
Differences in activity budgets and social behaviours of
three male alternative reproductive tactics in the African
striped mouse (*Rhabdomys pumilio*)

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Abstract

Alternative reproductive tactics (ARTs) have evolved in various animal taxa. For individuals of these species choosing the right reproductive tactic is very important as depending on the tactic chosen, individual fitness will differ. Recent studies have focused their interest on ultimate factors driving the evolution of ARTs. However, despite those efforts the phenomenon of ARTs remains largely unexplained. For instance, little research has been conducted to investigate behavioural differences between reproductive tactics, which have been found to influence the amount of energy available for an individual and thus its reproductive success. In this study, I investigated differences in activity budgets and social behaviours of three ARTs in the African striped mouse (*Rhabdomys pumilio*): territorial dominant males, roaming individuals and adult natively philopatric males. I expected group living males (philopatrics and breeders) to show higher sociopositive behaviour than roamers but simultaneously I expected territorial males to present high aggressiveness towards intruders in order to defend their females' harem. Besides, I predicted activity such as foraging and time spent at nest to be significantly higher in breeders and philopatrics rather than roamers. I also expected roamers to be less aggressive than breeders, to present bigger home range sizes and overlapping areas with other males and to spend more time travelling to find females than the other tactics. In order to investigate these predictions I collected behavioural data through focal-animal observations in the field and I performed experiments in an artificial arena to study possible differences in aggressive response patterns of roamers and breeders. Furthermore, I measured testosterone and corticosterone plasma levels to investigate concentration differences between ARTs and to compare these data with aggressiveness of territorial and roaming males. I found that I) philopatric individuals allocate their energies in survival rather than reproduction. Males following this tactic show high level of sociopositive behaviours, possibly aiming to promote the safety stay with the natal group. II) The behaviour of roaming males is a trade-off between survival and mating i.e., roamers intrude other male territories to seek copulations but at the same time they try to avoid risky encounters with territory owners. III) Territorial males use most of their resources for reproduction showing high levels of aggressiveness towards roamers but amicable behaviours towards individuals of their family, aiming to increase their own fitness. The hormone analysis did not support the behavioural results, suggesting that other studies are needed in this direction in order to explain the complex mechanisms that might underlie the variation of plasma androgens in striped mice adopting different ARTs. This study revealed significant behavioural differences between male ARTs in striped mice, especially regarding their activity budgets and correlated energy budgets, providing interesting data for further investigation of the evolution of this phenomenon.

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1. Introduction

Reproductive success in animals is the result of a sexual conflict whereby the number of available eggs to be fertilized limits male reproduction and female reproduction is limited by the presence of food resources. This is based on the fact that females are usually the sex that invests more energy in offspring, giving rise to few expensive gametes, the eggs, whereas males invest less energy producing several small sperm cells (Bateman, 1984). In such case, males would then be the sex that competes for the access to females and females would compete for access to food resources. As a consequence, the reproductive tactic that a male adopts has a main impact on his own fitness so that the male adopting the best tactic will mate and sire more offspring than the others. When this happens within the same population and within the same sex, i.e. when the adaption of divergent allocation tactics can optimize the fitness of an individual, alternative reproductive tactics (ARTs) evolve (Taborsky *et al.*, 2008). The utilization of a different tactic by a specific male is observed to be often status and condition-dependent (Scantlebury *et al.*, 2008; Tomkins and Hazel, 2007), relying on factors such as environment, population density, developmental stage and social status. ARTs represent a very fascinating and still largely unknown phenomenon and are an interesting opportunities to study the evolution and causes of behavioural and physiological variation in reproductive patterns between individuals of the same species.

Several studies focused on ultimate factors of ARTs, such as heritability and fitness differences (Clutton-Brock *et al.*, 2006; Zamudio and Sinervo, 2000). For instance: quantitative evidences for the success of discrete male tactics have been tested on three male lizard (*Uta stansburiana*) mating tactics. In this study, nuclear microsatellites have been used to estimate the difference of paternity rate of the three lizard tactics (Zamudio and Sinervo, 2000). A hierarchic social system was found, with the most aggressive and territorial male having the highest paternity rate.

In mammals, a study carried out on Japanese macaques (*Macaca fuscata yekui*) demonstrated that non-troop males often reduce the reproductive success of high-ranking males, siring more than the half of the troop's offspring (Hayakawa,

2008). Thus, in these two examples, not all breeding males were adopting the same reproductive tactic and as a consequence they did not have the same fitness output.

