyads (Gm4–Gm9) respectively, as soon as Ta decreased to 15 °C. The remaining dyad (Gm1–Gm2) started transferring nest material to one of the nests when temperature dropped to 5 °C.

Discussion

The aim of this study was to assess whether unfamiliar female woodland dormouse dyads huddle at low ambient temperatures, as proposed by the socio-thermoregulation hypothesis (Ebensperger 2001). I also tested whether these dyads would form huddling groups that persist after increasing Ta.

Four out of five female woodland dormice dyads did not share a nest or interact with each other on the first 5 days of encounters under high Ta. These results revealed an important contributor of sociality in female woodland dormice. Female dormice may indeed have group-living tendencies, and could be inclined to form groups regardless of Ta, as

observed in one dyad. However, the latency to form these social groups might require longer time for a majority of individuals. Therefore, it is conceivable that the length of exposure to conspecifics may increase familiarity and the motivation to associate. For example, observed by Wills *et al.* (1983), familiarity facilitated affiliative behaviours such as huddling in albino rat pups (*Rattus albus*). This could well happen independently of temperature constraints, but the latter seem to be a more powerful driver of association, as discussed further, below.

As predicted, all dyads huddled together and shared a nest as soon as the temperature was set at 5 °C, even for pairs that were not co-habiting in nests on previous days under slightly higher temperature regimes. This suggests that social huddling is initiated at the very least by very low temperatures, with a threshold possibly lying between 5 and 9 °C. Dyads actively transported and shared nest material with decreasing ambient Ta, which indicates that there exist Ta thresholds under which nest sharing and nest material transfer occurs. Both huddling and nest building increase thermal insulation (e.g. in the European ground squirrel *Spermophilus citellus*; Gedeon *et al.* 2010) and can substantially reduce energy expenditure of rodents housed at low Ta (Muul 1968; Stapp 1992; Merrit *et al.* 2001; Tompkins 2003). Several studies demonstrated that huddling increased with decreasing Ta, such as in Siberian hamsters *Phodopus sungorus* (Jefimow *et al.* 2010), Alpine marmots *Marmota marmota* (Arnold 1988), striped mice (*Rhabdomys pumilio*) (Scantlebury *et al.* 2006) and flying squirrels *Glaucomys volans* (Thorington & Weigl 2011).

Female dyads continued to co-nest, huddle, and share nest material even after the temperature was increased, with the exception of one dyad for which no information could be obtained during the final phase of the experiment. The most parsimonious explanation for these observations is that it could be energetically costly to construct nests, and therefore individuals preferred to continue sharing a nest. However, such cohabitation was observed up to 3 months after the temperature experiment, and despite surplus nest material being provided daily, females continued to share nests and nesting material. This shows a motivation for joint nest construction in dyads previously cohabiting at low temperatures. It is thus conceivable that co-nesting in dormice creates the emergent outcome of collaborative nest building, which in turn reduces the energetic costs of individual nest building. Therefore, latent sociality (i.e. social behaviours that lead to group formation unintentionally) possibly exists in female woodland dormice, and its onset is triggered by low temperatures.

A significant increase in nest temperature of huddling dyads was recorded. Huddling affected the rate of heat change in nest temperature. Through active formation of huddling pairs, dormice increased nest temperature by a median of between 1.25 °C and 7.25 °C. These

results indicate that there are acquired thermoregulatory benefits of huddling. Similar findings were recorded for short-tailed field voles *Microtus agrestis*, in which huddling individuals increased nest temperature by 5 °C (Hayes *et al.* 1992).

In conclusion, this study examined potential co-nesting as a thermoregulatory strategy utilised by female woodland dormice and whether co-nesting enhanced familiarity, thus strengthening social bonds amongst initially unfamiliar individuals. Female dormice appeared to employ social huddling in response to very cold ambient temperatures, and females transferred nest material to a communal nest under these low ambient temperatures. These results indicate that huddling might be a process that promotes familiarity in woodland dormice, which might then lead to co-ordinated activities and group-living (Kleiman 1977). The time spent huddling may be foundational for reinforcement of these behaviours, leading to other activities, such as communal nursing and even allo-parental care (as demonstrated in edible dormice; Pilastro 1992; Pilastro *et al.* 1996; Marin & Pilastro 1994; Sevianu & David 2012) and ultimately to fitness benefits. Social huddling could function as a platform through which emergent social behaviours lead to group formation. More generally, huddling in heterothermic species could serve as a precursor or transition phase to social hibernation, and group-living might then be an emergent consequence of such huddling.

