

**Behavioural responses of male woodland dormice  
(*Graphiurus murinus*) towards communicatory cues  
of same-sex conspecifics**

By

**Sinah Maswoba**

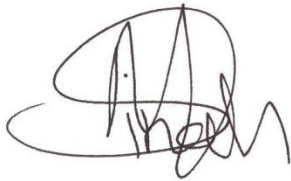
A dissertation submitted in fulfilment of the requirements  
for the degree of **MASTER OF SCIENCE (DISSERTATION)**  
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# DECLARATION

I **Sinah Maswoba**, student number **1280831** hereby declare that this dissertation titled **“Behavioural responses of male woodland dormice (*Graphiurus murinus*) towards communicatory cues of same-sex conspecifics”** submitted for the Degree of Master of Science at the University of Witwatersrand is solely my own, unaided work. It has never been submitted for any degree or examination at this University or other Institution.

A handwritten signature in black ink, appearing to read 'Sinah Maswoba', is written above a horizontal line.

**Sinah Maswoba**

Signed on the 4th day of November 2019 at the University of the Witwatersrand, Johannesburg

# **DEDICATION**

I dedicate this thesis to my nephew and nieces. I trust that this thesis will inspire you to reach your dreams and goals. All the best!!

# ACKNOWLEDGEMENTS

First and foremost, I thank God almighty for His grace and for His guidance throughout my studies to complete this thesis.

I would like to express my sincere gratitude to my supervisor Dr. Kim Madikiza for giving me the opportunity to do this research with her. I value her patience, guidance and insightful comments in writing this thesis. This was indeed a period of insightful learning and writing for me, and I am grateful you made this journey possible and an enjoyable one.

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# ABSTRACT

Broadcasting state and actions by means of communicatory cues is essential for mediating different important behaviours such as declaring social status, territory ownership or species or individual identification. The aim of this study was to investigate the behavioural responses of male woodland dormice (*Graphiurus murinus*) towards communicatory cues of same-sex conspecifics from the same or from different populations. I performed three experiments: 1) Three-chambered paradigm test for sociability and preference, which allows a focal animal to select between stimulus animals on the basis of visual, olfactory, and auditory cues, excluding tactile cues. 2) Acoustic test, which allows dormice to be exposed to auditory, olfactory and visual cues of conspecifics through social dyadic encounters. 3) Olfactory discrimination test, which allows animals to choose between stimulus odours only. Wild-caught dormice were obtained by means of live-trapping in three independent stretches (and therefore dormouse populations) of riverine *Combretum* forest at the Great Fish River Reserve (Eastern Cape, South Africa).

The three-chambered paradigm test revealed that male woodland dormice are able to discriminate between intra-population and inter-population male conspecifics. In my study it seems that recognition is achieved by means of multi-modal communicatory stimuli excluding physical contact of animals. Intra-population encounters showed significantly more affiliative (sitting next to conspecific), exploratory and grooming behaviours. Inter-population encounters displayed significantly more grooming behaviours only.

Acoustic tests showed that all four major acoustic signals recorded for woodland dormice species were emitted in this study. Across both intra-population and inter-population encounters, variation in behaviour correlated with variation in the type of vocalization. Inter-population dyads significantly vocalized and produced more aggressive (shriek/kecker) sounds, accompanied by aggressive (biting of wire) behaviours, exploratory/avoidance behaviours and sitting and grooming next to conspecifics. Olfactory discrimination tests revealed that male woodland dormice can discriminate between non-scented and scented areas by same-sex conspecifics from different populations. Males in scented tests showed more aggressive and investigative behaviours, while males in unscented tests displayed more exploratory/avoidance behaviours. This study has demonstrated that male woodland dormice

are not tolerant to males from different populations, and communicatory signals play an important role in mediating social interactions.

**Keywords:** acoustic behaviour, aggressive behaviour, *Graphiurus murinus*, non-vocal behaviour, olfactory cues, vocalization

# 1. INTRODUCTION

Most animal species live in complex social structures that are developed and maintained over space and time through communication (Portfors and Perkel 2014). Communication is described as an event whereby signals are released by individuals directed towards members of their own or of different species, therefore influencing the behaviour of the recipient (Ehret 1980, Seyfarth and Cheney 2003). In addition, communication requires the receiver to pick up the signal, though they might not respond to it (Francescoli 2000, Seyfarth and Cheney 2003). Many mammalian species spanning from solitary to social, primarily use acoustic, olfactory and visual cues to exchange information and to broadcast their intentions and actions with conspecifics (Francescoli 2000). These signaling cues (i.e. acoustic, olfactory and visual) are essential for mediating social behaviours, eliciting contacts with conspecifics, identifying individuals or species, signaling status (reproductive, dominance, territorial) as well as stimulating sexual behaviours (Schleich and Busch 2002). In addition, many of the signaling cues virtually enable individuals to resolve contests and disputes without physical harm through ritualised displays emanating from non-signaling behaviours (Van Staaden *et al.* 2011).

Acoustic signals include both audible (Schleich and Busch 2002, Simeonovska-Nikolova and Bogoev 2008) and ultrasonic sounds (Nyby *et al.* 1976, Blumberg and Alberts 1990). Audible sounds are vocalizations audible to the human hearing threshold (Holy and Guo 2005), whereas ultrasonic sounds are defined as acoustic or infrasonic signals above the human hearing range (Roberts 1975, Ancillotto *et al.* 2014, Seffer *et al.* 2014). Rodent acoustic signals are highly variable, and can reveal an individual state corresponding with specific non-acoustic behaviours (Keesom *et al.* 2015). As an example, the striped field mouse (*Apodemus agrarius*) vocalizations differ in structure and intensity ranging from loud and harsh vocalizations to relatively low clucks calls suggesting their different functions during intraspecific interactions (Simeonovska-Nikolova and Bogoev 2008). Loud and harsh vocalizations are used during hostile encounters to encourage threat behaviours before attacks and fights; while low clucks sounds are essential in reducing aggressive behaviours towards the dyad partner (Simeonovska-Nikolova and Bogoev 2008). On the other extreme, agonistic calls emitted in staged dyadic social encounters were linked to the stimulation of aggressive behaviours towards male opponents in the Siberian hamster (*Phodopus sungorus*) (Keesom *et*

al. 2015). Additionally, bicolored shrew (*Crocidura leucodon*) vocalizations were associated with retreating behaviours and mutual avoidance responses of the dyad partner (Simeonovska-Nikolova 2004).

Intrinsically, acoustic signals are important in defining territorial boundaries (Lupanova and Egorova 2015) and facilitating conflict resolutions (Seyfarth and Cheney 2003). For example, American red squirrels (*Tamiasciurus hudsonicus*) vocalizations coupled with overt aggressions in the form of fights and pursuits allow for territory holders to defend their territories against intrusion by strangers (Dantzer *et al.* 2012). The performance of ritualised signals in the form of repertoires of vocal signals particularly in group-living species often reduce intragroup conflicts and maintain social relationships among conspecifics (Seyfarth and Cheney 2003).

Most rodents have a well-developed olfactory sense used for social communication through chemical signals (Ralls 1971). The importance of olfactory signals is that, scent cues are typically long-lasting and degrade over a long period of time, making them ideal for conveying information in social as well as in solitary species (Hurst 2005). For example, the scent of an individual can be carried over long distances before exerting its effect upon another animal (Von Holst and Buerger-Goodwin 1975). There are different types of olfactory signals that animals use as potential sources of odour (Johnson 1973, Kapusta and Sales 2009, Schaal and Al Aïn 2014). For example, house mice (*Mus domesticus*) use urine (Hurst 1990), and Mongolian gerbils (*Meriones unguiculatus*) use salivary secretions as odours cues (Block *et al.* 1981). On the other hand, Libyan jirds (*M. libycus*) use various sources of odour emanating from abdominal glands to broadcast their scent (Wolff and Sherman 2007). However, urine and anal glandular secretions emerge as the most commonly used sources of odour in small mammals (Robert 2007).

Scent cues are individually distinct and may provide significant information that can influence a wide range of behavioural patterns (Ferkin 2015). For example, meadow voles (*Microtus pennsylvanicus*) are able to distinguish between individual conspecifics, indirectly via exposure to olfactory cues, exhibiting more amicable and less agonistic behaviours towards familiar than unfamiliar conspecifics (Ferkin 1988). In addition, such ability to discriminate individuals solely on the familiarity of odour cues could be a valuable social skill that provides conspecifics with the necessary information for decision making under different social circumstances such as during agonistic interactions (Huck and Banks 1979).

In other group-living mammals, the presence of scents from unknown individuals elicit investigatory sniffing and aggression as reported in the territorial beaver (*Castor fiber*)

(Rosell and Bjørkøyli 2002). In contrast, the presence of scent marks in an unfamiliar area might act as a threat, discouraging approach and increasing latency to enter scented areas, as observed in the golden hamsters (*Mesocricetus auratus*) (Alderson and Johnston 1975).

Visual cues are an important mode of communication for diurnal rodents such as the tree squirrels (*Paraxerus palliatus ornatus*) (Viljoen 1983), kangaroo rats (*Dipodomys spectabilis*) (Randall 1984, Randall and Matocq 1997), and great gerbils (*Rhombomys opimus*) (Randall *et al.* 2000). Visual signaling animals often use body postures to convey state of emotion (Viljoen 1983). For example, the displaying of tail pilo-erection and tail flicks in a visual obstructed habitat signals alertness and also maintains visual contact with conspecifics (Viljoen 1983), whereas foot-drumming cues (a quick up and down movement of the hind feet) are associated with territorial defense and advertisement (Randall 1984).

Signaling though visual cues mostly take the form of conspicuous, stereotyped, ritual features (e.g. leaping, open mouth, tail flagging) to communicate intent such as conflict resolution (Mackintosh and Grant 1963, Cheney *et al.* 1986), attracting potential mates (Bergman *et al.* 2009), or predator deterrence (Randall *et al.* 2000). In confrontational situations for example, the displaying of submissive postures such as body crouch, in the presence of aggressive conspecifics, inhibit attacks and appeases the aggressive animal (Mackintosh and Grant 1963). Visual cues are potentially affected by the social environment, relying closely on individual proximity to trigger immediate responses (Hödl and Amézquita 2001, Hartman *et al.* 2005). Additionally, visual signaling in complex environments such as dense vegetation or in dim light becomes ineffective for a well-developed communication (Myhre *et al.* 2013).

### **1.1. Biology of the woodland dormouse (*Graphiurus murinus*)**

The African woodland dormouse (hereafter woodland dormouse) is an arboreal, small nocturnal rodent belonging to the family Gliridae (Figure 1.1). Colour characteristic of the upper parts of the body is uniform grey to buffy-grey, whereas the under parts including cheeks, hands and feet are buffy-white (Webb and Skinner 1994, Kryštufek *et al.* 2004). Adult woodland dormice weigh between 24 and 34 g, with a head-body length of 78–113 mm and tail length of 58–94 mm (Skinner and Chimimba 2005). The woodland dormouse is described as heterothermic and utilizes communal huddling, multiple-day torpor bouts and

even hibernation in the nests to reduce thermoregulatory demands (Webb and Skinner 1996, Whittington-Jones and Brown 1999, Mzilikazi *et al.* 2012).

Woodland dormice have a promiscuous mating system and are seasonal breeders that exhibit communal breeding (Madikiza 2010, Madikiza *et al.* 2011). Sexual receptivity in females is asynchronous and mating season start from early October until late February (Qwede 2003, Madikiza 2010). Female gestation period lasts up to 24 days, resulting in litters of 3–6 pups (Lynch 1989). Neonates have a body mass of 3.5 g and a tail length of 18–40 mm, respectively (Kingdon 1974).

The woodland dormouse is considered a social rodent with some sex-specific differences in its social behaviour, thus indicating the different behavioural motivations between sexes for forming social groups (Madikiza 2017). Specifically, dormice males are intrasexually more aggressive, displaying both signs of overt and ritualised aggression, and appear to be more territorial than females (Madikiza 2017). Females are more amicable and are motivated to affiliate with conspecifics in comparison to males, even in the absence of extrinsic drivers such as low ambient temperatures known to promote sociability (Madikiza 2017). In addition, familiarity through associations (e.g. sleeping sites) and mating is an important factor in determining the outcome of social interactions among conspecifics.



**Figure 1.1.** Woodland dormouse (*Graphiurus murinus*) with noticeable buffy-white underbelly and bushy tail (Photo: Emmanuel Do Linh San).

Woodland dormice make use of olfactory cues through repeated rubbing of their ano-genital areas during encounters with conspecifics to broadcast presence and state (Madikiza 2017). Acoustic signaling coupled with visual, and tactile cues signifies an important means of communication in the woodland dormice, whose vocal repertoires are linked to non-vocal behaviours such as territoriality (Madikiza 2017), conflict resolutions (Hutterer and Peters 2011), aggression and spacing behaviour (Ancillotto and Russo 2016).

Extensive mark-recapture studies and nest box monitoring data within a female-biased population in the riverine *Combretum* revealed extensive same- and opposite-sex home range overlaps of adults throughout the year (Madikiza *et al.* 2011). Male home ranges are twice as large the size of female ranges, particularly before and during the mating season, therefore allowing males access to more than one sexually receptive female (Madikiza *et al.* 2011).

Detailed assessment on the woodland dormouse regarding the species taxonomy, distribution, population, habitat and ecology as well as conservation were described by Madikiza *et al.* (2016) (see Appendix).

## **1.2. Aims, objectives and predictions**

### *1.2.1. Aims*

1. My aim in this study was to investigate the behavioural responses of male woodland dormice (*Graphiurus murinus*) towards communicatory cues of same-sex conspecifics from the same or from different populations.

### *1.2.2. Objectives*

1. To determine the behavioural responses of male woodland dormice to the auditory, olfactory and visual cues of same-sex conspecifics from the same or from different populations.
2. To describe recorded acoustic signals between same-sex conspecifics from the same or from different populations, and to ascertain the behavioural conditions under which each signal is produced.
3. To determine the effects of odour on the behaviour of adult male woodland dormouse to the olfactory cues from the ano-genital areas of conspecific males.

### *1.2.3. Predictions*

1. Male woodland dormice will be behaviourally motivated to interact with previously encountered conspecifics from the same population compared to conspecifics from different populations.
2. Interactions between dormouse males from different populations will be more agonistic than interactions between dormice from the same population.
3. Dormice will show an intrinsic motivation to interact with males from different populations rather than being alone.
4. Vocal signals emitted during aggressive and amicable encounters are expected to have different functions in relation to the non-vocal behaviours exhibited by dormice.
5. Upon encountering a scented cloth, males will display more aggressive behaviours characterised by ritualised aggression and scent marking.