However, little is known about proximate mechanisms that cause the existence of variation in tactics, such as ontogenetic and behavioural processes.

Links between hormone levels and the adoption of a particular tactic have been demonstrated in several studies (Arlet *et al.*, 2009; Rasmussen *et al.*, 2008). As an example, the plainfin midshipman fish (*Porichthys notatus*) presents two male reproductive morphs. Males can either produce vocalization to court females and defend aggressively nest sites or they can be sneakers that try to fertilize eggs from females defended by territorial males (Arterbery *et al.*, 2010). This recent study discovered a link between the utilization of one of those two tactics and both glucocorticoid and mineralcorticoid levels present in the central nervous system of males. Thus, in males of this teleost fish, corticosteroid levels are linked to behavioural and physiological variations. A similar result was found in the gray-cheeked mangabey, *Lophocebus albigena* (Arlet *et al.*, 2009) and the study of Rasmussen *et al.* (2008) on African elephants (*Loxodonta africana*) also confirmed this hypothesis. Territorial and thus aggressive males presented higher level of androgens and intermediate level of glucocorticoids.

Factors that influence the choice of the ART have been studied in rodents. Male Cape ground squirrels (*Xerus inauris*) may follow two different mating tactics: they may remain with the natal group or, alternatively, disperse and search for females to mate with (Scantlebury *et al.*, 2008). Usually, mating possibilities of staying with the natal group are limited, but energetic costs associated to dispersal are avoided. The choice of the reproductive tactic depends on several factors such as age, relatedness among the natal group, reproductive suppression by the dominant individual and reproduction success in the natal group (Scantlebury *et al.*, 2008). This study suggests therefore that the two reproductive tactics are cost-dependent, as they require different amount of energy invested. Thus, physiological and behavioural differences between males determine the choice of the reproductive tactic: each male would then adopt the best tactic depending on the trade-off between costs and benefits in terms of fitness that the tactic would bring.

In spite of all the cited studies describing physiological variations between ARTs linked with their relative fitness, still little is known about behavioural differences between them. Given that the choice of a determinate tactic is energy-dependent (Scantlebury *et al.*, 2008), behaviours and activity budgets can be expected to play an important role in this trade-off. Energy investment in activities such as foraging, resting and defending the territory may vary from tactic to tactic. In addition, sociopositive and aggressive behaviours involve differences in energy investment too and they also may differ depending on the mating tactic. Therefore researching on differences in behaviours and in activities budgets between males showing ARTs becomes very important trying to gain a better and deeper understanding of this phenomenon.

Male ARTs have been observed in several rodent species (Cameron *et al.*, 2009; Scantlebury *et al.*, 2008; Schradin *et al.*, 2009a). Representing almost half of all mammalian species (Wilson and Reeder, 1993), rodents are a very interesting model to understand how the current variety of mammalian mating systems is linked with individuals' behaviour and physiology. Nevertheless, their mating mechanisms are largely unknown because rodent species are mostly small and nocturnal and the research on them is therefore difficult.

I focused my research on a wild population of African striped mice (*Rhabdomys pumilio*) in the South African Succulent Karoo. In fact, striped mice living in the Succulent Karoo represent a very good model to study ARTs because this muroid species is diurnal and presents different male alternative reproductive tactics. In the Succulent Karoo of South Africa they are known to be territorial, to live in groups but to forage alone and to have communal breeding and helpers at the nest (Schradin, 2007; Schradin and Pillay, 2004b). Family groups in the breeding season could reach the size of about 30 mice: 1 breeder male, up to 4 breeder females and their adult offspring of both sexes. Mice sleeping at the same place are considered to be part of the same group and they interact amicably with one another, forming an egalitarian social system (Schradin, 2004). Males often participate in infant care (Schradin and Anzenberger, 1999; Schradin and Pillay, 2003; Schradin and Pillay, 2004a) and females rear the offspring cooperatively (Schradin and Pillay, 2004b). Striped mouse males may follow three alternative reproductive tactics (Schradin *et al.*, 2009b; Tab. 1). First, young adult males may

adopt the philopatric tactic. This tactic consists in remaining with the natal group, delaying natal dispersal to the next year, helping to rear offspring of the breeding individuals (which might be siblings, half-siblings or cousins of the helpers) and defending the territory. Philopatry in striped mice includes benefits, such as predator avoidance because of increased vigilance during nest sharing and thermoregulatory benefits (Schradin, 2005). Usually, all males go through the philopatric stage during the breeding season in which they are born but in order to breed they have to leave the nest, losing their philopatric-status. Secondly, individuals may become territorial breeders, with just one of these dominant males living in the group and defending the group's territory, which includes breeding females and adult philopatric offspring (Schradin and Pillay, 2004b). Breeder males are older and heavier than the others (Schradin *et al.*, 2009a). Finally, males may follow a roamer tactic: these individuals leave their natal group and live alone, invading breeders' territories to search for females to mate with.