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CHAPTER 7
General Discussion

The literature on the African woodland dormouse *Graphiurus murinus* suggests that the species nests communally in trees and nest boxes, with nests being occupied by several adults (e.g. Kingdon 1974; Madikiza 2010; Madikiza *et al.* 2011). However, in-depth studies confirming these nesting associations and importantly the mechanisms driving these social groups are lacking, rendering it difficult to characterise the form of social system of this species. My over-arching aim was to investigate sociality in the woodland dormouse *G. murinus* and to position the species along a continuum of sociality, within the two extremes of solitary and social, and to further understand the drivers of its social system. I conducted both field and laboratory studies, and revealed new information on the behaviour and sociality of the species. In my discussion below, I summarise the key findings, and then reflect on the current understanding of social systems, focusing on both extrinsic and intrinsic mechanisms driving sociality. I used my findings to generate a model of sociality in the woodland dormouse and I compared my results with that obtained on other Gliridae and rodent species generally, emphasizing similarities and differences and finally putting forward avenues for future studies.

Key findings

I described the demographic and seasonal patterns of sleeping associations in a free-living population of woodland dormouse. I found that females showed higher frequencies of associations than males. Female–female sleeping associations were more frequent than expected in spring and winter and less frequent than expected in summer. Male–male sleeping associations took place almost exclusively during the mating season in spring and summer, and male–female sleeping associations were particularly high during the mating season but were also observed in the non-breeding autumn and winter seasons. The sleeping associations may be reflecting the reproductive and thermoregulatory priorities of the species. Having shown association patterns between individuals within my study population, in Chapter 3, I investigated the nature of these sleeping associations within the study population. I found that woodland dormice groups were highly composed of same-sex individuals, with female–

female dyads having a greater index of association than male–female and male–male dyads. Social network diagrams revealed a complex web of relatively even associations between adult males and females, as well as the presence of pairs and trios of associated females. To complement my field findings, I performed laboratory experiments to investigate the pertinent proximate mechanisms driving sociality in woodland dormice. In Chapter 4, I studied dyadic social interactions of same sex encounters, which are often used to test the degree of sociality within animal species. I found that males and females differed in the way they responded to the presence of a same-sex unfamiliar dormouse. Males were more aggressive, displaying both overt (e.g. chasing, biting and wrestling) and ritualised (e.g. raised tails, tail wagging and scent marking) aggression, and performed more social investigation behaviours than females. Females were more amicable and exhibited more exploration and avoidance behaviours than males. Next (Chapter 5), I investigated whether there was an intrinsic motivation to be social and whether this motivation was modified through familiarity. I found that woodland dormice are motivated to associate with conspecifics intrinsically under optimal environmental conditions in captivity. However, the motivation to be social differed between the sexes: female dormice had an affinity for both strangers and unfamiliar woodland dormice, whereas males showed an affinity for familiar male woodland dormice. Finally (Chapter 6), I tested whether thermal challenges (extrinsic factor) modified the social behaviour in females, thus promoting group-living, as proposed by the socio-thermoregulation hypothesis (reviewed in Ebensperger 2001). In support, I found that low temperatures (<5 °C) are potential triggers for nest cohabitation in female dyads, which persist for extended periods even when temperatures were restored to ambient conditions. Furthermore, my study revealed that cold temperature is indeed one of the factors leading to familiarity, and coordinated activities such as co-nesting and social huddling in female woodland dormice.

Social systems

Social systems of a species describes the social organisation (the composition of groups, e.g. solitary or family groups), the mating system, and the social structure (describing which individuals interact (social behaviour) with each other; Struhsaker 1969; Kappeler & van Schaik 2002; Schradin *et al.* 2012). Social systems are not fixed, and can change in space (populations of the same species) and time (within species; Lott 1991). Social systems are influenced by extrinsic and intrinsic factors (Happold 1976), and are therefore subject to evolutionary change and are adaptive because of the fitness benefits derived by individuals

(Barash 1989). As stated by Wilson (1975), social systems are not distinct options, but instead occur along a continuum where the extreme endpoints can vary between solitary at one end to extremely social on the other, and animal social systems can be positioned anywhere along this continuum (Happold 1976) and even vary temporally (Schradin *et al.* 2012). Below, I consider the extrinsic and intrinsic mechanisms possibly driving and shaping the social system of woodland dormouse (Figure 1).