## 2. MATERIAL AND METHODS

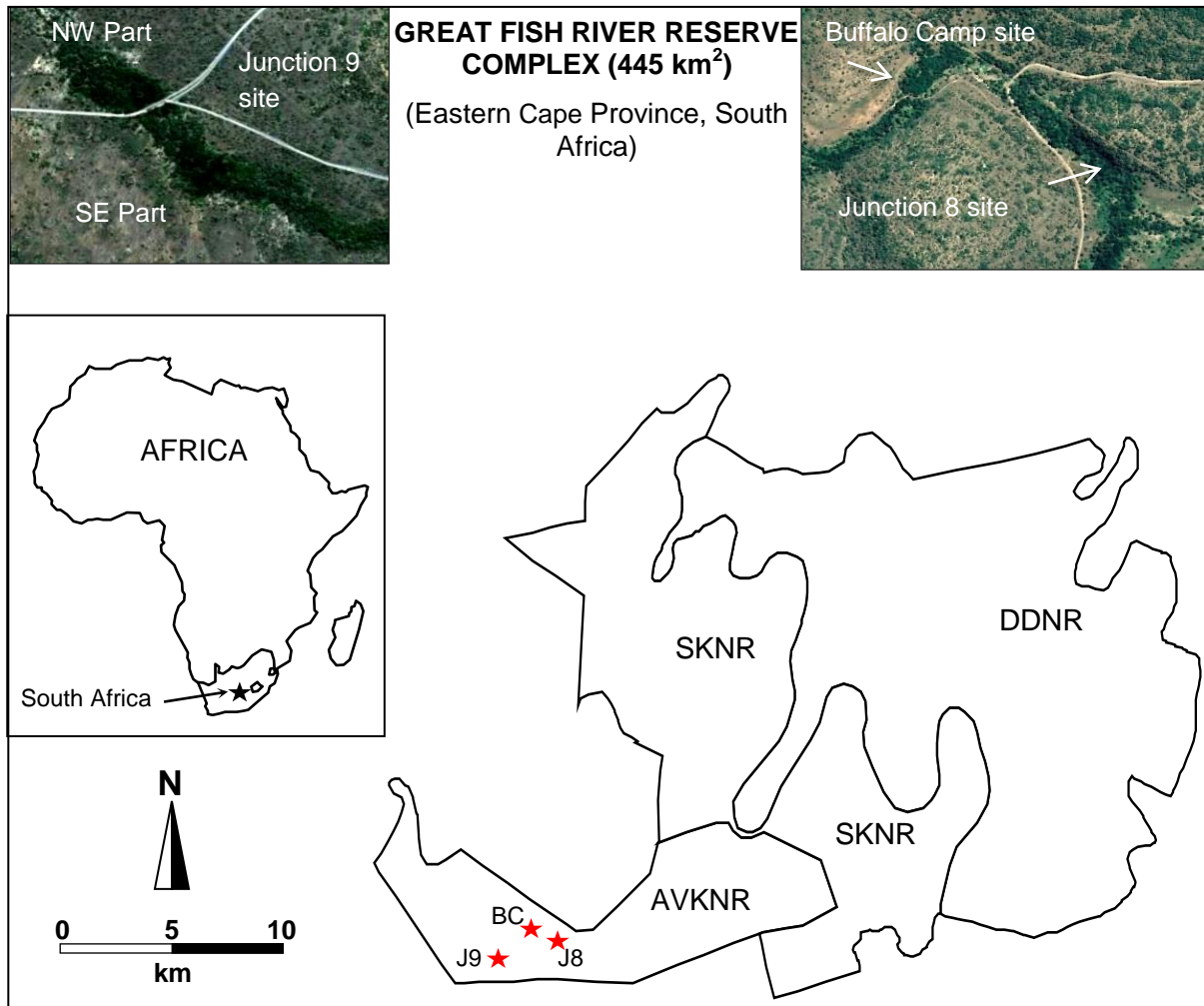
### 2.1. Laboratory studies at the Great Fish River Reserve (GFRR)

#### 2.1.1. Sampling sites

This study was conducted in the Great Fish River Reserve complex (GFRR; 33°04'–33°09'S, 26°37'–26°49'E), situated approximately 40 km northeast of Grahamstown and 50 km southeast of Fort Beaufort, Eastern Cape Province, South Africa. The reserve complex (total combined size 445 km<sup>2</sup>) is composed of three entities: the Andries Vosloo Kudu Nature Reserve, the Sam Knott Nature Reserve and the Double Drift Game Reserve (Figure 2.1).

Sampling took place in the western part of the reserve, namely, the Andries Vosloo Kudu Nature Reserve (AVKNR) (E 26.675430, S 33.126846; altitude: 300 m a.s.l.). My sampling sites were Junction 9 (2.5 ha; breadth × length: 100 × 250 m), Junction 8 (3 ha; b × l: 100 × 300 m) and Buffalo Camp (3.5 ha; b × l: 100 × 350 m). These sites were situated at least 500 m apart from one another to avoid removing individuals from the same population. Based on trapping data, home range sizes of free-ranging woodland dormice reach a maximum of about 0.4 ha (100 × 40 m) for males and 0.2 ha (50 × 40 m) for females (Madikiza *et al.* 2011). It could therefore be safely assumed that individuals trapped in different sampling sites did not have prior encounters.

All sampling sites were typically located in a dry riverine *Combretum* forest fed by an underground water table. Surface water is temporary except after heavy rainfalls. The three stretches of the riverine forest were dominated by stands of thickbush willows *Combretum* which are prone to rotting from the inside resulting in numerous natural cavities used by small arboreal animals including dormice (Madikiza *et al.* 2010, Lamani 2011). Other tree species found within my sampling sites include *Euphorbia bothae*, *Portulacaria afra*, *Schotia afra*, *Grewia* spp., *Euclea undulata*, *Crassula* spp., *Ptaeroxylon obliquum*, and *Phyllanthus verrucosa*.



**Figure 2.1.** Location of the Great Fish River Reserve complex on the map indicated by a black-shaded star. The three sampling locations; Junction 9 (J9), Junction 8 (J8) and Buffalo Camp (BC) are indicated by the red-shaded asterisks. The top left inset shows an aerial view of the riverine *Combretum* forest at the Junction 9 sampling site. Junction 8 and Buffalo Camp sampling sites are indicated by the aerial inset on the upper right-hand side. AVKNR: Andries Vosloo Kudu Nature Reserve, SKNR: Sam Knott Nature Reserve, DDGR: Double Drift Game Reserve.

### 2.1.2. Trapping

Live-trapping of woodland dormice took place in summer between November and December 2017, and was conducted for a period of two weeks. A total of one hundred Sherman folding aluminium live-traps (H. B. Sherman Traps, Tallahassee, Florida, USA; length  $\times$  breadth  $\times$  height: 23  $\times$  8  $\times$  9 cm) were set at each station (J9, J8 and BC). Traps were distributed along an irregular trail on the tree branches and on logs at heights between 1 and 2 m above ground depending on the suitability of the site. Traps were positioned at  $\sim$ 15 m from each other so as to cover as much of the sampling area as possible to maximize trapping success of woodland dormice. Sherman traps were baited with a mixture of rolled oats and sunflower seed oil, and

set in the evening for 4–5 consecutive nights. Traps were checked early in the morning (from 07:00) and late in the afternoon (from 15:00) and were rebaited and reset when necessary. When checking traps, other unintended rodent species found inside the traps were released without further manipulation.

### *2.1.3. Handling and identification of dormice*

In total, the number of woodland dormice trapped from each sampling site during trapping sessions which lasted for 5 consecutive nights were: 12 females, 4 males and 6 juveniles at Junction 9; 6 females, 3 males and 1 juvenile at Junction 8; and 5 females, 2 males and 1 juvenile at Buffalo Camp. Each caught woodland dormouse was flushed directly from the trap into a pre-weighed Ziploc plastic bag and then weighed to the nearest gram with a 60 g or 100 g spring balance (Pesola, Baar, Switzerland). For each dormouse captured, the following factors were recorded: trap location, trap number, sex, age (adult vs. juvenile), mass and reproductive status. Females were differentiated from males based on the presence or absence of nipples, appearance of the genitalia (e.g. open and perforated vagina) (Table 2.1), and by visually measuring the distance (much shorter in females) between the anal and genital apertures. Sexes of juveniles were sometimes allocated retrospectively by palpating the genital apertures. Following Madikiza (2010), the ages of individuals were determined based on body mass (< 20 g for juvenile, < 25 g for sub-adult and > 25 g for adult). In this study, dormice were considered familiar if they were trapped within the same sampling site, while unfamiliar woodland dormice were considered to be individuals trapped from different sampling sites within the GFRR complex. I only considered adult males with visible, scrotal testes and body weight > 25 g to avoid any possible influences of behavioural dominance over juveniles during dyadic interactions. All trapped females and juveniles were excluded from the study and were released immediately after capture at the same trap location. All the above mentioned handling of dormice were approved by the Animal Ethics Screening Committee (AESC) of the University of Witwatersrand (Ethical clearance No. 2017/07/48/B).

**Table 2.1.** Summary of physical characteristics used to differentiate sex and reproductive condition of trapped woodland dormice (*Graphiurus murinus*) (adapted from Madikiza 2010).

<b>Classes</b>	<b>Reproductive condition</b>	<b>Mass</b>
Scrotal male adult	Testes fully developed and descended	>25 g
Non scrotal male adult	Testes not descended and not fully developed	>25 g
Perforate female adult	Vaginal orifice opened	>25 g
Imperforate female adult	Vaginal orifice sealed	>25 g
Sub-adult	Either sex	20–25 g
Juvenile	Either sex	<20 g

#### 2.1.4. Animal maintenance and housing conditions

A total of 9 adult male woodland dormice were individually kept in clear conventional cages (l × b × h: 26 × 20 × 14 cm) fitted with stainless steel wire bar lids to prevent animals from escaping. Dormice were transported by a motor vehicle to the research house located between 2.5 and 4 km from the sampling sites. Dormice were housed in three separate rooms according to the trapping sites to avoid indirect interactions and familiarisation. Animals were kept at the research house for a period of 48 hours so that they habituate to the conditions prior to the commencement of the experiments. During the housing period, dormice in the same room were isolated from one another; therefore visual, olfactory and direct interactions were restricted, but animals could communicate with conspecifics acoustically. Captured dormice were subjected to a natural dark–light cycle and ambient temperatures ~27°C. Shredded paper towels (~10 g) were provided as nesting material. During this time, dormice were provided with apples, boiled egg and water *ad libitum*. All captured animals were kept for a maximum period of 7 days at the research house before being returned back to their exact trapping site to prevent disruption of their natural activities.

## **2.2. Laboratory studies at Milner Park Animal Unit (University of the Witwatersrand)**

### *2.2.1. Animal maintenance and housing conditions*

A total of 9 adult male woodland dormice housed at Milner Park Animal Unit, University of the Witwatersrand, Johannesburg, were used in my experiments. Woodland dormice housed were wild-caught individuals from free-living populations within the Eastern Cape Province, South Africa (Madikiza 2017), and were individually kept in metal cages (l × b × h: 0.5 × 0.5 × 1 m). Woodland dormice were maintained under the following environmental conditions: reversed 12L: 12D light–dark cycle (lights on at 19:00 and off at 07:00), 22–24°C and 30–60% humidity. Wood shavings (~3 cm long) were provided as bedding material. Branches and logs were made available as additional natural materials for environmental enrichment inside the cages. Food (Versele hamster muesli; Belgium) and water were provided *ad libitum*. Approximately 10 g of a combination of mealworm, peanuts, boiled egg, fruits and vegetables were given as occasional supplements each week (Madikiza 2017).

### *2.2.2. Scent collection*

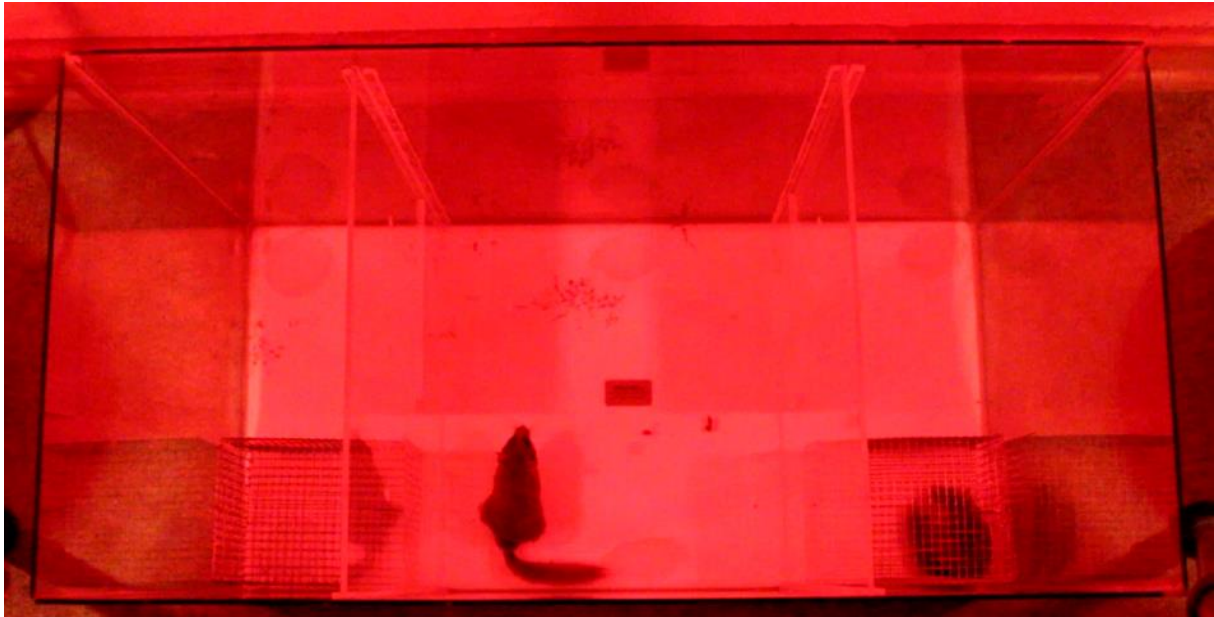
During my experiments, 9 “donor” male dormice were removed from their home cages, each was placed in an individual pre-weighed Ziploc plastic bag and weighed to the nearest gram using a spring balance (Pesola, Baar, Switzerland). In order to access the animal and collect scent, I used gloved hands while restraining the animal gently. Odour samples were collected from donor males by rubbing an unscented cotton cloth against the ano-genital areas. No sedation was required. Dormice were returned to their home cages immediately after collecting scent. The scented cloths were stored for 30 minutes until use in separate labelled Ziploc bags to preserve scent freshness and to avoid contamination. This study was approved by the Animal Ethics Screening Committee of the University of Witwatersrand (Ethical clearance No. 2012/34/2A).

## 2.3. Experimental design

### 2.3.1. Experiment 1: Behavioural responses of male woodland dormice towards same-sex conspecifics from the same and from different populations

Dyadic social interactions between adult male woodland dormice ( $n = 9$ ) at GFRR consisted of individuals from the same population (intra-population) and from different populations (inter-populations). First tests (intra-population interactions), were between same-sex conspecifics trapped within the same sampling site. Second tests (inter-population interactions), were between same-sex conspecifics trapped at the different sampling sites within the reserve. All males used in this experiment were sexually mature with visible scrotal testis and were matched with a similar body weight of the opponent (within 10%) during tests. To increase the sample size, each dormouse was used more than once, but participated as a stimulus or a focal dormouse that was always paired with a different same-sex conspecific from the same or from different populations. Intervals between each behavioural test were at least 3 hours. The order in which test individuals were used in the first and second tests was assigned systematically to avoid repeated testing of the same dyad.