As in other mammals with ARTs, some studies on striped mice demonstrated that the differences between hormone levels are also linked with the adopted tactic (Schradin, 2008; Schradin *et al.*, 2009b), but surprisingly in a rather different way than in other species. In the study of Schradin *et al.* (2009b), breeding striped mouse males had lower testosterone level than roamers, indicating a trade-off between amicable behaviour needed to gain access to females (low testosterone level) and dominance (high testosterone level). In addition the testosterone levels of breeders may be in trade-off with the prolactin level, necessary for parental care (Schradin and Pillay, 2004a). Philopatric individuals had a very low testosterone level but a higher corticosterone level, which was correlated with their low competitive status. Roamers showed the highest testosterone level, which might promote risky behaviours such as invading territory defended by breeding males.

The habitat of my study species was the South African Succulent Karoo, where the dominant shrub species are *Zygothymum retrofractum* and *Lycium cinerum*. Succulent plants like *Mesembryanthemum guerichianum* are also present, providing an important food resource for mice. The Succulent Karoo has an environment ranging from desert to semi-desert, which receives mainly during

the winter season (May-August) up to 160 mm rainfall (Rösch, 2001). The breeding season of striped mice occurs during spring (September-November) and is characterized by maximal plants growth, hence maximal food availability (Schradin and Pillay 2005b). Spring is followed by a long and dry summer (December-April) with consequently decreasing in food availability and therefore in mice body weight (Schradin and Pillay, 2005b). Temperatures at the research site range between 24° and -1.5°C in winter and between 40° and 5°C in summer (Schradin, unpubl. data).

Table 1: Male ARTs in striped mice during the breeding season

ARTs	Characteristic	Results of my study
Philopatrics	<ul style="list-style-type: none"> - Offspring individuals living with the natal group - Weight: 30-40 g - Participating in rearing siblings or half siblings, defending and building the nest - Delayed reproductive season (constrained reproduction as long as they remain philopatrics) 	<i>Investing in survival:</i> higher sociopositive behaviours towards group members probably in order to be accepted by them. The safety of the group allow philopatrics to reach the next breeding season in good condition and thus increase their reproductive success
Breeders	<ul style="list-style-type: none"> - Territorial breeder males, living with their harem and offspring - Scrotal - Weight: 60-70 g - Participating in infant care - Defense of the territory and family group 	<i>Keeping the monopoly on the female group:</i> social interactions with females and offspring but high aggressive behaviours towards intruders that might represent reproductive competitors or threat offspring's survival (infanticide)
Roamers	<ul style="list-style-type: none"> - Solitary individuals, they live alone and do not have a specific territory - Scrotal - Weight: 50-60 g - Try to steal copulations from breeders' females 	<i>Trade-off between survival and reproduction:</i> avoidance of risky encounters with breeders but at the same time they try to intrude breeders' territories to seek matings

1.1 Aims and predictions

My main goal was to investigate energy-dependent behaviours and activities of the three male ARTs and find if males adopting different tactics are allocating their energies in specific behaviours or activity budgets.

Sociopositive behaviours

Territorial males show amicable behaviours towards females (Schradin and Anzenberger 1999, Schradin 2004, Schradin and Pillay 2004b) to keep their harem and gain mating success. I expected breeders to show high levels of sociopositive behaviours in the field, thus I made a similar prediction for philopatrics: due to habitat saturation (Schradin and Pillay 2004b, Schradin and Pillay, 2005) they are forced to remain with the natal group and not reproduce in order to avoid inbreeding depression (Pillay, 2002) and because of reproductive suppression by breeders. Consequently, I expected them to show high sociable interactions towards other group members (grooming, body contact and close proximity). Besides, I expected both philopatrics and breeders to spend considerable time in the nest participating in the upbringing of pups. Moreover, as infanticide by intruders could happen (Palanza *et al.*, 1996; Kiyota and Okamura, 2005), breeders and philopatrics should visit the nest in order to defend it against intruders.