Possible mechanisms driving social behaviour in the woodland dormouse

A number of factors influence the social behaviour of animals. Intrinsic factors, such as the life history characteristics (e.g. sex of individuals, age, reproductive status) and physiology, have direct influences on the regulatory processes shaping social behaviours by influencing the motivation to associate or avoid conspecifics (Hofmann *et al.* 2014). These motivations are causally linked to neuroendocrine and genetic mechanisms that regulate the decision making rules to be social or not (Rubenstein & Hofmann 2015). In synergy with these internal processes are a variety of external factors, such as the presence of another individual or stranger, or an animal's immediate environment (reviewed in Curtis *et al.* 2007). Ecological factors (e.g. habitat structure, resource distribution, ambient temperatures) and social factors (e.g. kinship, familiarity, demography) are possibly the main extrinsic factors influencing social systems, although stochastic processes have some regulatory role (Schradin 2013). For instance, ecological factors such as resource availability can affect the behavioural responses of individuals, sexes or group members by changing the spatial patterns and social organization of a population (Emlen & Oring 1977). Social factors, such as the presence of familiar and unfamiliar conspecifics, can affect behavioural responses of individuals, leading to attraction or avoidance (Beery & Kaufer 2015). Stochastic factors such as changes in demography (e.g. death and dispersal), could alter the entire social organisation, and thus shape the social system. Combined, intrinsic and extrinsic factors interact to shape the spatio-temporal variation in associations between individuals and thus shape the social system (Schradin *et al.* 2012). Below, I consider the pertinent intrinsic and extrinsic factors that shape sociality in woodland dormice, as summarized in Figure 1.