Dyadic interactions were conducted indoors at the research house in a separate room from where other dormice were kept. Tests were carried out in a rectangular glass tank ( $l \times b \times h$ :  $60 \times 30 \times 30$  cm), comprising of three internal chambers ( $l \times b \times h$ :  $20 \times 30 \times 30$  cm) which were partitioned by two clear removable parallel walls made of Plexiglass (Figure 2.2). The two small openings at the bottom of the parallel Plexiglass walls allowed test animals to move freely in and out of the chambers. Two squared wire-mesh cages ( $130 \times 105 \times 95$  mm) were placed simultaneously in each of the two outer chambers with one cage empty and another enclosing a stimulus dormouse. The wire-mesh cages allowed test individuals (focal and stimuli dormice) visual, auditory and olfactory communication, but restricted direct physical interactions. Prior to the tests, each dormouse was given 24 hours to acclimatize alone to the experimental three-chambered apparatus to minimize possible effects of testing them in an unfamiliar environment and at the start of each experiment, the barriers were removed after an acclimatization period of 5 minutes and the focal dormouse moved freely across the chambers. During the habituation process, animals were provided with food (apples and boiled egg), water and shredded nesting materials *ad libitum*. Prior to taping, food, water and nesting materials were removed, and the glass tanks were wiped down using soapy water and cloth and air dried completely to reduce carry-over odour effects of test individuals.



**Figure 2.2.** An aerial view of the experimental set-up with three internal chambers separated by two removable parallel walls made of Plexiglass. The focal woodland dormouse (*Graphiurus murinus*) in the middle chamber could move freely between the chambers through two small passages at the bottom of the walls. A stimulus same-sex dormouse enclosed in a squared wire-mesh cage ( $130 \times 105 \times 95$  mm) in the first tests (intra-population interactions) or second tests (inter-population interactions), was placed in a selected (left or right) chamber. An identical empty wire-mesh cage was simultaneously placed on the opposite side of the chamber.

At the beginning of each experiment, the test dormouse (focal dormouse) was restricted to the central chamber by placing removable ceramic tile barriers on the entries of the two outer chambers. A stimulus same-sex dormouse enclosed in a squared wire-mesh cage ( $130 \times 105 \times 95$  mm), was placed in a selected (left or right) chamber (Figure 2.2). An identical empty wire-mesh cage was simultaneously placed on the opposite side of the chamber. All experiments at GFRR were conducted during the peak activity period of dormice i.e. evening between 20:00 and 22:00 (see Lombard 2013) for 3 successive nights.

Since dormice are nocturnal rodents, behavioural tests were recorded under the red light (light intensity = 71 lux). Behavioural interactions between focal and stimulus dormouse from the same population (first tests), and from different populations (second tests) were video-taped for 20 minutes with a camcorder (Canon, HF-R806) mounted on a tripod stand in front of the cage above floor level with no observer present. At the completion of each test, the chamber floor and walls were cleaned with water and disinfectant soap, air dried to reduce carry-over odour effects of previous tests subjects.

I observed and recorded occurrence, duration and the type of behaviours exhibited by focal males during interactions with stimulus dormouse from the same or from different populations (Table 2.2). I recorded also the number of entries into, and the time spent (in seconds) by the focal males in each chamber. Scoring of different behaviours was conducted for 15 minutes, starting after the acclimatization period of 5 minutes. I scored different behaviours from the video-recordings after taping was concluded. All the observed behavioural components in Table 2.2 were assigned into the four main behavioural categories based on previous studies on mice (Perrin *et al.* 2001, Vekhnik 2018). All behavioural components were scored as either point (i.e. occurrence) or event (i.e. occurrence and duration).

**Table 2.2.** Behavioural categories and their related behavioural components scored during interactions between same-sex focal and stimulus woodland dormouse ( $n = 9$ ) from the same or from different populations.

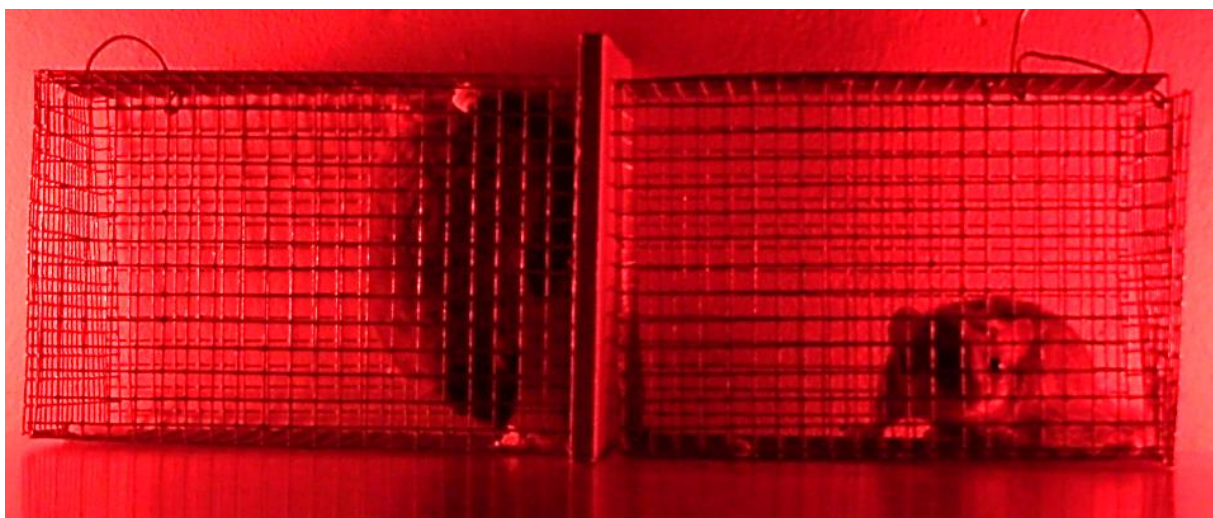
<b>Behavioural categories</b>	<b>Behavioural components</b>
Aggression	Tail wagging; biting wire of stimulus dormouse's cage; scent marking.
Vocalization	Vocalizations ranging from loud sharp shrieks to soft twitter calls.
Attraction	Naso-nasal sniffing; sitting next to stimulus dormouse; grooming next to stimulus dormouse's cage.
Exploration/avoidance	Exploring the arena; avoiding interactions with stimulus dormouse by sitting in an empty cage.

### 2.3.2. *Experiment 2: Vocal behaviour of male woodland dormice towards same-sex conspecifics from the same and from different populations*

Dormice ( $n = 9$ ) used in the vocal behaviour tests were the same individuals which participated in Experiment 1 as focal and stimulus animals. As in the previous experiment, first tests (intra-population interactions) were between same-sex conspecifics trapped within the same sampling site. Second tests (inter-population interactions) were between same-sex woodland dormice trapped at the different sampling sites within the reserve. Dyadic interactions in the first and second tests took place after a resting period for 24 hours from Experiment 1 inside the squared wire-mesh boxes ( $130 \times 105 \times 95$  mm) to avoid injury or

heightened overt aggressions during interactions (K. Madikiza pers. comm.). In order to increase the sample size, each dormouse was used more than once and was always paired with a different dyadic partner from the same or from different populations. All animals participated in both the first and the second tests with at least a 3-hour interval between each test. The order in which test individuals were used in the first and second tests was assigned systematically to avoid repeated testing of the same dyad. Behavioural interactions were conducted during the peak activity period of dormice i.e. evening between 20:00 and 22:00 (see Lombard 2013) for the duration of one night.

Prior to the experiments, dormice were placed individually inside the wire-mesh cages ( $130 \times 105 \times 95$  mm) and a removable tile barrier was placed between the two squared cages for the duration of one minute, to avoid interactions (Figure 2.3). Tests began immediately after the barrier was removed and dyadic interactions in the first and second tests were taped for 5 minutes thereafter. Behavioural responses of dyads in the first and second tests were recorded under a red light (light intensity = 71 lux) with a camcorder (Canon, HF-R806) mounted on a tripod stand in front of the cage above floor level with no observer present. Between each complete test, the wire-mesh cages were cleaned with water and disinfectant soap, air dried to reduce carry-over odour effects of the previous test subjects. After the experiments, all dormice were released back at the same recorded location during their peak activity times (i.e. evening; 20:00) (Lombard 2013).



**Figure 2.3.** A picture of the woodland dormice during intra- or inter-population interactions between same-sex conspecifics which took place inside the squared wire-mesh boxes ( $130 \times 105 \times 95$  mm). A removable tile barrier was placed between the two squared cages for the duration of one minute, to avoid interactions prior to the tests.

I observed and recorded occurrence, duration, type of non-vocal behaviours together with the different vocal signals displayed during interactions between same-sex dormice from the same or from different populations (Table 2.3). Scoring of non-vocal behaviours (Table 2.3) and their associated vocalizations (Table 2.4) took place immediately after taping and thereafter conducted for 5 minutes. I manually recorded all the four different audible vocalizations from the video-tapes saved on a personal computer using head-phones. All the behavioural components assigned into the four behavioural categories were scored as either point (i.e. occurrence) or event (i.e. occurrence and duration).

**Table 2.3.** Behavioural categories and their related behavioural components scored during dyadic interactions between same-sex woodland dormice ( $n = 9$ ) from the same or from different populations.

<b>Behavioural categories</b>	<b>Behavioural components</b>
Aggression	Tail wagging; biting wire; scent marking; open mouth.
Vocalization	Twitter; chirp; rapid down-sweep; shriek/kecker.
Attraction	Naso-nasal sniffing; sitting next to each other; grooming next to each other.
Exploration/avoidance	Exploring cage; sitting away or avoiding interactions by changing direction when approaching dyad partner.

**Table 2.4.** Classification and description of the vocal repertoire of woodland dormice based on physical structural characteristics (modified from Hutterer and Peter 2001, and Ancillotto and Russo 2016).

<b>Vocalization type</b>	<b>Description</b>
Shriek/kecker	Explosive sounds with varying pitch, noise and duration.
Twitter	Very short tonal twittering sounds occurring in regular rapid series.
Chirp	Faint, high-pitched, short tonal sounds varying in frequency and rapid series.
Rapid down-sweep	Characterised by short and very faint audible sounds.

### 2.3.3. *Experiment 3: Behavioural responses of male woodland dormice to the olfactory cues of same-sex conspecifics from different populations*

Behavioural responses of adult male dormice to the scent of same-sex conspecifics took place at Milner Park Animal Unit, University of Witwatersrand, Johannesburg. The experiments consisted of two tests: scented (presence of cloth rubbed with scent from ano-genital areas of same-sex conspecifics) and unscented (absence of both cloth and scent). First tests (scented experiments), were between a woodland dormouse male and a scented cloth placed on a wooden block that was positioned at one corner of the experimental neutral glass chamber ( $l \times b \times h$ :  $46.5 \times 31 \times 31$  cm). In the second tests (unscented experiments), dormice were provided only with an unscented wooden block placed inside the chamber also without the presence of a cloth and conspecific scent. Both scented and unscented experiments involved the use of a single test dormouse ( $n = 9$ ). All animals participated first in the scented experiments, followed by unscented experiments with at least a 3-day interval between each test. All scent donors were unrelated and unfamiliar to the test males. The order in which test individuals were used in scented tests was assigned systematically to avoid repeated testing with the same scent. Prior to the tests, dormice were singly habituated overnight in the experimental neutral glass chamber with no cloth, wooden block and conspecific scent present. During the habituation process, individuals were provided with food (Versele hamster muesli; Belgium), water and shredded nesting materials *ad libitum*. However, food, water and nesting materials were removed during the actual experiments and the glass tanks were wiped down using soapy water and cloth before the experiment started.

Before experiments began, a scented cloth was removed using gloved hand from the Ziploc plastic bag to prevent transference of human scents and was placed onto a wooden block positioned at one corner of the experimental neutral glass chamber ( $l \times b \times h$ :  $46.5 \times 31 \times 31$  cm). During tests, a test dormouse was released into the neutral glass chamber containing scented cloth placed on a wooden block (first tests) or containing a wooden block without the presence of a cloth and scent (second tests) positioned at one corner of the chamber (Figure 2.4). Tests were conducted under a red light (light intensity = 71 lux) during the dark phase of the reversed light cycle when dormice were most active.



**Figure 2.4.** A picture of the experimental set-up showing a test dormouse in a neutral glass chamber ( $l \times b \times h$ :  $46.5 \times 31 \times 31$  cm) with scented cloth placed on a wooden block positioned at one corner of the chamber during scented experiment (first tests, left) or containing a wooden block without the presence of a cloth and conspecific scent during unscented experiment (second tests, right).

Behavioural responses of the test dormice in scented and unscented tests were video-taped for 20 minutes with a camcorder (Canon, HF-R806) mounted on a tripod stand in front of the cage above floor level. No observer was present at the time of recording. In order to reduce carry-over odours, the chamber floor and walls were cleaned with water and disinfectant soap between each complete test. Cages were then left to air dry completely before introducing test dormice. After experiments were completed, dormice were returned to their home cages at Milner Park Animal Unit, University of Witwatersrand, Johannesburg.

I observed and recorded occurrence, duration and the type of behaviours displayed by the test dormice between scented and unscented tests (Table 2.5). All the observed behavioural components in Table 2.5 were classified into the four main behavioural categories based on previous studies on mice (Perrin *et al.* 2001, Vekhnik 2018). Scoring of different behaviours was conducted for 15 minutes, starting after the acclimatization period of 5 minutes. I scored different behaviours from the video-recordings once taping was concluded. All the behavioural components were scored as either point (i.e. occurrence) or event (i.e. occurrence and duration).

**Table 2.5.** Behavioural categories and their related behavioural components scored between scented and unscented tests with an individual woodland dormouse.

<b>Behavioural categories</b>	<b>Behavioural components</b>
Ritualised aggression	Scent marking through rubbing cheeks and hind legs.
Overt aggression	Biting scented cloth.
Investigation	Alertness in the presence of scented cloth; approaching scented cloth or wooden block; sniffing scented cloth or wooden block.
Exploration/avoidance	Locomotion; individual climbs walls of the arena; grooming.

## 2.4. Data analysis

All statistical analyses were conducted using IBM SPSS Statistics 25.0 (SPSS Inc.). In all statistical analyses, differences were considered significant at  $p < 0.05$ . Unless stated otherwise, data are reported as mean  $\pm$  standard error. Since my data were not normally distributed (Kolmogorov-Smirnov test and/or Shapiro Wilk's test,  $p < 0.05$ ), non-parametric Wilcoxon matched-pairs signed-ranks tests were assigned in all cases to compare differences between intra-population stimulus dormouse chamber vs. empty cage chamber, and again between inter-populations stimulus dormouse chamber vs. empty cage chamber in the number of entries into and time spent by focal dormice in the test chambers during Experiment 1. These same tests were used to compare the duration of behavioural categories exhibited by test dormice with stimulus dormouse; duration of vocal and non-vocal behavioural categories (Experiment 2); as well as duration of behavioural categories in scented and unscented tests (Experiment 3). Due to small sample size, Mann-Whitney tests were used to assess variation in the duration of each type of vocalization in Experiment 2.

Intrasexual comparisons in the pooled data (total occurrences) of different behavioural categories recorded in Experiments 1, 2 and 3 were analysed with chi-square tests of independence. Goodness-of-fit tests were used to test for intrasexual differences in the total occurrences of behavioural components exhibited by focal males with stimulus dormouse (Experiment 1), and by test dormice in Experiment 2 and Experiment 3, respectively. Similarly, a goodness-of-fit test was performed to assess differences in the total occurrences of vocal repertoires emitted under different behavioural situations by dormice during the 5 min dyadic encounters in Experiment 2.