Because roamers are not part of any group they should not have any need to show sociable behaviour towards other mice. The only sociable behaviour that would bring an advantage to them would be the one towards females, in order to mate. Anyway, females are observed to be aggressive towards stranger males (Schradin, 2006), therefore I expected very little sociable interaction from roamers. The same prediction can be applied concerning the time that roamers would spend in their nest. Roamers usually sleep alone: the nest does not represent an area where they can find females. They should leave their sleeping site as soon as they can, searching for females to mate with and returning just at the end of the day.

Socionegative interactions

Territorial males were expected to show aggressiveness towards stranger males (roamers or neighboring breeders; Schradin, 2004) because they have to defend their territory and their harem. I expected them to show less avoidance when encountering other mice than other individuals because they should be alert and ready to chase away possible intruders. Besides, with presentation experiments in an artificial arena, I wanted to test my hypothesis about the higher aggressiveness of territorial males and demonstrate that encounters between breeders present a higher level of aggressiveness than encounters between roamers and breeders. That would indicate simultaneously that roamers are more careful than breeders and assume some kind of submissive behaviour trying to prevent stranger mice (in this case the breeder stimulus-mouse) from starting an aggressive encounter, which could be very risky for them given their lower body mass.

I expected philopatrics to participate in territorial defense (Schradin, 2004; Schradin and Pillay, 2004b). This behaviour, combined with other kind of collaborations with the family group such as helping in rearing pups and nest construction is thought to fall within the “helping behaviour” category because it increases the inclusive fitness of the philopatric males (Schradin and Pillay 2004b).

Activity budgets

As energy dependent activity budgets I recorded foraging rate, daily traveled distance, basking behaviour and resting behaviour.

I expected foraging rate for striped mouse males to be a trade-off with searching for females. Normally, breeders are the heaviest males in the group (Schradin *et al.*, 2009b) due to their age (they are usually the oldest males in the group). However, their larger body mass could also mean that they feed more than the other mice. I argued that breeders invest more time on feeding than roamers because they do not have to travel to find females. Therefore I expected breeders to have a higher feeding rate than roamers. In addition, breeders’ aggressiveness might require more energy and thus a larger amount of food. At the same time, I expect philopatrics males to have the highest feeding rate, assuming that they

invest little in obtaining matings. Instead, philopatric males should forage more in order to gain weight and become breeders during the next breeding season: it has been shown that a diet consisting of high proteins influences scrotality (Schneider, 2005).

I expected roamers to have a smaller feeding rate because they have to invest more in travelling to search for females reducing time available for foraging.

I expected roamers to show a larger travelling distance than group-living males: as they do not possess any harem they should be interested in finding females to mate with and thus they are forced to travel further. I expected breeders to have a smaller travelling distance than roamers as they have already females inside their territory; anyway my expectation was a relevant travelling distance, as they have to be alert and travel inside their territory to check for intruders. Philopatrics are the ones that should present the smaller travelling distance, as mating possibilities are not thought to push them to travel far away from the nest.

As for my prediction about feeding rate, I expected philopatrics to be the ones spending more time in basking and resting than breeders and roamers, given that they are not investing time in mating attempts (Schradin and Pillay, 2004b). In the same way, I expected roamers to invest little in basking and resting but more in travelling and I expected breeders to show an intermediate level of resting and basking behaviours.

Home ranges

My expectation was that roamers should have larger home range sizes than breeders as already shown in a previous study (Schradin *et al.*, 2009b), because they are forced to travel further searching for matings and intrude in breeders' territories.

Moreover, I expected roamers to show bigger overlapping areas with other male individuals than breeders. Even though breeders as well could be interested in intruding neighboring territories in order to sire offspring (Schradin *et al.*, 2010b), the need of roamers to intrude is expected to be higher because they do not control a territory with females. They are thus forced to intrude other males'

territories and consequently they will share a bigger percentage of their home range with other individuals (both breeders or roamers) than breeders.