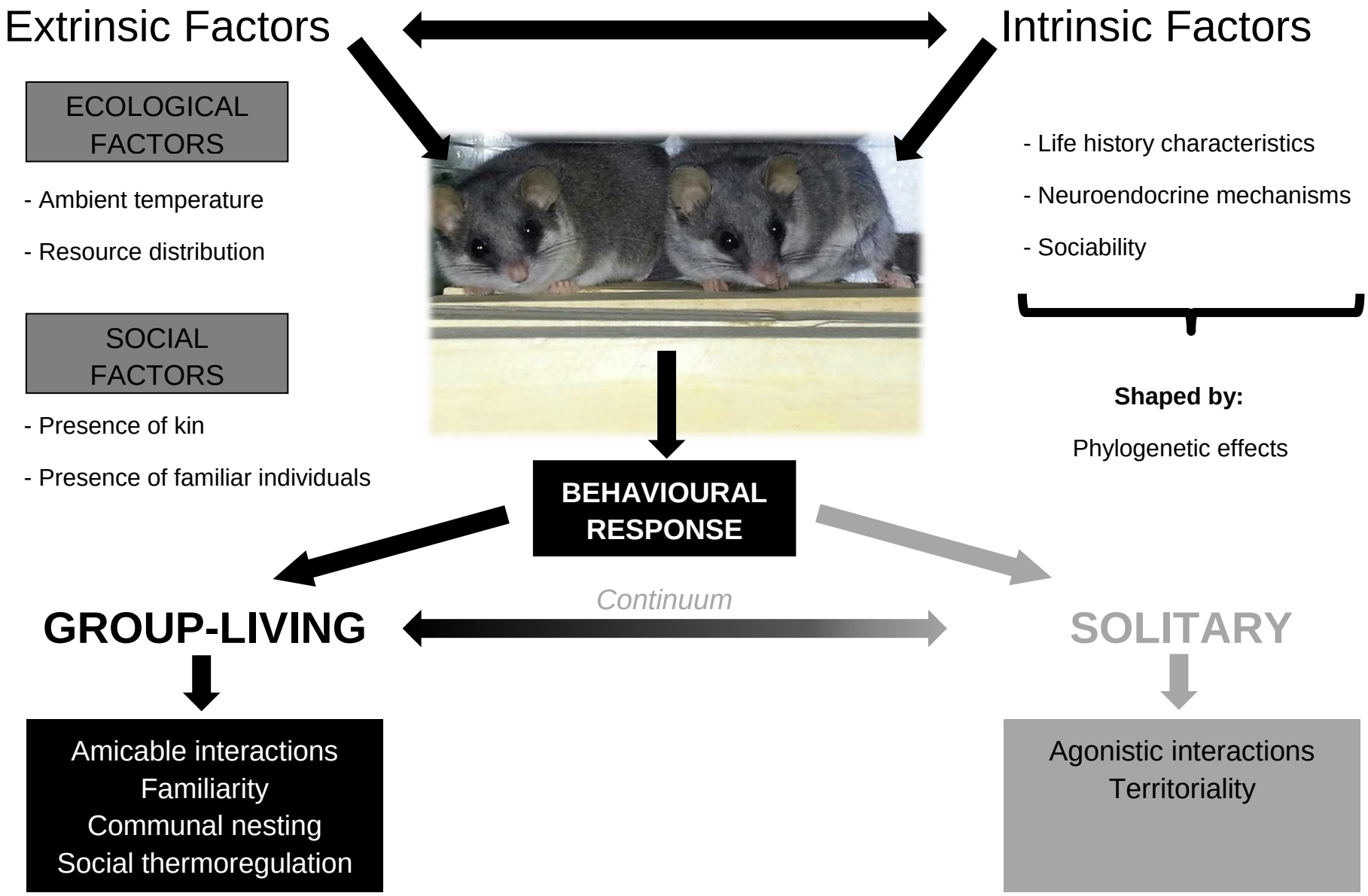


Figure 1. Schematic representation of the extrinsic and intrinsic factors I hypothesise to shape group-living in the African woodland dormouse *Graphiurus murinus*.

Intrinsic factors

Life history influences

Life history characteristics may have direct influences on the regulatory processes shaping social behaviours and the extent of sociality (Figure 1). For example, certain life history traits such as longevity of a species could lead to the development of long term bonds and associations, thus shaping sociality (Arnold & Owens 1998). The life history hypothesis proposes that high longevity (i.e. low mortality) has direct significance on establishing a territory by offspring, through limited breeding territories for offspring, thus leading to natal philopatry (Brown 1987). This hypothesis is supported by studies on social birds, where greater longevity leads to sociality (Arnold & Owens 1998). Woodland dormice, as a heterothermic species, can live up to 6 years in nature (pers. obs.), which is aligned with the theory of Turbill *et al.* (2011) that heterothermic species have a greater life expectancy than homeothermic species of similar size. Additionally, female woodland dormice can have up to two litters in a breeding season (Madikiza 2010). Taken together, these two above mentioned life history characteristics could have at least three implications on the social behaviour and sociality of the species. 1) High survival in adult woodland dormice could cause low territory turnover rates, thus leading to a shortage of new territories for juveniles. 2) A shortage of new territories in the population, constrains the two litters to share the mother's territory, thus limiting dispersal and promoting natal philopatry. 3) Sharing of space predisposes the pooled litter to be tolerant and social (e.g. in the case of male–male associations). Therefore, the observed patterns of sleeping site association, and the overall network structure (Chapter 2 & 3) showing male–male (brothers?), females–female (sisters?) and juvenile–juvenile (siblings?) sleeping association could be a result of high longevity, limited territories and natal philopatry.

Neuroendocrine mechanisms

Hormones orchestrate and modify the behavioural responses expressed, in concert with the ecological, social and physiological status of individuals (Figure 1) (Crews 1997). Well known candidate mechanisms linked to social behaviour are neuropeptides (e.g. oxytocin and arginine vasopressin) and sex hormones (e.g. testosterone; Adkin-Regan 2005).

For group living to exist, proximate mechanisms orchestrate the expression of pro-social behaviours, such as tolerance of the presence of other individuals and social recognition of partners, and induce behavioural responses that increase sociability (reviewed in Soares *et al.* 2010). It has been shown that arginine vasopressin and oxytocin are involved in the

regulation of sociable behaviours such as approach and aversion (Porges 2001), cohabitation, pair bonding and affiliation (reviewed in Lim & Young 2006). In my study, the high degree of intrinsic motivation to be sociable (Chapter 4 & 5) to strangers (as in the females) or familiar conspecifics (as in both males and females), could have been mediated by oxytocin which is known to reduce stress in response to unfamiliar conspecifics. Under such circumstances, it is then expected that woodland dormice would be less aggressive to non-threatening conspecifics, thereby promoting tolerance, amicable behaviours and co-nesting in the species. Indeed, empirical evidence shown in goldfish *Carassius auratus*, indicated that administration of oxytocin encouraged sociable approach behaviours, while arginine vasopressin inhibited sociable acts (Thompson & Walton 2004). Other evidence is provided in studies of Mongolian gerbil (*Meriones unguiculatus*) in which artificial injections of oxytocin caused an increase in sociability (Razzoli *et al.* 2003) and reduced aggression to female intruders (Harmon *et al.* 2002).

The ability of animals to distinguish between familiar and unfamiliar conspecifics may serve as an important catalyst in creating social groups, as the type of social interactions may highly be dependent how well a social partner is known (reviewed in Soares *et al.* 2010). In this case, oxytocin and vasopressin play very important roles in social recognition, especially since vasopressin is known to be involved in olfactory social recognition (Bielsky & Young 2004; Winslow & Insel 2004). In Chapter 5, social preference tests indicated that male woodland dormice had preferred familiar over unfamiliar males, even when familiarity occurred for a short term.