Chi-square tests for pooled occurrences ( $df = 1$ ) were performed to compare differences between focal males from the same population vs. empty cage, and again between

focal males from different populations vs. empty cage (Experiment 1), assuming that focal males would choose the chamber with stimulus dormouse or empty cage equally i.e. 50% of observations in each chamber. Absolute occurrences were interpreted as percentages.

### 3. RESULTS

#### 3.1. Behavioural responses of male woodland dormice towards same-sex conspecifics from the same and from different populations (Experiment 1)

##### 3.1.1. Behavioural response comparisons

Intra- and inter-population focal males did not differ in the number of entries into and the time spent in the chamber whether occupied by stimulus dormouse from the same population or from different populations in comparison to the chamber with an empty cage (Table 3.1).

**Table 3.1.** The number of entries into, and the duration (in seconds) spent by focal woodland dormouse males ( $n = 9$ ) in the chamber occupied by a same-sex stimulus dormouse from the same or from different populations vs. empty chamber during 20-min tests. Values for the number of entries into, and the duration (s) are reported as medians. Ranges are presented in parentheses. Wilcoxon's test results to compare both chambers types are provided at the bottom of the table.

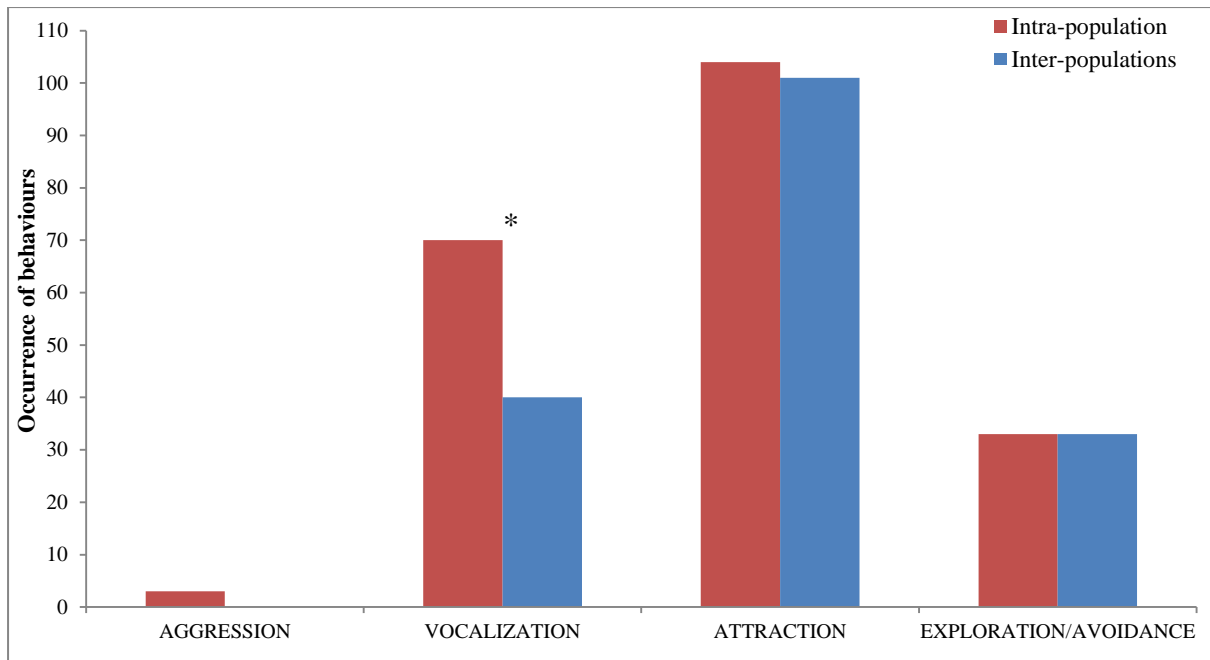
Chamber	Number of entries		Duration in the chamber	
	Intra-population	Inter-populations	Intra-population	Inter-populations
Chamber with stimulus dormouse	0.0 (0–6)	0.0 (0–3)	477 (0–900)	34.0 (0–900)
Chamber with empty cage	0.0 (0–4)	0.0 (0–3)	119.5 (0–900)	103.0 (0–900)
Wilcoxon's test → $W$	3	81	57	107
→ $p$	0.18	0.83	0.56	0.61

Woodland dormice focal males from the same or from different populations similarly approached, sniffed and made contact equally often in the presence of a stimulus dormouse compared to an empty cage (Table 3.2). Dormice males from the same or from different populations groomed themselves significantly more often when in the presence of a stimulus dormouse than in an empty cage alone. This difference in grooming behaviour was slightly pronounced in intra-population than in inter-population interactions. Intra-population focal males preferred sitting by the stimulus dormouse cage than sitting alone in an empty cage.

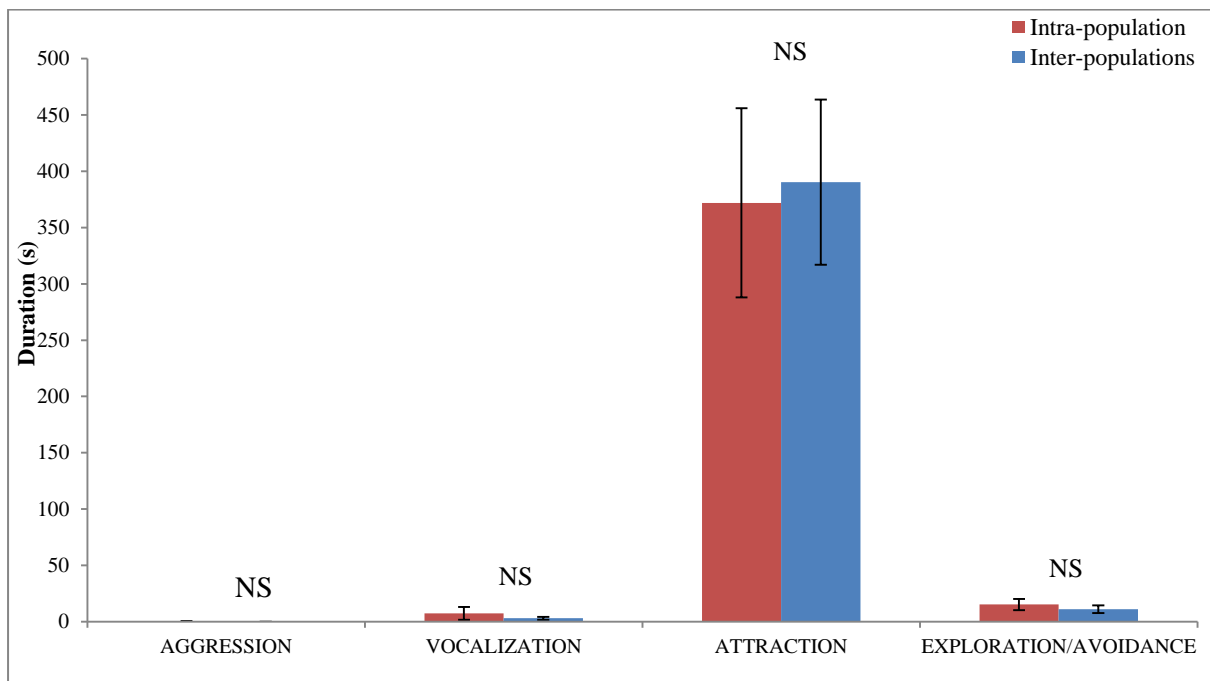
**Table 3.2.** Comparison of specific behavioural components between the focal male and a same-sex stimulus dormouse from the same or from different populations vs. empty cage during a 20-min test. Chi-square goodness-of-fit tests ( $df = 1$ ) for pooled data were run, assuming that focal males would equally choose between both cages (50% of observations). Absolute frequencies of occurrence data are provided in parentheses. Bold values indicate significant differences. NS = Non-significant with  $p > 0.05$ .

<b>Behavioural comparisons</b>	<b>Intra-population</b> ( $n = 9$ )	<b>Inter-populations</b> ( $n = 9$ )
Sitting next to stimulus dormouse's cage	<b>18% (38)</b>	22% (40)
Sitting next to empty cage	0% (0)	12% (21)
	$p < 0.05$	$p = 0.166$
	$\chi^2 = 9.36$	$\chi^2 = 1.92$
Sniffing stimulus dormouse's cage	2% (4)	3% (8)
Sniffing empty cage	1% (3)	1% (3)
	$p = 0.070$	$p = 0.981$
	$\chi^2 = 3.28$	$\chi^2 = 0$
Approaching stimulus dormouse	3 % (8)	3% (7)
Approaching empty cage	1% (2)	2% (5)
	$p = 0.819$	$p = 0.262$
	$\chi^2 = 0.05$	$\chi^2 = 1.26$
Contact with stimulus dormouse's cage	4% (10)	7% (16)
Contact with empty cage	1% (3)	2% (4)
	$p = 0.573$	$p = 0.429$
	$\chi^2 = 0.32$	$\chi^2 = 0.63$
Grooming next to stimulus dormouse's cage	<b>37% (62)</b>	<b>36% (59)</b>
Grooming next to empty cage	15% (25)	11% (18)
	$p < 0.001$	$p < 0.001$
	$\chi^2 = 42.13$	$\chi^2 = 72.70$

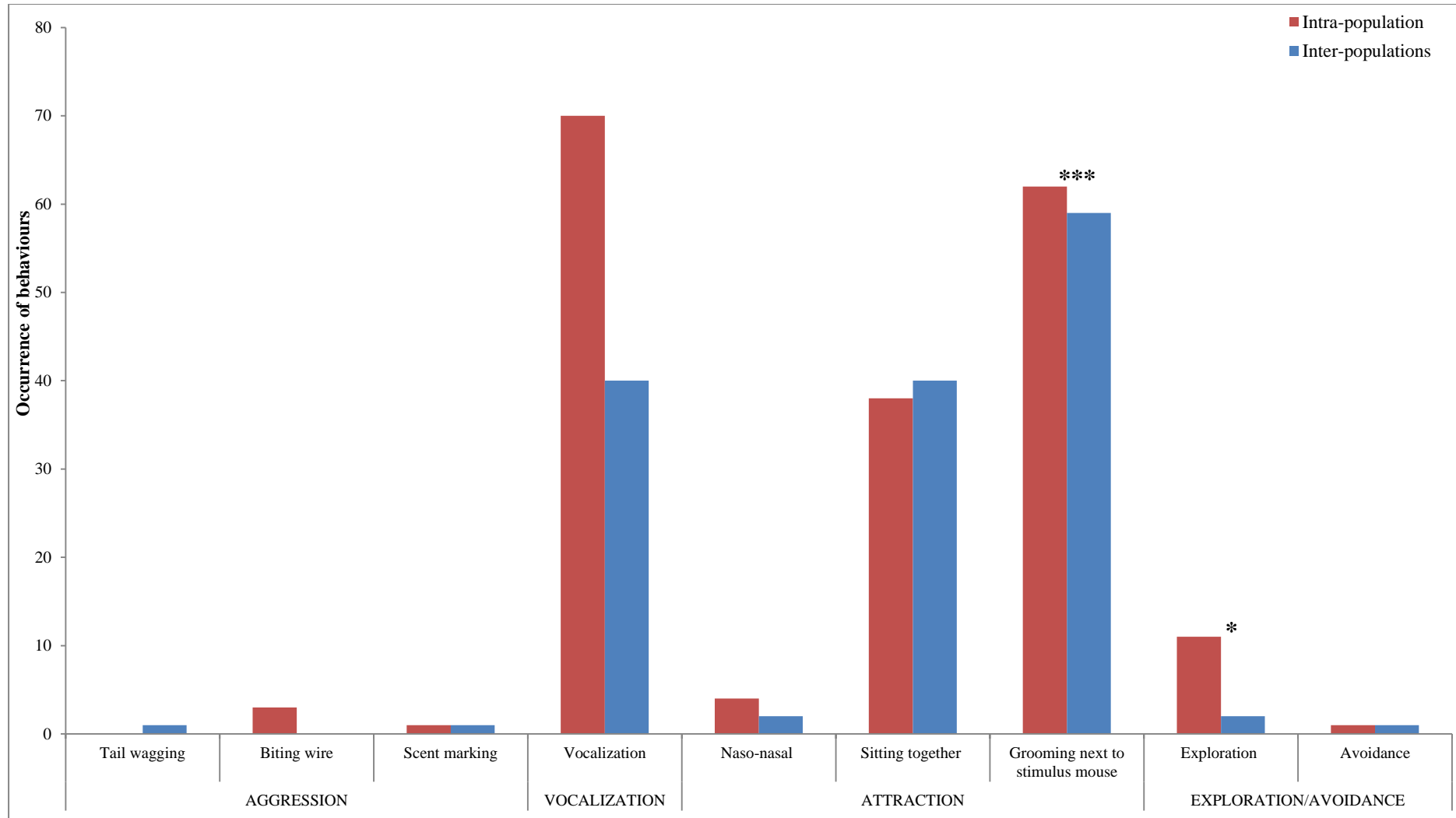
Focal males from the same population vocalized significantly more often than focal males from different populations. There were no differences observed between dormice from the same population or from different populations in the way they performed aggressions, attraction or exploration/avoidance behaviours (Figure 3.1). As shown in Figure 3.2, there were no differences found in the duration of all behavioural categories between focal dormice from the same population and focal dormice from different populations (Wilcoxon matched-pairs signed-rank tests:  $p > 0.18$  in all four categories; Figure 3.2). In Figure 3.3, focal woodland dormice significantly exhibited grooming behaviour and explored cage significantly more often in the presence of a stimulus dormouse from the same population than in the presence of a stimulus dormouse from different populations.



**Figure 3.1.** Occurrence of four broad behavioural categories recorded during a 20-min test between a focal male woodland dormouse ( $n = 9$ ) and a same-sex stimulus dormouse from the same or from different populations. Behavioural categories between intra- and inter-population males with significant differences (chi-square tests of independence) are indicated with \* ( $p < 0.05$ ).



**Figure 3.2.** Duration (mean  $\pm$  SE) of four broad behavioural categories recorded during a 20-min test between a focal male woodland dormouse ( $n = 9$ ) and a same-sex stimulus dormouse from the same or from different populations. No significant differences (NS) were found across all behavioural categories between intra- and inter-population males (Wilcoxon matched-pairs signed-rank tests:  $p > 0.05$ ).



**Figure 3.3.** Occurrence of behavioural components exhibited during interactions between focal male woodland dormouse ( $n = 9$ ) and a same-sex stimulus dormouse from the same or from different populations in a 20-min test. Behavioural components between intra- and inter-population males that differed significantly (chi-square goodness-of-fit tests) are indicated with \* ( $p < 0.05$ ) or \*\*\* ( $p < 0.001$ ).