Hormones and behaviours

I analyzed the amount of testosterone and corticosterone levels in plasma of focal-breeders and -roamers that I tested for aggression patterns in the arena experiment. Usually in species with ARTs the dominant male reports the highest androgen level (Arlet et al., 2009; Rasmussen *et al.*, 2008). For striped mice the results of researches carried out to date did surprisingly show the opposite (Schradin *et al.*, 2009b). I thus had the same expectation: testosterone contents in plasma of breeders and roamers were expected to differ significantly, with a higher level shown by roamers. I expect no significant difference in corticosterone level of these two ARTs (Schradin *et al.*, 2009b). In such a case, it would be possible to associate the predicted aggressiveness of breeders and the predicted caution of roamers to tactic mechanisms (such as lighter roamers risking their life intruding heavy territorial males' areas), rather than strictly to behaviours.

2. Materials and methods

2.1 Study site and research period

My data was collected within groups of a wild population of striped mice in the Goegap Nature Reserve in Namaqualand (29° 41.56' S; 18° 1.60' E), Northern Cape Province, South Africa, at an elevation of 950 m. Data was collected during the breeding season 2009 from the end of August to the middle of December. The field work was carried out in the so called main field site (ca. 20 ha of size; Fig.1) situated in front of the research station and characterized by a dry riverbed, sandy earth and shrubs. The vegetation type and the environmental conditions for this site are the ones described as Succulent Karoo (Rösch, 2001) and no habitat manipulation has ever been carried out in this area.

2.2 Study species

The African striped mouse (*Rhabdomys pumilio*, Sparman 1784) is a diurnal muroid rodent species with a small to medium body size (adult body weight varies from 40-80 g). It is one of the most common mammals in southern Africa and is widely spread in all the rest of Africa. This is thought to be because of its ability to adapt to different kinds of habitats i.e., adaption takes place from moist grasslands to deserts (Schradin, 2005). Furthermore, striped mice present a very



Fig. 1: The main field site during Spring 2009. Shrubs and flowers that provide food for striped mice can be seen.

interesting and highly flexible social system, which varies depending on the type of habitat they inhabit (Schradin and Pillay, 2005). In the mesic (moderately moist) grassland of South Africa striped mice are solitary and associations between sexes are limited to mating (Schradin, 2005). In contrast, in the arid Succulent Karoo African striped mice

could be described as living in territorial groups with a solitary foraging behaviour, communal breeding and helpers at the nest (Schradin and Pillay, 2004b).

African striped mice have a breeding season which is rainfall dependent and which lasts about 3-4 months over spring. Mice usually start breeding when they are around 10-12 months old (Schradin and Pillay, 2005a) with females typically rearing around 2-3 litters (Schradin and Pillay, 2005) per season. In the Succulent Karoo food availability is provided all year-round, the highest pick is in spring (maximal flowering) and during the dry summer Succulents and other plants provide food resources, even though very little amount is present. Moreover, mice are also known to feed on seeds and insects (Schradin, 2005).

2.3 Field data

2.3.1 Trapping and marking of animals

Mice were trapped using metal live traps (26 x 9 x 9 cm, Sherman traps) and a bait mixture of bran flakes, sea salt and salad oil (Schradin and Pillay, 2004b; Schradin, 2006). Traps were placed in the shade under bushes (Fig. 2) just in front of nests. I performed trapping during mornings and afternoons thereby avoiding the hottest times of the day. I checked traps twice during the morning (beginning at sunrise, when mice are observed to start their daily activities) and once in the afternoon (right before sunset, when mice are returning to their nest



Fig. 2: Traps used during the trapping sessions. Traps were placed in front of the nest and checked every 30 minutes.

to sleep). Traps were left open for at least 30 min during each round. Trapped mice were sexed, weighted and individually marked using combinations of black, blond or red hair dye (Inecto Rapid, South Africa) to distinguish individuals during

subsequent nests and focal-animal observations. Furthermore, all trapped mice were permanently marked using ear tags (National band and tag Company, USA) carrying an ID number.

2.3.2 Nest observations

Nest observations are a useful method to establish group compositions as mice observed to feed together form part of the same group and individuals are easily recognizable thanks to their different color marking. Nest observations took place over the whole period of data collection. Mice were observed in front of their nest in the morning during the time they began to be active (at sunrise) and in the afternoon just before sunset, when they return to the nest.

Observations took place from a distance of 5-10 m, using 10 x 25 field binoculars or with naked eye.

Nest observations lasted for at least 30 minutes and a scale covered in peanut butter was put in front of the nest to bait mice.