Social recognition can act as a platform on which the formation and maintenance of social relationships can exist (reviewed in Soares *et al.* 2010). Recognition of individuals allows for animals to build preferential relationships with selected members in a population. In Chapter 3, the existence of specific sleeping associations, as well as the strength of the associations (as shown by an association index), could have been determined by the levels of social preferences associated with certain individuals in the population. Such strong relationships with certain individuals could lead to social bonds, thus facilitating cooperative behaviours such as social huddling (males and females) and communal nursing/nesting in females.

Testosterone is known to modulate behaviours such as mating, territory defence and group formation in both sexes (Wolff 1994; Faulkes & Abbott 1997; Clarke & Faulkes 1998). In birds and mammals, the sexual motivation of females has been linked to testosterone, while in all male vertebrate taxa, testosterone influences agonistic and/or sexual behaviours

(reviewed in Soares *et al.* 2010). In Chapter 4, the high aggression observed in dyadic interactions between males is likely to be regulated by the levels of circulating androgens, and frequent encounters between males potentially stimulates testosterone secretion, and subsequently increasing aggression (Wingfield *et al.* 1997). This is in agreement with the Challenge Hypothesis (Wingfield *et al.* 1990), which proposes that aggression is in direct association to androgen levels, along with the context at which the behaviour takes place.

My field studies do not appear to support the Challenge hypothesis. In Chapter 2, male woodland dormice were intra-sexually tolerant towards conspecifics (thus possibly lower androgens) during the mating period when males are expected to compete for access to receptive females, and therefore show intense aggression (thus high testosterone levels). Several studies have shown that during the breeding season, high male testosterone levels effectively regulated the mating behaviours of males through attraction to females and moderation of male intra-sexual interactions (Cavigelli & Pareira 2000; Dunlap *et al.* 2002; Emerson 1997; Goodson & Bass 2001; Wingfield *et al.* 1990). Therefore, the occurrence of male–male associations during the breeding season in my study implies that other factors (e.g. familiarity) are at play. Indeed, the sociability tests (Chapter 5) indicated that males associate with familiar over unfamiliar males even when familiarity occurred for a short term. This potentially means that familiarity could be one factor that overrides the modulating influences of testosterone, thus contradicting the Challenge Hypothesis.

Tolerance of other males is also apparent during the hibernation period in my studies. Based on the energetic demands linked to thermoregulation, it is possible that being aggressive or showing tendencies of agonistic behaviours during hibernation might prove to be costly for male woodland dormice. Aggression could adversely affect the process of torpor or hibernation through increased metabolic rates and glucocorticoid levels of animals (Goymann & Wingfield 2004). Empirical evidence is provided in male Siberian hamsters *Phodopus sungorus*, which when injected with testosterone, were unable to enter torpor (Ruby *et al.* 1993). Similar findings were noted for the edible dormice *Glis Glis* (Fietz *et al.* 2010) in field studies. Therefore, in heterothermic species, such as the woodland dormouse, physiological thermoregulatory adaptations may directly affect hormonal levels (Wingfield 1994).

Sociability

Formation of groups and the maintenance of social relationships may also be influenced by the motivation of the organism to seek, approach and spend time in social contact with

conspecifics (i.e. sociability- Figure 1) (Kohn *et al.* 2013). Sociability can be measured at an individual level, by the motivation of animals to gain access to conspecifics (e.g. silver foxes *Alopex lagopus*: Hovland *et al.* 2008), and through observations of how individuals respond to isolation (e.g. in cattle: Hopster & Blokhuis 1994).

In Chapter 5, the distinct inclination to interact with conspecifics may have been driven by an innate motivation to be social. Both males and females consistently were motivated to be in close proximity to conspecifics even in the absence of extrinsic factors (e.g. low ambient temperatures) that are known to promote sociability (see Chapter 6). Matthews *et al.* (2013) argued that social animals are expected to be socially motivated, which can be used to distinguish between social or solitary animals. In other words, social species should seek out conspecifics and as a result implement behaviours that increase social contact in comparison to solitary species, as seen in social prairie voles *Microtus ochrogaster* vs solitary meadow voles *Microtus pennsylvanicus* (Matthews *et al.* 2013). However, the extent of sociability exhibited by individuals is generally influenced by several factors such as the sex of the individual and the level of relatedness/familiarity of individuals (Scott *et al.* 2005), which must be considered studies of sociality.