## 3.2. Vocal behaviour of male woodland dormice towards same-sex conspecifics from the same and from different populations (Experiment 2)

### 3.2.1. Association between different vocalizations and non-vocal behaviours

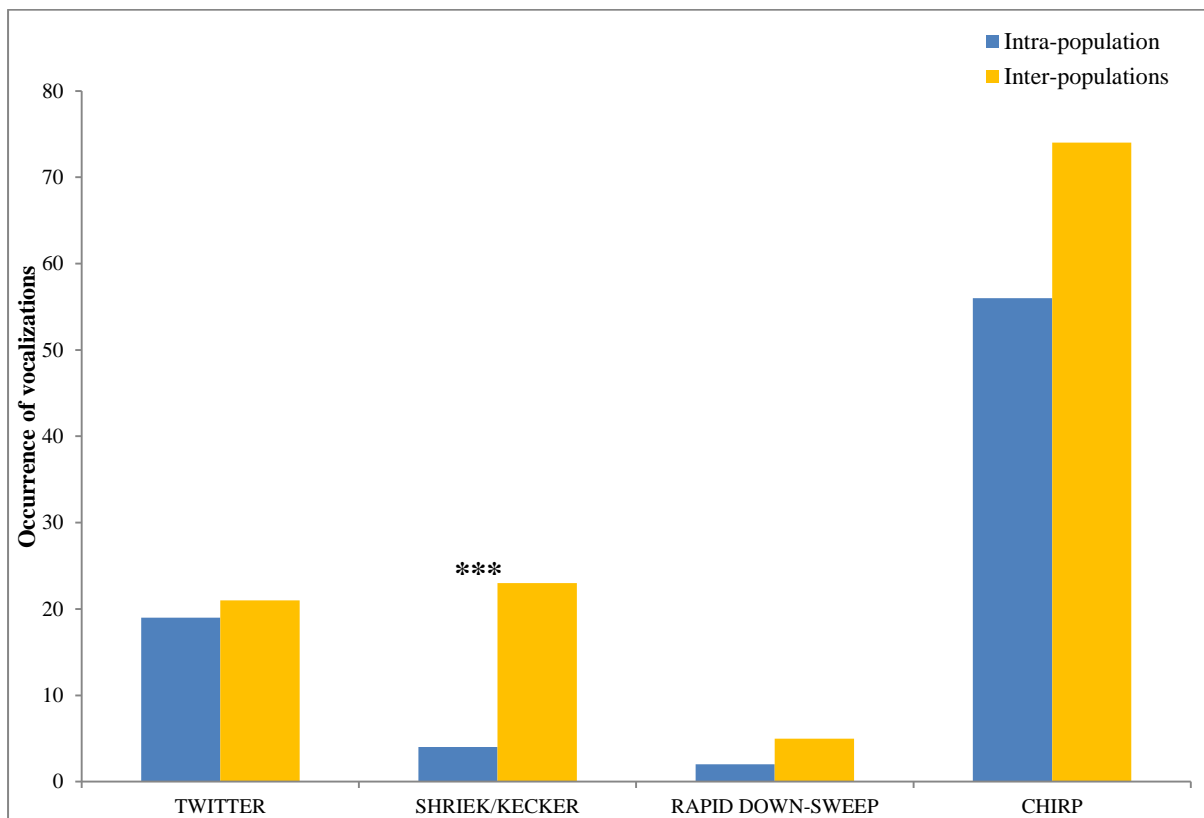
In total, 204 vocalizations (intra-population,  $n = 100$ ; inter-populations,  $n = 104$ ) were recorded and allocated into four different vocal types (Table 3.3). The four vocalization types recorded in this study were established based on their physical structural characteristics similar to those reported by Hutterer and Peter (2001) and were associated with a particular non-vocal behaviour (Table 3.3).

Males from different populations emitted soft twitter vocalizations that were often accompanied by affiliative signals displayed by dormice when sitting together less than 5 cm to each other in comparison to males from the same population (Table 3.3). Dormice in this study did not vocalize while grooming themselves next to another. Chirp vocalizations were regularly emitted with the displaying of moving ears and an open mouth directed towards the dyad partner. The chirp calls were emitted across different dyadic encounters and therefore these calls could not be associated with a specific behavioural context. Rapid down-sweep vocalizations were associated with avoidance behaviours and were emitted as soon as the animals were separated by a distance of more than 5 cm from one another (Table 3.3).

**Table 3.3.** Number ( $n$ ) and vocalization types of male woodland dormice ( $n = 9$ ) and their related non-vocal behaviours exhibited during dyadic interactions between same-sex conspecifics from the same or from different populations.

Vocalization type	Associated non-vocal behaviour	Description of non-vocal behaviour	Behavioural category	Population type	$n$
Shriek/kecker	Biting wire	Dormouse aggressively uses teeth to bite wire of cage	Aggression	Intra-population	4
	Open mouth	Dormouse continuously open mouth towards dyad partner		Inter-populations	23
Twitter	Sitting next to each other	Dormouse sit <5 cm from another	Attraction	Intra-population	19
				Inter-populations	21
Chirp	open mouth and ear movement	Individuals continuously open mouth towards each other, moving ears	Varied behavioural contexts	Intra-population	75
				Inter-populations	55
Rapid down-sweep	Avoidance	Sitting away (>5 cm) not interacting with dyad partner	Exploration/avoidance	Intra-population	2
				Inter-populations	5

On the other hand, aggressive vocalizations between dormice from different populations were more pronounced (Figure 3.4), and were emitted particularly before performing aggressive behaviours such as biting wire of cage, and mouth opening. Immediately after aggressive encounters, dormice exhibited more of avoidance behaviours ultimately orienting themselves >5 cm apart from each other (Table 3.3). In another situation, dormice emitted aggressive vocalizations in an attempt to approach the dyad partner directly. Twitter, chirp and rapid down-sweep vocalizations did not differ significantly in the total number of times dormice were observed vocalizing with intra- and inter-population males (Figure 3.4). Dormice did not differ in the time spent vocalizing in any of the four vocalization types between intra- and inter-populations encounters (Mann-Whitney tests:  $p > 0.10$  in all four vocal types; Figure 3.4).



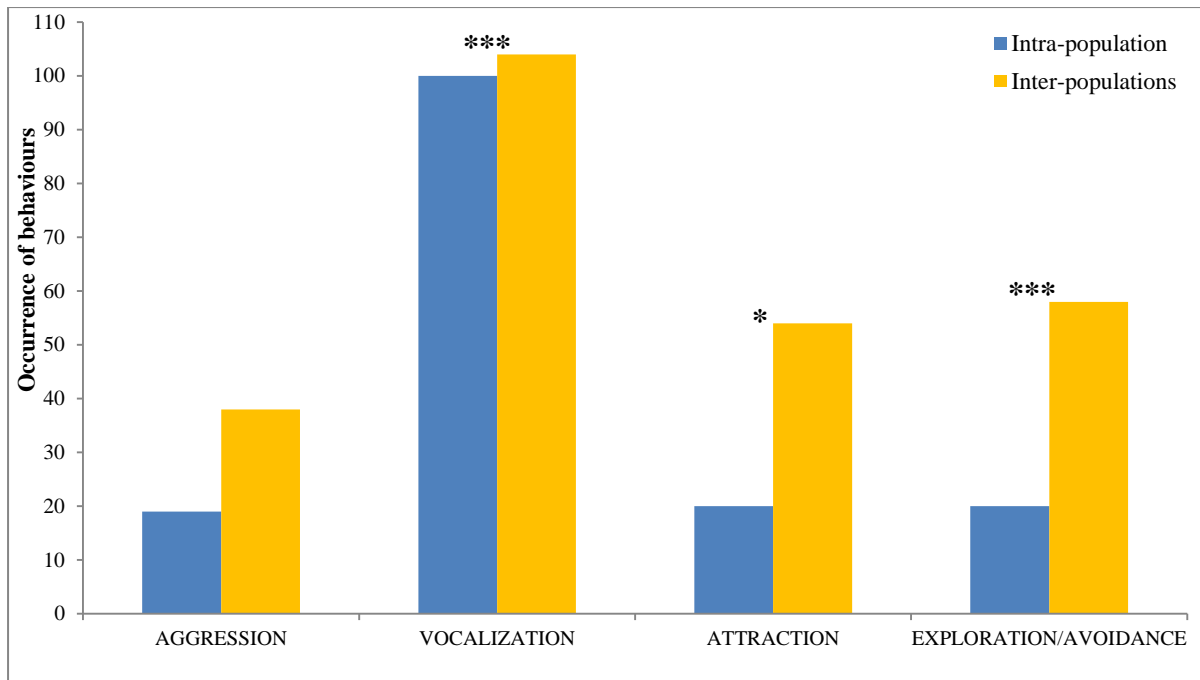
**Figure 3.4.** Occurrence of different vocalizations of woodland dormouse ( $n = 9$ ) emitted under different behavioural contexts during dyadic encounters between same-sex conspecifics from intra- or inter-populations in a 20-min test. Vocalization types between intra- and inter-population males that differed significantly (chi-square goodness-of-fit tests) are indicated with \*\*\* ( $p < 0.001$ ).

### 3.2.2. Behavioural response comparisons

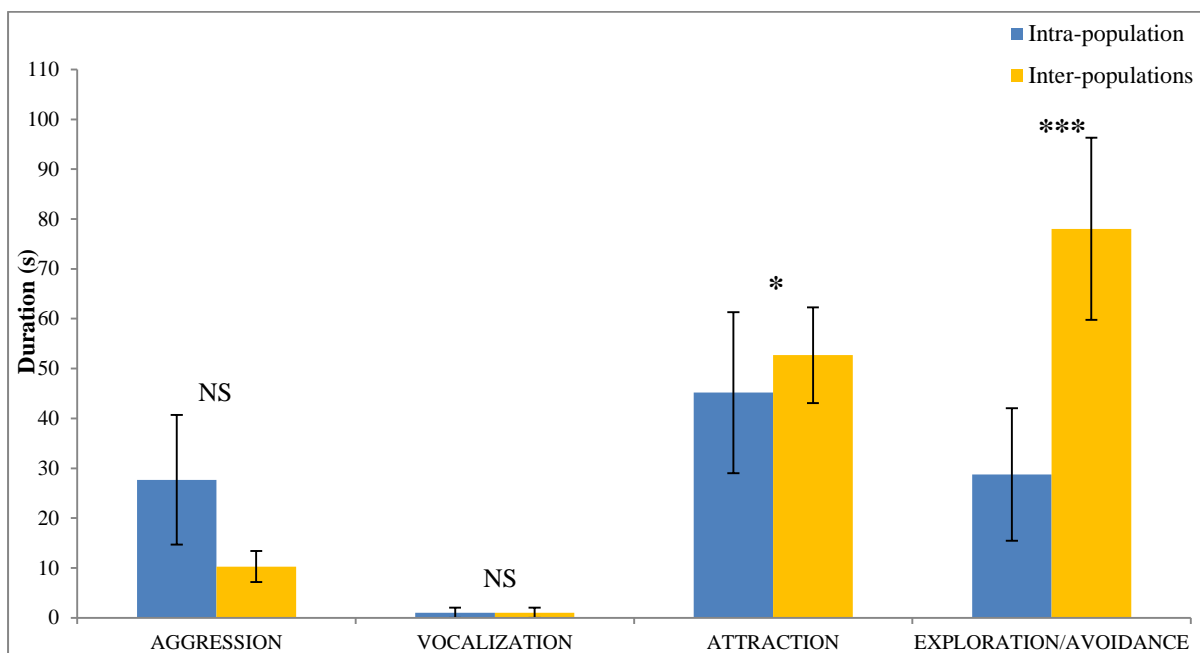
Woodland dormice males from the same and from different populations showed both differences and similarities in the behaviours displayed towards same-sex conspecifics. Male woodland dormice from different populations vocalized, performed more of attraction behaviours and exhibited significantly more exploration/avoidance behaviours compared to males from the same population. Dormice males from the same and from different populations did not differ in the way they performed aggressive behaviours towards same-sex conspecifics (Figure 3.5).

The time that the woodland dormice spent performing attraction behaviours to males from different populations (mean  $\pm$  SE: 53  $\pm$  10 s; range 0–141 s; Figure 3.6) was significantly longer than the time spent with males from the same population (mean  $\pm$  SE: 45  $\pm$  16 s; range 0–137 s; Wilcoxon matched-pairs signed-ranks tests:  $W = -2.26$ ,  $p = 0.02$ ). Similarly, different populations males (mean  $\pm$  SE: 78  $\pm$  15 s; range 0–240 s) spent significantly more time displaying exploration/avoidance behaviours compared to the same population males (mean  $\pm$  SE: 29  $\pm$  10 s; range 0–122 s; Wilcoxon matched-pairs signed-ranks tests:  $W = -2.26$ ,  $p = 0.02$ ). No differences were found in the time spent between intra- and inter- population males performing aggressive behaviour or vocalization (Figure 3.6).

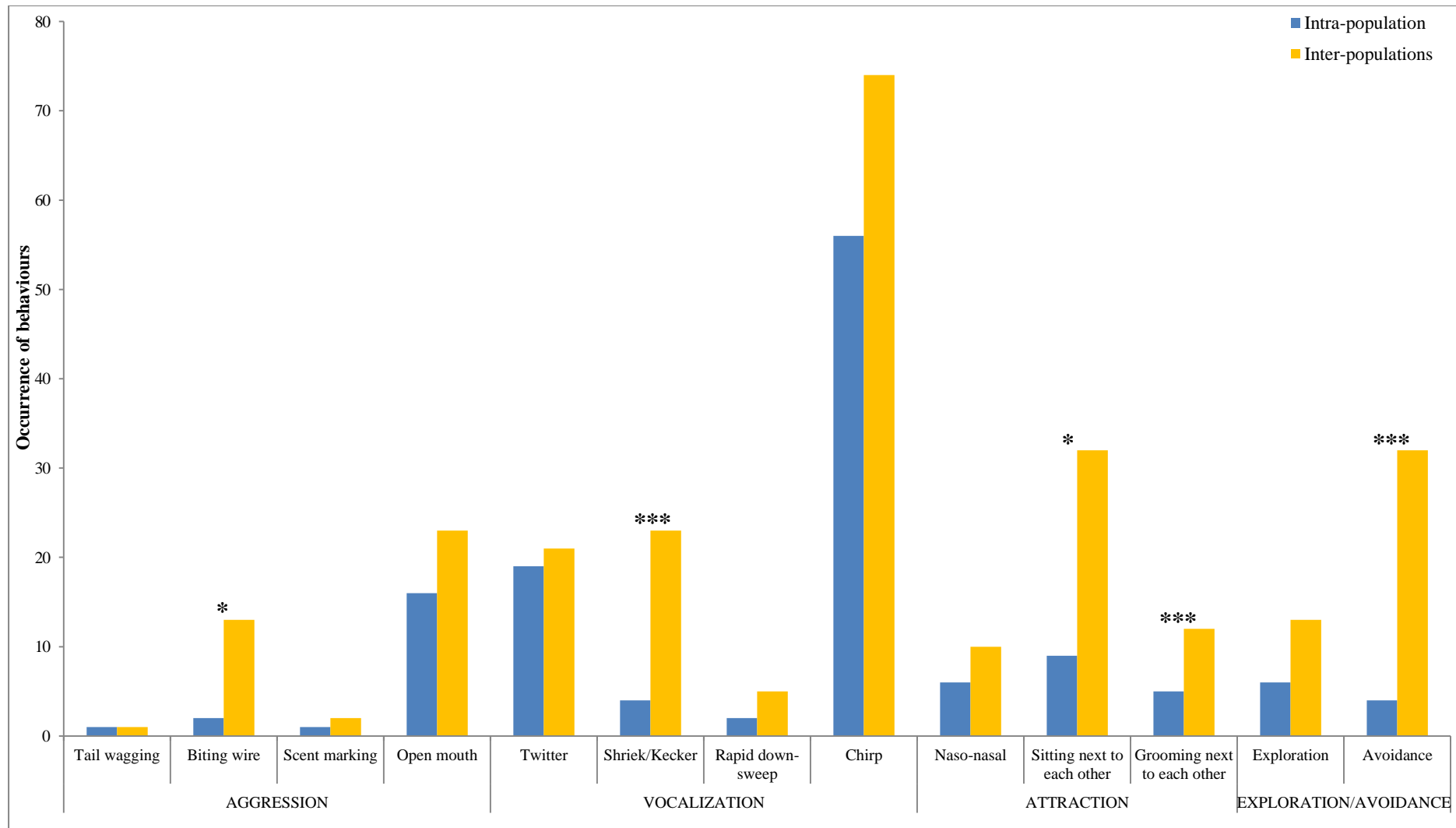
Inter-population males were often engaged in biting the wire of the cage aggressively, and significantly exhibited aggressive shriek/kecker vocalizations in comparison to intra-population males (Figure 3.7). Similarly, males from different populations significantly preferred grooming themselves more often while sitting next to each other, but also displayed more avoidance behaviours than intra-population males (Figure 3.7).