2.3.3 Radio-tracking and focal-animal observations

I used radio-tracking to determine differences in home range sizes, overlapping territorial areas, travelling distances as well as location of sleeping sites of males following the three reproductive tactics. Home range sizes and subsequent overlapping areas have not been calculated for philopatric individuals: due to their relatively higher mortality rate it was too risky to keep the radio-collars on them long enough to provide home range data. The data revealing sleeping sites was used to describe the composition of groups, the reproductive tactic that different males were following and to know where to trap focal-individuals. Identified and trapped focal-individuals were thereafter fitted with radio-collars. Following the literature, the weight of a radio-collar did not exceed 10% of the total body weight (Schradin, 2005). In my case two different sizes of radio-collars were used: mice which weighed less than 45 g were provided with a small radio-collar (2.5 g), whereas mice which weighed more than 45 g were provided with a bigger radio-collar (4.5 g). Radio-tracking was performed using an AR 8000 wide range receiver and an H antenna.

To check for home ranges I recorded the GPS position of each focal-mouse during a control-tracking which was performed on a daily base. Control was alternated

between morning and afternoon, the presence/absence in the field site and the survival of mice were checked. Thereafter, I processed GPS data with different computer programs (Map Source and Range 6) to calculate short-term home range sizes based on data corresponding to the month in which I followed a certain individual (28 days). To create home range sizes a minimum of 13 and a maximum of 22 GPS points with 95% core and the Harmonic Mean Center (Dixon and Chapman, 1980) were used.

Radio-tracking was also used to conduct focal-animal observations, helping to track the focal-individual e.g., when hidden in the bushes. Focal-animal observations lasted 3 hrs and were performed during the time of their main activity: the morning observation was starting at sunrise and the afternoon observation was starting about 3 hours before sunset (Schradin and Pillay, 2004b). Mice were followed from a distance of 5-10 m. I performed focal-mice observations of 10 philopatrics, 10 breeders and 10 roamers following each individual twice (morning and afternoon). All the observations were performed directly, using 10 x 25 field binoculars when necessary. During observations, I recorded the behaviour of mice using a "one minute interval" (1/0 sampling) for a total amount of 180 minutes, in each interval it was possible to record more than one behaviour. Afterwards, I calculated the frequency of each event (event observed/total events outside the nest).

The following behaviours were recorded (Schradin, 2006; Table 3 in Appendix): aggressive interactions such as chasing other mice (one mouse running after another mouse and the other escaping), biting (one mouse touching another mouse with its teeth), fighting (two mice standing on their hind legs and touching each other with their forelegs), being chased (one mouse running away when another mouse chases him) and avoidance (mouse moves away if another mouse comes in its proximity); sociopositive interactions such as grooming other mice (one mouse touching the other mouse body with the nose and cleaning it), sitting in body contact (one mouse sitting next to another mouse and touching it), close proximity with other mice (one mouse sitting less than one mouse length from the next individual), in nest (mouse observed to be in the nest), or proximity (mouse observed to be in the same bush with another individual). Additionally, the following activities budgets have been recorded: feeding

(feeding on seeds, plants, flowers or insects), basking (mouse sitting in the sun, no movements), mating attempts (male trying to mount a female), resting (mouse sitting in the shade, no movements), sniffing (one mouse touching another mouse with its nose), in nest of another group (when being in another mice group's nest), in bush (when hidden in a shrub that is not its nest), auto grooming (cleaning itself) and travelling (mouse moving from bush to bush, without feeding or showing any social interactions). Travelled distances of each mouse were recorded with a GPS device and considered as activity budget as well.

2.3.4 Determination of ARTs

I determined the reproductive tactic of each male mouse combining data of trapping, radio-tracking and nest observations. I considered mice sleeping in the same nest as being part of one family and therefore as group-living mice (breeder males with their breeding females and their offspring). Striped mice are considered sexually mature at 4-6 weeks of age, when they reach a body weight of 30 g (Brooks, 1982), I thus considered as philopatrics male individuals reaching this body weight but still living with the natal group. The heaviest, oldest and stranger (not born in the same group) male of a family was considered to be the breeder. On the other hand, male mice sleeping alone were considered as to be roamers. Roamers are observed to change nests more often than group living mice, sometimes they would even share the nest for a couple of nights with a female, although this never happens in the presence of a breeding male (personal communication of Ed Yuen).

2.4 Presentation experiments: response of a threat

2.4.1 Individuals tested

To test for differences in aggressiveness response of ARTs, I performed presentation experiments using as focal-individuals 12 breeding and 7 roaming males trapped in the main field site.