Ecological factors

Ambient temperature

Ambient temperature has a direct effect on the behavioural responses of animals (Figure 1). Unfavourable ambient temperatures are considered as environmental stressors that can illicit physiological and/or behavioural responses in animals (Killen *et al.* 2013). In the woodland dormouse, individuals respond to environmental stressors, such as food deprivation and low ambient temperatures, physiologically by utilising torpor or hibernation and behaviourally through social huddling (Ellison & Skinner 1991; Webb & Skinner 1996, Madikiza 2010; Mzilikazi *et al.* 2012). The observed temperature related sleeping association patterns in natural population of woodland dormice (Chapters 2), as well as social huddling by previously unfamiliar female dyads under low (<5 °C) ambient temperatures (Chapters 6) suggested that woodland dormice were behaviourally motivated to huddle with conspecifics. In free-living dormice, this motivation to huddle coincides with a drop in ambient temperatures (autumn and winter) coupled with low food availability during this time of the year (Chapter 2). My findings are aligned with the social thermoregulation hypothesis (see review by Ebensperger 2001), and is supported by several mammalian studies on social huddling in bank voles *Clethrionomys glareolus* (Gerbczynski 1969), marmots (Armitage

2007), striped mouse *Rhabdomys pumilio* (Schradin *et al.* 2006), neotropical bats *Noctilio albiventris* (Roverud & Chappell 1991), Indian bats *Myotis sodalist* (Boyles *et al.* 2008), sugar gliders *Petaurus breviceps* (Quin *et al.* 2010) and pygmy possum *Cercartetus nanus* (Namekata & Geiser 2009).

Energy expenditure differs between huddling and torpor/hibernation. Communal huddling is less energetically costly than the maintenance of torpor or hibernation (Barton *et al.* 1992). Therefore, minimising the use of torpor could reduce the energy costs associated with this strategy, and thus increase individual fitness. Hwang *et al.* (2007) indicated that heterothermic species that utilise huddling tend to enter torpor less often than those that are solitary. In Chapter 2 & 6 of my study, the availability of social partners allowed for social huddling thermoregulatory strategy by woodland dormice, as a consequence possibly saving energy. Indeed, in striped skunk *Mephitis mephitis*, groups of skunks utilized social huddling and entered torpor less frequently, thus reducing energy expenditure as compared to solitary skunks who entered torpor frequently (Hwang 2005). Similar results were also reported for Siberian hamster *Phodopus sungorus* (Jefimow *et al.* 2011), whereby social huddling reduced body mass loss, as well as the frequency and duration of torpor bouts in the species (Jefimow *et al.* 2011).

However, heterothermic species, such as the woodland dormouse may face what is termed as the "energetic conundrum" (McAllan & Geiser 2014), describing the fact that thermoregulation and reproduction are different biological entities that have dissimilar energetic and hormonal demands. In woodland dormice, the breeding season follows soon after winter (Madikiza 2010), so that in winter individuals must conserve energy for the subsequent mating season. Since torpor is energy costly and huddling is less energy consuming, huddling would save energy in winter that could be channelled into reproduction later. I therefore argue that if woodland dormice utilised behavioural thermoregulatory strategies (thus shorter and shallower torpor bouts) then energy savings through huddling could be re-channelled into reproductive activity by both males and females. Indeed, in the edible dormouse *Glis glis*, sexually active males socially huddle during winter in order to counterbalance the high thermoregulatory costs associated with reproductive activity (Fietz *et al.* 2004). Supporting evidence for females has been found in the little brown bats *Myotis lucifugus*, whereby the torpor bouts of pregnant and lactating females were found to be shorter in comparison with post lactating females (Dzal & Brigham 2012).

Resource distribution

The formation of social groups and the stability of these groups is highly dependent on the characteristics and qualities of key resources (King 2015). If these resources (e.g. nesting sites, mating partners) are clumped, more stable social groupings form (Clutton-Brock 1989; Wolff 1993). For example, male aggregations in grey-sided voles *Myodes rufocanus* is a direct consequence of the clumped distribution of receptive females (Ims 1988). Contrary to this, if the resources are evenly distributed and predictable, unstable social grouping occur, made up of transitory associations, and low competition within groups (Gowans *et al.* 2008), as occurs in Gunnisson's prairie dogs *Cynomys gunnissoni* (Slobodchikoff 1984). Furthermore, the distribution of important resources can modulate the behaviour towards conspecifics (males and females or group members) (Figure 1). For instance, the distribution of resources will affect and determine spatial distribution of one sex (e.g. quality food and protective nesting areas for females), which will in turn influence the spatial patterns and behaviour of another sex (e.g. availability of mating partners for males) (Emlen & Oring 1977). In my study site, there was surplus of nest sites (natural and artificial nestboxes) and these were not clumped, which might explain the transitory or ephemeral nature of association in this population.