**Figure 3.5.** Occurrence of four broad behavioural categories recorded during dyadic encounters between same-sex woodland dormice ( $n = 9$ ) from the same or from different populations in a 5-min test. Behavioural categories between intra- and inter-population males that differed significantly (chi-square tests of independence) are indicated with \* ( $p < 0.05$ ) or \*\*\* ( $p < 0.001$ ).



**Figure 3.6.** Duration (mean  $\pm$  SE) of four behavioural categories recorded during dyadic encounters between same-sex male woodland dormice ( $n = 9$ ) from the same or from different populations in a 5-min test. Behavioural categories between intra- and inter-population males that differed significantly (Wilcoxon matched-pairs signed-rank tests) are indicated with \* ( $p < 0.05$ ) or \*\*\* ( $p < 0.001$ ).



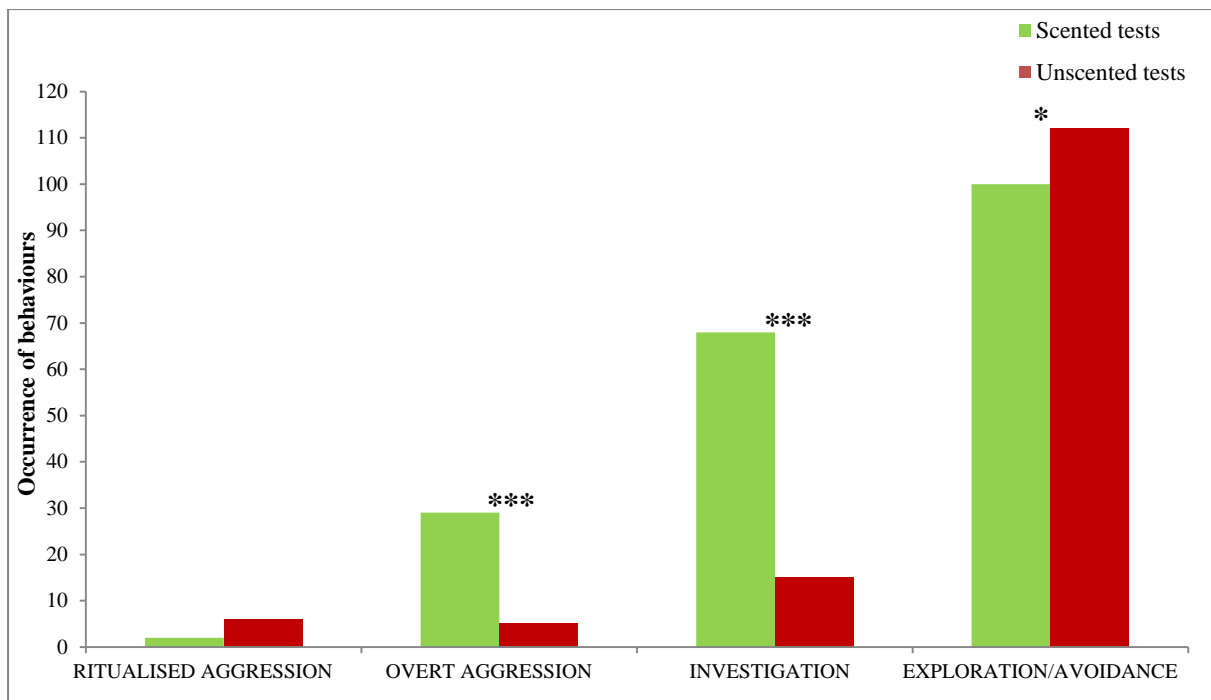
**Figure 3.7.** Occurrence of behavioural components exhibited by male woodland dormice ( $n = 9$ ) during dyadic encounters between same-sex conspecifics from the same or from different populations in a 5-min test. Behavioural components between intra- and inter-population males that differed significantly (chi-square goodness-of-fit tests) are indicated with \* ( $p < 0.05$ ) or \*\*\* ( $p < 0.001$ ).

### **3.3. Behavioural responses of male woodland dormice to the olfactory cues of same-sex conspecifics from different populations (Experiment 3)**

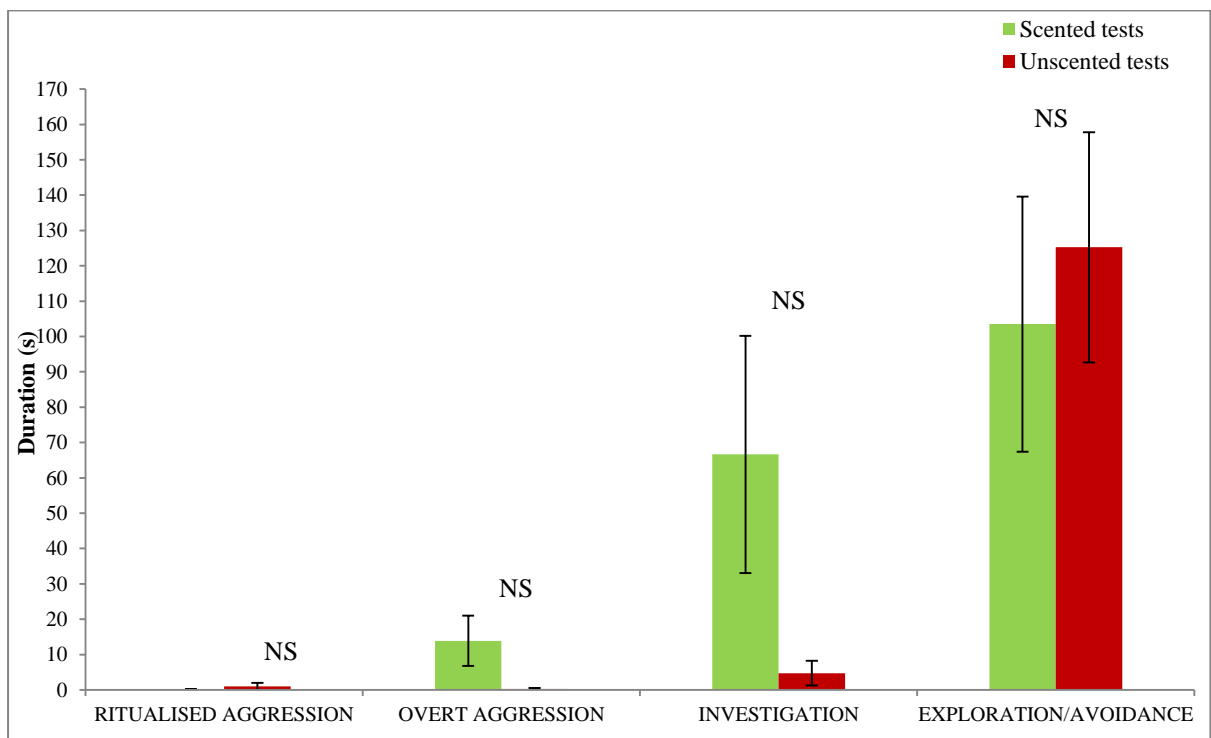
#### *3.3.1. Behavioural response comparisons*

Test dormice observed during non-social encounters with scented cloth or in the absence of scented cloth differed significantly in their behavioural responses (Chi-square of independence:  $\chi^2 = 50.41$ ,  $df = 5$ ,  $p < 0.001$ ; Figure 3.8). Specifically, males in scented tests were more aggressive, displaying signals of overt aggression followed by investigative behaviours towards scented cloth than did males in unscented tests. Male woodland dormice in unscented tests displayed more of exploration/avoidance behaviours than males in scented tests (Figure 3.8). Ritualised aggressions did not differ between scented and unscented tests. During tests however, dormice would explore first the arena and then start scent marking around the cloth and around the arena within the first five minutes of recording. No significant differences were found between scented and unscented tests in the duration of all behavioural categories (Wilcoxon matched-pairs signed-ranks tests:  $p > 0.05$ ; Figure 3.9).

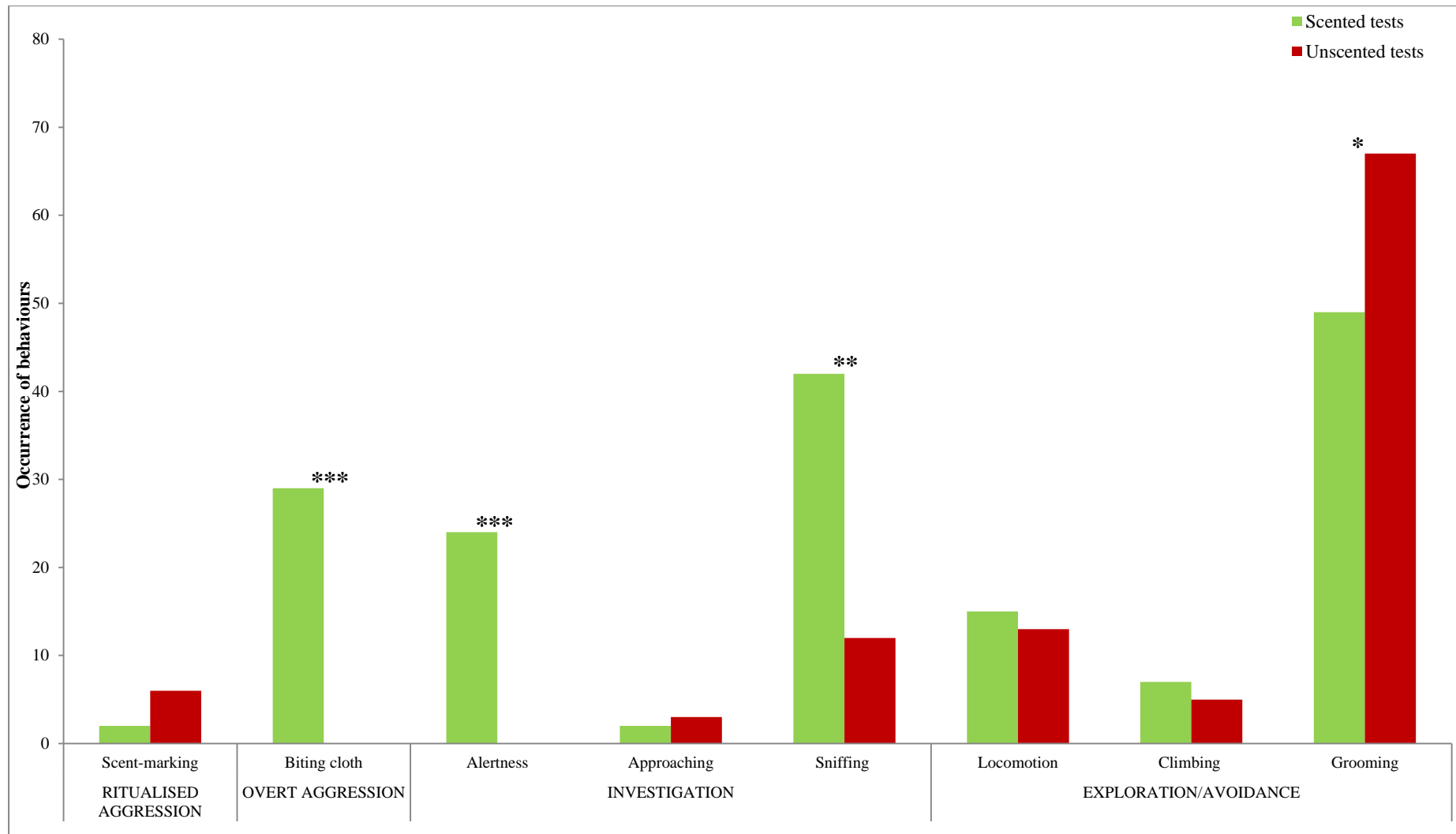
Figure 3.10 represents observed differences and similarities in the occurrences of behaviours exhibited by test dormice during scented and unscented tests. Woodland dormice in both tests displayed similar behaviours with exceptions of some behavioural components developing under specific conditions. Male dormice in unscented tests engaged regularly in grooming behaviour than males in scented tests (Figure 3.10). Biting of scented cloth aggressively and alertness behaviours were more developed in scented than unscented tests. Similarly, males were attracted to the scented cloth which was signified by higher rates of sniffing behaviour in scented tests than unscented tests.



**Figure 3.8.** Occurrence of four broad behavioural categories recorded during scented and unscented tests with an individual male woodland dormouse ( $n = 9$ ) in a 20-min test. Behavioural categories between scented and unscented tests that differed significantly (chi-square tests of independence) are indicated with \* ( $p < 0.05$ ) or \*\*\* ( $p < 0.001$ ).



**Figure 3.9.** Duration (mean  $\pm$  SE) of four broad behavioural categories recorded during a 20-min test with a single male woodland dormouse ( $n = 9$ ) during scented and unscented tests. No significant differences (NS) were found between scented and unscented tests across all behavioural categories (Wilcoxon matched-pairs signed-ranks tests:  $p > 0.05$ ).



**Figure 3.10.** Occurrence of behavioural components exhibited by a single male woodland dormouse ( $n = 9$ ) during scented and unscented tests in a 20-min test. Behavioural components between scented and unscented tests that differed significantly (chi-square goodness-of-fit tests) are indicated with \* ( $p < 0.05$ ), \*\* ( $p < 0.01$ ), or \*\*\* ( $p < 0.001$ ).

## 4. DISCUSSION

### 4.1. Behavioural responses of male woodland dormice towards same-sex conspecifics from the same and from different populations (Experiment 1)

My aim in this study was to investigate the behavioural responses of male woodland dormice (*Graphiurus murinus*) towards communicatory cues of same-sex conspecifics from the same and from different populations. In order to achieve my aim, I first used a three-chambered paradigm test for sociability and preference, which allows a focal animal to select between stimulus animals on the basis of visual, olfactory, auditory cues, and excluding tactile cues. My results in this experiment first showcase that male woodland dormice are able to distinguish between intra-population and inter-population conspecifics. Similar outcomes have been reported for other rodent species, where discrimination by focal animals was made through the use of stimulus animals (Nevo and Heth 1976). Based on my results, it seems that social recognition was attained through multi-modal communicatory stimuli from living individuals, with the exclusion of physical contact. Even though there were no significant differences in the number of entries and the time spent in the chamber with a stimulus dormouse, one cannot conclude that focal animals were not able to discriminate between conspecifics; instead it is possible that focal males explore both stimuli up until the point where they could distinguish between the two males. Similar findings on increased exploratory behaviour, resulting in less discrimination ability by *Peromyscus* males was observed by Smith (1965), as well as in male vlei rats (*Otomys irroratus*) (Pillay 1993).