I confronted these focal-animals with stimulus-animals. As stimulus-animals I used breeding males from the captive colony of the research station, with a weight similar or slightly bigger than the focal-mouse (from 0 to 8 g of difference). The difference of weight was matched so that stimulus-mice would

represent a real threat for focal-mice and therefore would trigger a responsive behaviour as dominance is commonly linked with body mass (Schradin and Lamprecht, 2002). Furthermore, I never confronted stimulus-mice with the same reproductive tactic twice, except in one occasion.

2.4.2 Experimental design

The presentation arena size was 100 x 80 x 65 cm and was built from 10 mm thick chipboard veneered white (Fig. 3 and Fig. 14 and 15 in Appendix; Schneider 2005). Between every experiment I cleaned the arena with liquid soap (Dettol, South Africa) in order to remove any possible remaining olfactory cues. Experimental tests were performed during mornings at the research station. The focal-mouse was provided with some sunflower seeds and kept in a small cage for 15 minutes, before being put in the presentation box. This was done to allow the mouse to calm down before starting the test. Then, both mice were put in the arena for 3 minutes (habituation phase) being separated from each other by a removable partition board placed in the middle of the box, to avoid mice from seeing each other before the experiment would start.

The experiment began once the separation was removed and lasted 15 minutes. If males were showing a high level of aggressive behaviour (repeated biting) with the risk of injuring the other mouse, the test was ended immediately. The time from the beginning of the experiment until the first aggressiveness showed by mice was measured as "latency time". The time-span run from the beginning of the experiment until its end was measured and represented the "total duration". In those cases where males did not show a too high aggressive behaviour level, the experiment lasted until the end of the 15 minutes. I recorded the following behaviours (Table 8 in Appendix) in terms of frequency (times of behaviour observed/total duration of the experiment in sec): activity budgets (grooming itself, sniffing: nose to nose or nose to another part of the body) sociopositive behaviours (grooming the other mouse, body contact: mice sat with a part of their body in contact, approaching: moving in the direction of the other individuals), aggressiveness (chasing: running in the direction of one individual and the other escaping, fighting: mice on their hind legs leaning one on the other, biting: teeth in contact with the body of the other individual), neutral

behaviours (no interaction at all) and submissive behaviours (sitting far away from the other mouse, avoidance: mouse moving away from the other). Avoidance, approaching and aggressiveness (initiated or experienced) were then used in my analysis.



Fig. 3: Arena box used to perform presentation experiments (picture taken by Ed Yuen).

2.5 Blood sampling and hormone assays

In a window of about one week before or one week after the presentation experiment, blood samples of the focal mice have been taken. This allowed the mice to recover from the possible physiological change that either blood sampling or aggressiveness testing might comport. Ed Yuen and Carsten Schradin carried out all the blood sampling.

Mice were trapped at nest during the morning. Traps were watched at close distance (10 m) and as soon as a male entered a trap he was anesthetized with diethyl ether. Blood samples were taken from the mouse tongue without any damage. ID number, body mass and breeding status were recorded. Blood samples have been kept at room temperature for 1.5 hrs and than centrifuged to obtain serum for the analysis. Blood serum aliquots where then refrigerated until further analysis in the EIA (Enzyme Immunoassy) laboratory of the Zoological Institute, University of Zurich.

To analyze corticosterone and testosterone contents, commercial kits from IBL (Immuno Biological Laboratories) Hamburg have been used. Basically, we followed the procedure described in the manual of the kits. We added one

standard vial with a concentration of 0.1 ng/ml and we did not use the vial the concentration of 16 ng/ml (to be used in case of very high concentration of hormone). Because of the limited blood sample that we can get from one individual in the field instead to put 25 μ l of standards, control and sample we put 20 μ l (Schradin *et al.*, 2009b). For each hormone assay one kit was necessary. Intra-assay variability for corticosterone (17.7%, $N=8$) and for testosterone (3.3%, $N=8$) were calculated using one pool for each.

2.6 Data processing and statistical analysis

All the data was processed using the software R 2.10.1 for statistical computing environment (2009).