The resources that drive group formation usually differ between the sexes. Female spatial patterns are driven by food, whereas males search for females (Emlen & Oring 1977). Females may cooperate to exploit food or nesting sites, while males may cooperate in order to gain access to females (Trivers 1971). Female woodland dormice may face high energetic demands during pregnancy, lactation, and rearing offspring, primarily due to decreased foraging time (Millesi *et al.* 1999). Under such circumstances, females may benefit from cohabiting in order to minimise energetic costs. In previous studies of woodland dormice, adult females were recorded communally nesting with their young in nest boxes (Madikiza 2010). In male woodland dormice, the levels of tolerance and the spatial associations could be linked to mating opportunities as well as thermoregulatory demands. The low association levels between woodland dormouse males during non-breeding seasons and the peak in associations in winter (hibernation) and spring (breeding season) in my studies (Chapters 2 and 3) reflect an interesting mixed strategy to achieve and exploit mating opportunities on the one hand and meet thermoregulatory needs on the other. Such relationships could be established in two ways: 1) males tolerate and form coalitions and cooperate with one another (i.e. neighbouring males) in order to increase breeding opportunities (i.e. with receptive females) through joint mate attraction and nest guarding, as has been recorded in chimpanzees

Pan troglodytes (Watts 1998); and 2) after natal dispersal, males may still maintain close or overlapping home ranges with kin, deriving inclusive fitness through sharing huddling and mating opportunities.

Social factors

Presence of social (kin or familiar) individuals

The availability and the presence of social (related and unrelated familiar) individuals in a population can define and limit the extent of sociality in several ways. 1) Familiar or kin individuals can influence the nature of social interactions that take place, by reducing the levels of agonistic behaviours amongst individuals and thus reducing stress e.g. domestic cats (Leyhausen 1965; reviewed in Bekoff 1981), and may further stimulate amicable behaviours and sociability (Figure 1) (Scott *et al.* 2005). In Chapter 4 & 5, focal dormice showed more amicability and reduced aggression to familiar conspecifics. 2) The presence of conspecifics can facilitate the tendency to participate in cooperative behaviours (Dugatkin 1997). In Chapter 5 & 6, the presence of familiar conspecifics not only increased amicable behaviours, but also encouraged cooperative behaviours (nest sharing and nest construction) in female woodland dormice. 3) The availability of familiar social partners plays a pivotal role in searching and securing potential mates (Douglas *et al.* 1976). In Chapter 2, it is possible that male-female partners that huddled in the same nest in winter, were potentially mating partners during the mating season in spring. Supporting evidence are available in the fat-tailed dwarf lemurs *Cheirogaleus medius* (Dausmann & Glos 2014) and sugar gliders *Petaurus breviceps* (Suckling 1984).

Cooperative behaviours between familiar social partners could be explained by the mutual benefits model (Lima 1989, Maynard-Smith 1983) or the "prisoners delight" (Binmore 2004) model, whereby cooperating with conspecifics (social partners) is the best choice for both individuals. From a thermoregulatory perspective, it seems implausible that sleeping alone would yield a higher pay-off than sleeping in groups in woodland dormice. Therefore, encounters between females are an important catalyst that facilitates cooperative behaviours and possibly sociability and group-living, while familiarity between males leads to tolerance in nest sites, again leading to cooperative behaviours.

Evolutionary explanations of sociality

Phylogenetic effects

The phylogenetic constraint hypothesis maintains that group-living re-appears in species that share a lineage even though constituent populations occur in different ecological contexts (McKitrick 1993; Rowe & Honeycutt 2002). A good example of phylogenetic constraints is shown in the equids (horses and zebra) whereby Linklater (2000) linked the variations in the socio-spatial organisation of equids to ancestor-descendant relationships rather than habitat differences.

Across the Glirids, formation of groups and the tendency to huddle during winter is well known in most of the studied species of dormice: edible dormouse *Glis glis* (Pilastro 1992; Marin & Pilastro 1994; Scinski & Borowski 2008; Fietz *et al.* 2010; Koppmann-Ruf *et al.* 2012; Sevianu & David 2012); common dormouse *Muscardinus avellanarius* (Likhachev 1966; Morris *et al.* 1990; Bright & Morris 1996; Juškaitis 1997); garden dormouse *Eliomys quercinus* (Viñals *et al.* 2017); forest dormouse *Dryomys nitedulla* (Juškaitis & Kertuka 2016); Japanese dormouse *Glirulus japonicus* (Kawamichi *et al.* 2000; Shibata *et al.* 2004); spectacled dormouse *Graphiurus ocularis* (Van Hensbergen 7 Channin 1990); and African woodland dormouse (Kingdon 1974; Qwede 2003; Madikiza 2010). Is it then possible that the observed similarities in the occurrence of group-living in the extant Glirids a consequence of shared ancestry (ancestor-descendant relationship)?