In terms of behavioural responses by males, intra-population encounters showed significantly more affiliative (e.g. sitting next to conspecifics) behaviours, exploratory behaviours, grooming behaviour and more vocalizations. In contrast, inter-population encounters displayed often more of grooming behaviour only. Focal males in both intra- and inter-population dyads groomed, approached, made contact, and sniffed stimulus dormice. However, grooming behaviour was slightly more pronounced in intra-population than in inter-population dyads.

In addition, focal males from intra-population dyads spent often more time sitting near the stimulus conspecifics as compared to inter-population dyads. It seems that behavioural components are important mechanism for discrimination in the species. Increased affiliative behaviour in intra-population relative to inter-population encounters

could be indicative of conspecific recognition. Indeed, failure to recognise familiar conspecifics on the basis of auditory, olfactory and visual cues may lead to detrimental effects during encounters. My results complement those by Madikiza (2017), where male woodland dormice under laboratory settings displayed a greater affinity for familiar males during dyadic encounters.

#### *4.2. Vocal behaviour of male woodland dormice towards same-sex conspecifics from the same and from different populations (Experiment 2)*

In my acoustic tests, males produced a wide range of acoustic signals, and all four major acoustic signals recorded in my study were also emitted by woodland dormice in a previous study (Hutterer and Peter 2001). Across both intra- and inter-population encounters, variation in behavioural conditions correlated with variation in vocalizations. Inter-population dyads vocalized more and produced more aggressive (shriek/kecker) sounds, accompanied by some aggressive (biting of wire) behaviours, exploratory/avoidance behaviours and attraction behaviours (sitting and grooming next to conspecifics). Aggressive vocalizations were very loud and were frequently produced more often than any other calls. It seems that these aggressive calls emitted by inter-population males while in close proximity (e.g. sitting less than 10 cm from the “dyad partner” dormouse) appear to convey a warning message to conspecifics, as the receiver frequently retreated to a corner following the emission of these calls. Aggressive vocalizations emitted in similar behavioural contexts as in my study have also been recorded in the American red squirrels (Lair 1990) and silvery mole rats (*Heliophobius argenteocinereus*) (Knotkova *et al.* 2009). It has been suggested that aggressive or territorial animals have a tendency to display aggressive sounds during encounters, as shown in the slender mongoose (*Herpestes sanguineus*) (Baker 1982).

It is also possible that the higher frequency of aggressive calls during inter-population encounters may be related to population differences in visual and olfactory cues regulating aggression in the species. Higher occurrence of aggressive calls may also show that woodland dormice use communication signals (i.e. vocalization) to facilitate resolutions during aggressive interactions (Hogstedt 1983). Previous research has suggested that male woodland dormice have developed ritualised aggressions (signified by tail wagging and open mouth), and that acoustic signals in combination with visual and tactile cues could be important in preventing physical confrontations, as well as reducing direct aggression that might lead to potential harm (Madikiza 2017). The display of succession of stereotyped vocal repertoires during staged male dyadic encounters by silvery mole rats (Knotkova *et al.* 2009) coupled

with body postures such as ear movements, lifting and turning head in Seba's short-tailed bats (*Carollia perspicillata*) (Fernandez *et al.* 2014) and scent marking in wild European rabbits (*Oryctolagus cuniculus*) (Monclus *et al.* 2014) would be some of the essential ritualised signals to minimize physical confrontations during conflictual situations.

Therefore, the intensity of aggressive vocalizations displayed by dormice further reveal the possibility of territoriality in males, since the calls reduced frequency of contact between individuals. Even though free-living adult male woodland dormice have large intra-sexually overlapping home ranges (Madikiza *et al.* 2011), nest box monitoring study revealed that cohabitation by adult males in the same nest box was not common except in winter and during the mating season (Madikiza *et al.* 2010, Madikiza 2010, 2017). This possibly shows that male dormice have smaller exclusive territories within these overlapping home ranges that they defend from time to time against intrusion by same-sex conspecifics. Indeed, empirical evidence of male dormice showing signs of territoriality in a form of overt (e.g. chasing and biting) and ritualised aggressions (e.g. tail wagging and open mouth) towards same-sex conspecifics were reported in the previous study by Madikiza (2017).

My results further showed that the frequency in occurrence of exploratory/avoidance behaviours when males encountered dormice males from different populations was more pronounced in comparison to intra-population males. Higher levels of avoidance behaviours could possibly be a passive behavioural response used by male woodland dormice to avoid conflicts with strangers from different populations, especially since this behaviour occurred directly after aggression. As noted by Randall (1989) and Rychlik and Zwolak (2005), infrequent interactions, freezing and withdrawal behaviours during threatening situations are probably passive conflict-resolution strategies for male rodents. It is also plausible that higher levels of avoidance behaviours coupled with aggressive vocalizations could be indicative of an aversion for strangers, thus assuming the existence of the dear enemy phenomenon in male woodland dormice (Temeles 1994). The dear enemy phenomenon has been reported to occur in a number of territorial species such as the root voles (*Microtus oeconomus*) (Rosell *et al.* 2008) and the Eurasian beavers (*Castor fiber*) (Rosell and Bjørkøyli 2002), where males display different levels of aggression and are less amicable towards unfamiliar conspecifics than neighbours. In natural populations, 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 (hence re-enforcing familiarity), and therefore are expected to be less tolerant to unfamiliar males that maybe competitors, as was

notably observed in the thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*) (Schwagmeyer and Brown 1983, Yahyaoui *et al.* 1995).

It is also possible that lower levels of aggression towards intra-population males in my study could be because aggressive behaviours are triggered by resource competition such as females, nesting sites or food. In my study I did not provide these resources. Indeed, Gray *et al.* (2002) observed lower levels of aggressiveness in male house mice when resources such as water, food or nests were absent. In addition, inter-male aggressions between different populations of Pampean grassland mice (*Akodon azarae*) were relatively low when dyadic encounters took place in the absence of females (Bonatto *et al.* 2013).

Pooled together, it is clear that there seem to be differences between intra- and inter-population males in the drive to be tolerant. My results indicate that male woodland dormice from the same population are more sociable than males from different populations. Therefore, it is plausible that prior associations between dyads could have an influence on male dyadic interactions. In other rodent species such as banner-tailed kangaroo rat (*Dipodomys spectabilis*) (Randall 1989) and Turkish hamsters (*Mesocricetus brandti*) (delBarco-Trillo *et al.* 2009), there is indeed evidence of familiarity suppressing agonistic behaviours and encouraging social tolerance among familiar male conspecifics.

#### *4.3. Behavioural responses of male woodland dormice to the olfactory cues of same-sex conspecifics from different populations (Experiment 3)*

Olfactory discrimination tests revealed that male woodland dormice can discriminate between non-scented and scented areas by same-sex conspecifics from different populations. Males in scented tests showed more aggressive and investigative behaviours, while males in unscented tests displayed more exploratory/avoidance behaviours. My results showed that males are able to discriminate on the basis of olfactory cues of conspecifics. Previous dyadic encounters of woodland dormice showed that males make use of repeated rubbing of their ano-genital areas during encounters to broadcast their presence and state (Madikiza 2017). My results indeed showed that males scent marked in the presence of unscented and scented areas, even though scent marking behaviour was considerably low. It was further interesting to note that individuals in my study frequently marked during the period of habituation, but did not mark as frequently on the scented cloth or in the unscented areas.

I further wanted to investigate the behavioural responses of adult males to the olfactory cues from the ano-genital areas of conspecific males. In my results, males frequently displayed overt aggressive behaviours characterised by biting of the scented cloth,

and this took place exclusively when presented with a scented cloth. My results indicate that 1) male behaviours in dormice are altered by scents of unfamiliar males, 2) unfamiliar scents of conspecific males elicits aggressive behaviours. My results are supported by several studies on European rabbits (Mykytowycz *et al.* 1976), house mice (Archer 1968) and red foxes (*Vulpes vulpes*) (Blizard and Perry 1979), in which exposure to the unfamiliar conspecific scents was associated with overt aggressive behaviours in males. It is plausible to assume that in natural populations, the presence of unknown conspecific scents may be interpreted as a threat which arouses aggressive behaviours; thus leading to territorial behaviour in males. In fact, laboratory studies on male–male dyadic interactions by Madikiza (2017) reported high frequencies of overt aggression between unfamiliar males. Therefore, pooled together one can possibly deduce that male dormice are not only intolerant towards unfamiliar males; but are also intolerant of scents from unfamiliar male conspecifics.

The presence of a scented cloth in the arena further prompted high levels of investigative behaviours in males, signified by alertness (i.e. standing still on all four paws while looking at the cloth or sitting with the head projected towards the scented cloth), as well as approaching and sniffing the scented cloth. By being alert dormice could be 1) visually scanning the surroundings, or 2) detecting potential threats and non-threats that might be posed by the scent. Sniffing of scented cloth shows that males are indeed aware and are able to pick up scents of conspecifics. My results concur with those reported for male dwarf hamsters (*Phodopus sungorus campbelli*) (Reasner and Johnston 1987) and thick-tailed galagos (*Galago crassicaudatus argentatus*) (Clark 1982) where sniffing was profusely elicited in the presence of conspecific odours.

There are several explanations one can link to my results; investigative behaviours displayed by males could possibly suggest that the odour of unfamiliar males is perceived as a warning, repellent or both towards other male conspecifics (Byrne and Keogh 2007). Investigations of the scented cloth could be further construed as gathering of information, as well as assessment of risks associated with the odour cues (Guillette *et al.* 2009, Tebbich *et al.* 2009). It is thus plausible that under natural populations male dormice use olfactory cues to distinguish between unfamiliar (inter-populations) and familiar (intra-population) male conspecifics; and possibly use these distinctions to avoid interactions that might be potentially risky and costly.

On the contrary, male dormice displayed high exploratory/avoidance behaviours during unscented experiments. Similar findings were observed in a study conducted on golden hamsters, where male hamsters exhibited high levels of exploratory behaviours in

unscented than scented areas (Alderson and Johnston 1975). High rates of grooming behaviour, involving all forms of body surfaces such as tail, genitals, paw and fur-licking, including washing the face with licked-fore paws and drawing fore-paws over the head to the tip of the snout were also observed in my study. It is possible that grooming behaviour was induced when dormice transition from one type of behavioural activity to another (Baker and Aureli 1997). Additionally, grooming by dormice could be a way of broadcasting their scents in a novel environment. As suggested by Ferkin *et al.* (2001), self-grooming by rodents may cause the release of particular chemical cues from the body and saliva that increases within an active space. Therefore, self-grooming may be another form of scent marking in male woodland dormice (Thiessen *et al.* 1976, Ferkin *et al.* 1996).

## CONCLUSION

My study has shown that male woodland dormice are able to discriminate between same-sex conspecifics from the same population and from different populations on the basis of visual, auditory, and olfactory cues. Male woodland dormice have a clear aversion for males from different populations, while displaying a heightened sociability for conspecifics from the same population. It seems that ritualised aggressive behaviours along with avoidance behaviour towards strangers allows for establishment and maintenance of the territories of individuals. Whereas sociable behaviours such as motivation to investigate conspecifics allows for social and spatial tolerance to develop

Acoustic signals in woodland dormice play an important role in mediating social interactions with members of the species. Male woodland dormice acoustic signals are predominantly associated with aggression and possibly used as a strategy in preventing physical confrontations as well as reducing direct aggression between conspecifics. However, future studies should make effort to use spectrographic analysis of recorded vocalizations, as in my study we cannot ascertain that the entire acoustic repertoire of the species has been identified. Olfactory tests revealed that scents of same-sex conspecifics from different populations elicit aggressive behaviours in males, and that male dormice scent mark to broadcast their presence and state (i.e. competitive ability or aversive state) towards conspecifics.

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# APPENDIX

**Appendix 1.** Detailed information on woodland dormouse; taxonomy, distribution, population habitat and ecology as well as conservation, as published in *The Red List of Mammals of South Africa, Swaziland and Lesotho* (2016).

# *Graphiurus murinus* – Woodland Dormouse



<b>Regional Red List status (2016)</b>	<b>Least Concern*</b>
National Red List status (2004)	Least Concern
Reasons for change	No change
Global Red List status (2016)	Least Concern
TOPS listing (NEMBA) (2007)	None
CITES listing	None
Endemic	No

#### \*Watch-list Data

The Woodland Dormouse uses daily torpor spontaneously to save energy when faced with unfavourable conditions like scarcity of food and low temperatures. Excluding the bats, it is currently the smallest known non-volant African mainland hibernator (Mzilikazi et al. 2012).

## Taxonomy

*Graphiurus murinus* (Desmarest 1822)

ANIMALIA - CHORDATA - MAMMALIA - RODENTIA - GLIRIDAE - *Graphiurus - murinus*

**Synonyms:** *alticola*, *cineraceus*, *cinerascens*, *collaris*, *erythrobronchus*, *griseus*, *isolatus*, *johnstoni*, *lalandianus*, *raptor*, *saturates*, *selindensis*, *soleatus*, *vulcanicus*, *zuluensis*. See full list in Holden (2013).

**Common names:** Woodland Dormouse, Forest African Dormouse (English), Boswaaierstermuis (Afrikaans), Mokomane, Nthuê, Nthufê, Nthuhê, Motsékêtsêkê, Tsikôtsikô (Tswana)

**Taxonomic status:** Species complex

**Taxonomic notes:** Taylor et al. (1994) reported that specimens from Mkhuze in KwaZulu-Natal, Simunye in Swaziland and Waterpoort in Limpopo differed morphologically (reduced upper molar, inflated bullae) from other specimens of *Graphiurus murinus* and from the Stone Dormouse (*G. platyops*). Similarly, recent evidence reported differences in the morphology of two populations

of *G. murinus* in the Eastern Cape (Kryštufek et al. 2004). Although karyotypes were the same for both populations, they differed from previously recorded karyotypes for this genus in Africa (Kryštufek et al. 2004). Additionally, a high degree of chromosomal diversity has been recorded in this species (Dippenaar et al. 1983; Holden 1993). Taxonomic research and DNA analysis is therefore necessary to carry out a systematic revision of this species complex (Skinner & Chimimba 2005; Holden 2013).

## Assessment Rationale

The Woodland Dormouse is listed as Least Concern in view of its wide distribution within the assessment region and presumed large population. It is present in many protected areas, and can co-occur with human habitation. Although the species is thought to occur in naturally low numbers, it is not suspected to be declining as there are no major threats. As this rodent is arboreal, it is difficult to trap on the ground, and thus may be more abundant than expected. For future surveys, it is recommended that traps are set in trees. This species may have to be reassessed as the species complex is disentangled through ongoing molecular work.

**Regional population effects:** Unless conditions are favourable, this species may occur in low numbers across the central, eastern and northern parts of the assessment area. Where it occurs in Mozambique, Zimbabwe, Botswana and Namibia, immigration is expected where continuous woodland is found or where patchy woodlands are connected by riverine forests or similar wooded corridors.