Phylogenetic studies by Montgelard *et al.* (2003) indicated that dormice originated from Europe, and *Graphiurus* colonised Africa approximately 11 Myr ago. Based on this analysis, the observed social thermoregulatory strategies in the woodland dormouse could have originated in a European ancestor already exhibiting this behaviour due to colder ambient temperatures in Europe in comparison to Africa. As such, social thermoregulation in woodland dormice could be a phylogenetic constraint rather than ecological adaptation (i.e. low ambient temperature). If so, the current distribution of woodland dormice in South Africa would coincide in areas where social thermoregulation is exploited.

Ecological constraints

The ecological constraint hypothesis maintains that the existence of sociality in rodents is directly linked to availability, heterogeneity and abundance of important resources (reviewed in Ebensperger 2001). Ecological constraints such as habitat heterogeneity may favour sociality by driving individuals to co-habit in suitable habitats (see Malizia 1998; Stallman & Holmes 2002). In other words, the accessibility and distribution of suitable breeding sites,

nesting/sleeping areas, foraging space, would have direct consequences on the existence and extent of group-living (Lott 1991; Travis *et al.* 1995). However, my findings, at least for nest site availability, does not support this hypothesis because 1) the number of cohabited nests was shown to be higher than the single vs unused nests in Chapter 2, and 2) previous studies on the sleeping site ecology have shown that sleeping site fidelity in this population of woodland dormice was low and that individuals changed sleeping sites on a daily basis, thus displaying higher availability of this resource (Lamani 2014). It would be important to study the extent of group-living in other woodland dormice populations in areas where such resources are poor (e.g. degraded habitats or forests). Moreover, it is important to consider whether other resources (e.g. distribution of food) contribute to spatial patterns and sociality.

Conclusion and future directions

The aims of my study was to investigate sociality, the mechanisms promoting sociality, and to position my species along the continuum of sociality. My study has provided new knowledge on the social system of the woodland dormouse *G. murinus,* which expands on the body of work on Glirids particularly and rodents generally. Group-living in the woodland dormouse is driven by intrinsic and extrinsic drivers associated with social thermoregulation and mating. Huddling has emerged in my study as an important behavioural strategy in response to very cold ambient temperatures and under these conditions, tolerance, familiarity, and as such co-ordinated activities and group-living emerged (at least in females).

Future studies must investigate the genetic/familial relationships of the population and particularly individuals in sleeping associations, in which benefits kin derive direct and inclusive fitness benefits (Michener 1983). If female and male woodland dormice associations are indeed kin based, elevated tolerance should exist, mirrored by non-random association patterns and network. Previous work on the same population revealed the occurrence of pregnant female–female aggregations in nest boxes (Madikiza 2010), and compelling evidence from other dormice species has shown that co-nesting exists between sisters (Pilastro 1992; Marin & Pilastro 1994).

It is possible that female association groups of woodland dormice could be a mixture of kin or non-kin groups rather than one or the other. The motivation to be sociable (Chapter 5) and nest co-habitation (Chapter 6) with non-kin suggest that groups can occur between non-kin. If so, the acquired benefits of group-living are not only restricted to related groups (kin selection hypothesis) and also the reciprocity hypothesis (Trivers 1971).

In my study, familiarity was an important factor driving associations, indicating the occurrence of social recognition (Winslow 2003). Perhaps frequent association in nests or sleeping groups may promote familiarity, leading to tolerance in the species. As such, familiarity might have a stabilising effect on the social structure in the population. I therefore ask whether group formation in woodland dormice is expedited by the presence or availability of familiar conspecifics (Wolff & Trillmich 2008).

I conclude that African woodland dormice display facultative sociality, characterised by small seasonally transient sleeping groups. In females, limited aggression, tolerance, nest sharing and construction under low temperatures could also lead to prolonged group-living. In males, aggression towards unfamiliar males possibly maintains intrasexual territoriality, whereas familiarity yields a tolerance, leading to group-living. My study has shown that woodland dormice tend towards being social along the two extreme end points of sociality and solitary living (Figure 1). Group-living in this arboreal rodent is mediated by the apparently phylogenetic energetic demands of thermoregulation, coupled with an inherent need to associate with conspecifics. The level of familiarity between conspecifics or the presence of social partners facilitates group formation and is shaped by prevailing ecological conditions. These conclusions will need a more intensive investigation of genetic relatedness and consideration of other populations in the geographic range of the species to assess the generalisability and evolution of sociality in woodland dormice.

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