## Distribution

The Woodland Dormouse has a scattered distribution that stretches from Ethiopia to South Africa (reaching as far west as the Western Cape) and Lesotho. Within the assessment region, it ranges across Limpopo, North West, Gauteng, Mpumalanga, KwaZulu-Natal, and Eastern Cape provinces and marginally into the Western and Northern Cape. It also occurs in Swaziland (Monadjem 1998) and Lesotho (Lynch 1994).

Within the North West Province, only one individual was captured recently (post-2000), which was taken in *Terminalia sericea* woodland near Mositha in the Mafikeng Bushveld vegetation type (Power 2014). However, numerous dead specimens were found throughout the province as Woodland Dormice often nest in electrical switchboxes and sometimes die when in torpor.

## Population

This species is thought to generally occur at low densities, although these can vary drastically where the species experiences “boom and bust” cycles, possibly in response to variations in rainfall and food availability. In the Great Fish River Nature Reserve (GFRNR), Eastern

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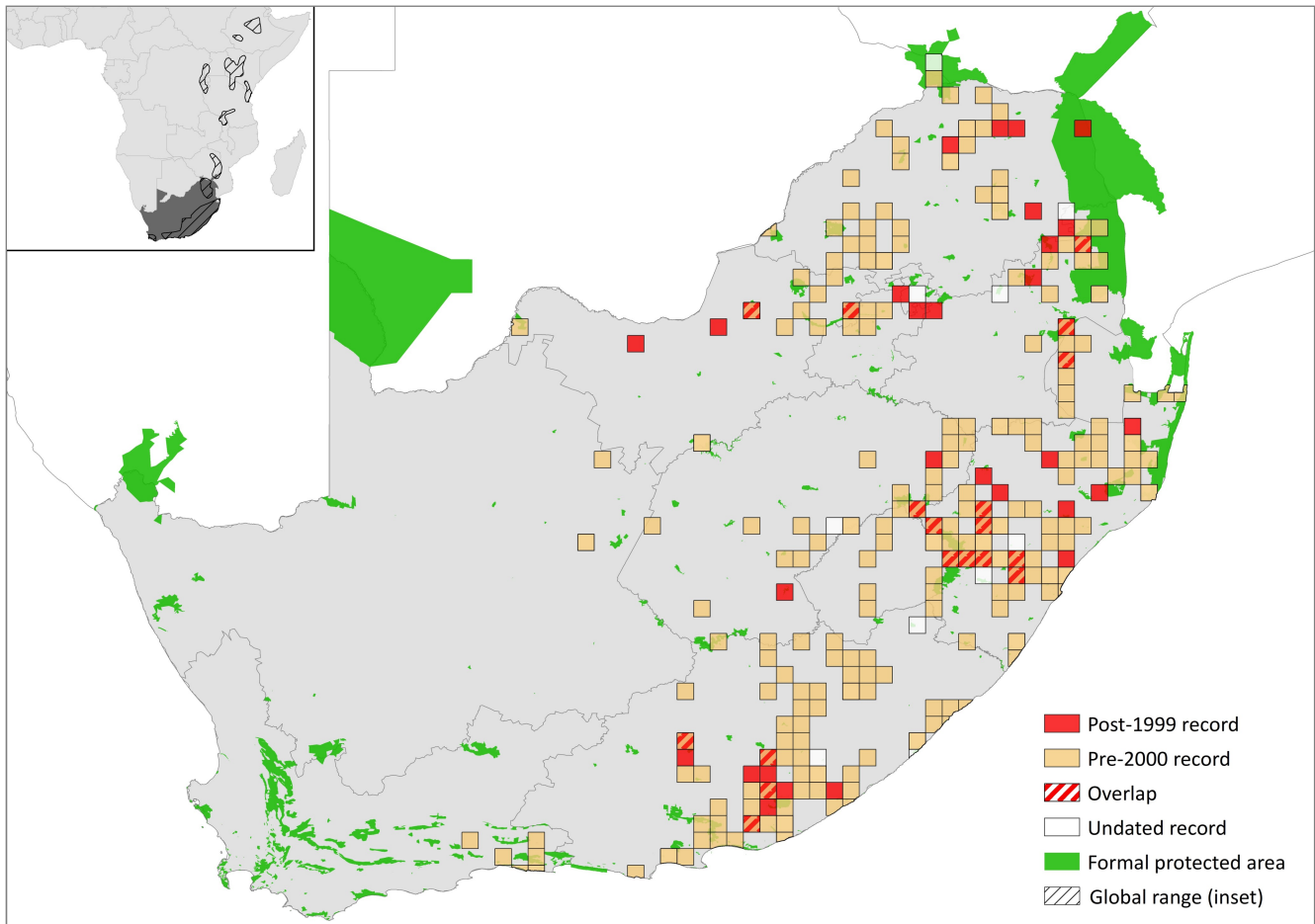


Figure 1. Distribution records for Woodland Dormouse (*Graphiurus murinus*) within the assessment region

Table 1. Countries of occurrence within southern Africa

Country	Presence	Origin
Botswana	Possibly extant	Native
Lesotho	Extant	Native
Mozambique	Extant	Native
Namibia	Absent	-
South Africa	Extant	Native
Swaziland	Extant	Native
Zimbabwe	Extant	Native

Cape, densities have been estimated to vary between 2 and 16 individuals / ha depending on the season and year (Madikiza 2010; Z.J.K. Madikiza pers. obs. 2006–2012) in riverine *Combretum* forests, where it can be the dominant small mammal. It is, however, unclear whether the presence of wooden nest boxes at the study site might have improved nesting conditions and offspring survival (Madikiza et al. 2010a), hence leading to overall higher densities than usual. Woodland Dormice exhibit low densities in Telperion Nature Reserve (Mpumalanga) in areas where large rocks are present, but have been recorded from various accommodation units at the study site (MacFadyen 2014).

Although it has been noted that this species is seldom caught in traps and is more commonly recorded from houses, it is likely because in most studies traps were set on the ground and not on logs or in trees. In GFRNR, Madikiza et al. (2010b) did not make a single capture on

the ground, either inside or outside the riverine forest, during a 13-month period. In contrast, trapping success in trees averaged 13.3 captures per 100 trap nights, with a minimum average of 5.1 captures in winter and a maximum average of 19.0 captures in summer. In a subsequent study in the same area, Lamani (2014) only recorded 10% of captures on the ground over the four seasons of the year.

**Current population trend:** Unknown, but probably stable due to lack of major threats to the species.

**Continuing decline in mature individuals:** Unknown, but probably not.

**Number of mature individuals in population:** Unknown

**Number of mature individuals in largest subpopulation:** Unknown

**Number of subpopulations:** Unknown

**Severely fragmented:** No

## Habitats and Ecology

This species inhabits woodland, savannah, grassland and rocky areas (Skinner & Chimimba 2005). In parts of its range it is found in either Afromontane forest or riverine forest dominated by *Combretum* (Qwede 2003; Kryštufek et al. 2004; Madikiza 2010; Photo 1). In Rolfontein Nature Reserve, Northern Cape Province, two specimens were caught in the *Acacia karroo* community (Jooste & Palmer 1982), as it is dependent on large trees for nesting. It can persist in secondary habitats, and in some regions occurs in various types of buildings. For example, it is recorded

regularly in buildings at Tswalu Kalahari Reserve (D. MacFadyen pers. obs. 2007) and can reach pest proportions in dwellings in the Soutpansberg. This species has also been recorded using piles of debris deposited by high floods near seasonal rivers (Skinner & Chimimba 2005). The diet has only been studied in GFRNR based on remains found in nest boxes. There, arthropods – mainly beetles and millipedes – were dominant (99% occurrence) in all seasons, followed by molluscs (16%) and the fruits of the Cross-berry (*Grewia robusta*) and the Buffalo Thorn (*Ziziphus mucronata*) (14%).

The species is nocturnal and arboreal, and to a lesser extent terrestrial (Lamani 2014; Lombard 2014). At night it forages singly in trees or on rocks – depending on habitat – in search of insects and other food items. In GFRNR, Lamani (2014) found that, in riverine forests, Woodland Dormice select areas with dense canopy cover and a high percentage of arboreal connectivity when active at night, possibly to reduce predation risk and facilitate movements. This species tends to be crepuscular on overcast days on the Highveld (D. MacFadyen pers. obs. 2009) and has been observed during the afternoon at Telperion Nature Reserve (D. MacFadyen pers. obs. 2009). It is inactive at low temperatures in the winter months on the Highveld (MacFadyen 2014). Woodland Dormice are competent thermoregulators (Ellison & Skinner 1991; Webb & Skinner 1996; Whittington-Jones & Brown 1999). In the Eastern Cape, they have been found torpid at different periods of the year (Madikiza 2010), even entering a state of hibernation during the colder months (Mzilikazi et al. 2012). The longest torpor bout that dormice can undergo without arousal is about 8 days, and torpid dormice can drop their body temperature to a minimum of 1.5°C (Mzilikazi et al. 2012).

During the day Woodland Dormice sleep inside branches and trunks (Lamani 2011; Photo 1), and locally in rock crevices. Dead logs and underground sites (burrows) are rarely used (Lamani 2011). In GFRNR, Cape Bushwillows (*Combretum caffrum*) are the predominant trees used for the resting sites, probably due to their abundance in the forest, and their propensity to rot from the inside and provide natural cavities. Woodland Dormice use several resting sites throughout the year, but site fidelity on consecutive days is very high during winter (Lamani 2011; Z.J.K Madikiza & E. Do Linh San unpubl. data). Specific resting sites (both natural and nest boxes) are used by several different dormice, and simultaneous sharing is frequent (Photo 2), taking place between all combinations of male, female and juvenile dormice, with different patterns observed depending on the season of the year (Madikiza et al. 2010a; Madikiza 2010, 2017).

Woodland dormice are seasonal breeders, starting from October up to February (Qwede 2003; Madikiza 2010), and females can produce up to two litters 6–8 weeks apart (Madikiza 2010). At least in some areas, reproduction seems to be associated with high availability and abundance of insects, fruits and high rainfall (De Graaff 1981). After a gestation of about 24 days (Kingdon 1974), females in natural populations give birth to 3–6 young (Lynch 1989). Using extensive trapping and nest box monitoring data, Madikiza et al. (2011) found high intra- and intersexual home range overlaps, with the home ranges of males twice as large as those of females. This, coupled with asynchronous sexual receptivity in females and a complex network and dynamics of sleeping associations (Madikiza 2010, 2017) suggests that



**Photo 1. Woodland Dormouse (*Graphiurus murinus*) peering out from a cavity in a Cape Bushwillow (*Combretum caffrum*) (Emmanuel Do Linh San)**



**Photo 2. Woodland Dormice (*Graphiurus murinus*) huddling in a nest box during winter (Emmanuel Do Linh San)**

Woodland Dormice have a promiscuous mating system. In addition, some females may engage in communal breeding (Madikiza 2010, 2017).

**Ecosystem and cultural services:** The Woodland Dormouse is one of the core small mammals in the forest ecosystem, as observed notably in some study sites in the Eastern Cape. It is therefore likely to play a significant ecological role, for example in seed dispersal and/or as a food source for small carnivores (Matolengwe 2010) and aerial predators.

## Use and Trade

The Woodland Dormouse seems to be growing in popularity in the pet trade in Europe and USA (see e.g. <https://www.thespruce.com/african-dormice-as-pets-1236775>). We suspect that a large majority of pet Woodland Dormice originate from captive breeding programmes rather than from the wild. There are also anecdotal records of schoolboys keeping them as pets in Zimbabwe (Skinner & Chimimba 2005).

## Threats

There are no major threats to this species. However, habitat loss and fragmentation from mining and agriculture is likely to cause local subpopulation declines. This species is unlikely to persist in agricultural monocultures with few or no trees. In transformed areas, it is only likely to remain within the rocky, inaccessible

**Table 2. Threats to the Woodland Dormouse (*Graphiurus murinus*) ranked in order of severity with corresponding evidence (based on IUCN threat categories, with regional context)**

Rank	Threat description	Evidence in the scientific literature	Data quality	Scale of study	Current trend
1	2.1.2 Annual & Perennial Non-Timber Crops: habitat loss and fragmentation from agricultural expansion.	-	Anecdotal	-	-
2	3.2 Mining & Quarrying: habitat loss and fragmentation.	-	Anecdotal	-	-

**Table 3. Conservation interventions for the Woodland Dormouse (*Graphiurus murinus*) ranked in order of effectiveness with corresponding evidence (based on IUCN action categories, with regional context)**

Rank	Intervention description	Evidence in the scientific literature	Data quality	Scale of evidence	Demonstrated impact	Current conservation projects
1	1.1 Site/Area Protection: protected area expansion to include woodland ecosystems.	-	Anecdotal	-	-	-
2	2.1 Site/Area Management: ensure corridors of woodland between agricultural monocultures.	-	Anecdotal	-	-	-

habitats, which are unsuitable for agriculture. However, it is adaptable and is known to make use of secondary habitats, including roofs of buildings or thatched huts, switch boxes, water pumps and transformers. Resultantly, it can become a nuisance by causing electrical short circuits (Skinner & Chimimba 2005).

**Current habitat trend:** Stable

## Conservation

Within the assessment region, the Woodland Dormouse is present within many protected areas across its range, including the Kruger National Park (Limpopo and Mpumalanga), Telperion Nature Reserve (Mpumalanga), Ezemvelo Nature Reserve (Gauteng), Tswalu Kalahari Reserve (Northern Cape), Silaka, Hluleka, Dwesa, Mpofu, Fort Fordyce and the Great Fish River nature reserves (Eastern Cape). It is also present in the forests of the Amathole Mountains. Although no specific conservation interventions are necessary, protected area expansion to ensure corridors of suitable woodland for movement would benefit this species.

### Recommendations for land managers and practitioners:

- Protect woodland areas.
- Influence agricultural policy to ensure connected patches of woodland are retained.

### Research priorities:

- Taxonomic revision is required to disentangle this species complex.
- The boundaries between *G. murinus* and *G. microtis* should be clearly defined.
- A better knowledge of the geographic distribution of this and other dormice species is needed. As trap placement is critical, with traps generally having to be set in trees in order to successfully catch this species, it means that Woodland Dormice could well be present in areas where they have not previously been detected.

A team of researchers at the University of the Witwatersrand and at the University of Fort Hare has been

running a long-term project on the biology, ecology and behaviour of the Woodland Dormouse. Contact details of the research coordinator: Dr Kim Madikiza, School of Animal, Plant & Environmental Sciences, Faculty of Science, University of the Witwatersrand, WITS 2050. Email: [kim.madikiza@wits.ac.za](mailto:kim.madikiza@wits.ac.za).

### Encouraged citizen actions:

- Report sightings on virtual museum platforms (for example, iSpot and MammalMAP), especially outside protected areas.
- Plant suitable indigenous trees in gardens and ensure corridors of natural vegetation remain to allow local movements.

## Data Sources and Quality

**Table 4. Information and interpretation qualifiers for the Woodland Dormouse (*Graphiurus murinus*) assessment**

Data sources	Field study (literature, unpublished), indirect information (literature, expert knowledge), museum records
Data quality (max)	Estimated
Data quality (min)	Inferred
Uncertainty resolution	Best estimate
Risk tolerance	Evidentiary

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Details of the methods used to make this assessment can be found in *Mammal Red List 2016: Introduction and Methodology*.