I tested the data for normality using the Shapiro test for each variable and for its residuals. Moreover, I also checked graphically whether the data were normal distributed (Quantil-Quantil plot). Just three of my variables were found to be normal distributed (data from the field: events outside the nest, bush behaviour and feeding behaviour; data from the arena experiments: weight difference in tested pairs), but given my small sample size and that the P -values for normality in those cases were not highly significant I decided to test all my data with non-parametrical statistical tests. In the Results section, data are thus presented as median \pm 1st/3rd quartile due to their non-parametrical nature. I presented behavioural data as rate: for behavioural data coming from the focal-animal observations, rates are presented as “observed behaviour/total amount of events happening outside the nest per day”, and I abbreviate it as “observed behaviour/day” or “times/day”. As “day” the 6 hrs-period of main activity of mice is meant. For behavioural data coming from the arena experiment I presented rate as “observed behaviour/second”.

For behavioural data coming from the focal animal observations I used the Kruskal-Wallis test, and as a post hoc test I used the test suggested by the manual of the R software (named “kruskalmc.test”; Siegel and Castellan, 1988). Mating attempt, fighting and biting were not tested any further because they are very rare behaviours and I could observe them with a frequency that did not enable to produce valuable tests. Travelling and close proximity behaviour were not taken into account either, because not reliable (personal observation). Bush behaviour

and autogrooming were not included in the results because not relevant for my own scientific questions.

In the statistical analysis I decided to excluded 3 of the roamers that I followed (Table 2 in Appendix): one individual was excluded because of his non-scrotality during the breeding season, indicating that he was not sexually mature and as a consequence not useful for the intention of my study. Other two individuals were excluded because observed to live in a bachelor group (only males) for nearly one month and thus they never followed a “pure” roamer tactic. This group used to have just one breeder female, but when she died the males remained together, living as bachelor group. When they acquired a new breeder female the male that used to be the territorial one returned to be the breeder: consequently, none of these mice could be consider as roamer.

For the behavioural data coming from the arena experiments I used the Mann Whitney U test. In the statistical analysis I had to exclude the same 2 roamers for the reasons described above (part of a bachelor group, Table 7 in Appendix).

For GPS data I had first to enter them in the software MapSource (Copyright © 1996 – 2010 Garmin Ltd. or its subsidiaries) and then import the tables in Ranges6 v1.081 (Anatrack Ltd). I applied the same normality tests already described and I then tested for differences using the Mann Whitney U test.

Of the twenty individuals from which I had the data points, I had to exclude 7 of them, parts because of lack of GPS points or because not following the roamer tactic (bachelor group).

3 Results

3.1 Behavioural data from the focal-animal observations

3.1.1 Activity budgets differences

Daily travelled distance

Travelled distance was significantly different between the three ARTs (Kruskal-Wallis test, $H_2 = 7.1$, $P = 0.02$; Fig. 4a). Philopatrics traveled $954 \pm 800 / 1147$ m per day ($N=7$), breeders $1347 \pm 1146 / 1736$ m per day ($N=10$) and roamers $1152 \pm 944 / 1219.5$ m per day ($N=10$). I found a significant difference between philopatrics and breeders (Kruskal-Wallis post hoc test, $P < 0.05$), while no significant difference was found between the other groups.

Basking behaviour

No significant difference between the three ARTs was found in basking behaviour (Kruskal-Wallis test, $H_2 = 1.2$, $P = 0.6$, Fig. 4b). Philopatrics basked $10.9 \pm 6.7 / 16.52$ times/day ($N=10$), breeders $12.8 \pm 9.95 / 14.6$ times/day ($N=10$) and roamers $15 \pm 10.8 / 18.9$ times/day ($N=7$).

Resting behaviour

No significant difference was found in resting behaviour between the three ARTs (Kruskal-Wallis test, $H_2 = 1.85$, $P = 0.4$, Fig. 4c). Philopatrics rested $0.6 \pm 0 / 1.75$ times/day ($N= 10$), breeders $0.53 \pm 0.2 / 1.15$ times/day ($N= 10$) and roamers $1.18 \pm 0.72 / 2$ ($N=7$).

Feeding behaviour

No significant difference was found in feeding behaviour rate between the three ARTs (Kruskal-Wallis test, $H_2 = 1.36$, $P = 0.5$, Fig. 4d). Even though the result was not found to be statistically significant philopatrics are the ones that showed in average the highest feeding rate: they fed $17.7 \pm 13 / 23.2$ times/day, ($N= 10$). Breeders fed $13.4 \pm 6.9 / 18.7$ times/day ($N= 10$) and roamers $15 \pm 12.73 / 21.56$ times/day ($N= 7$).

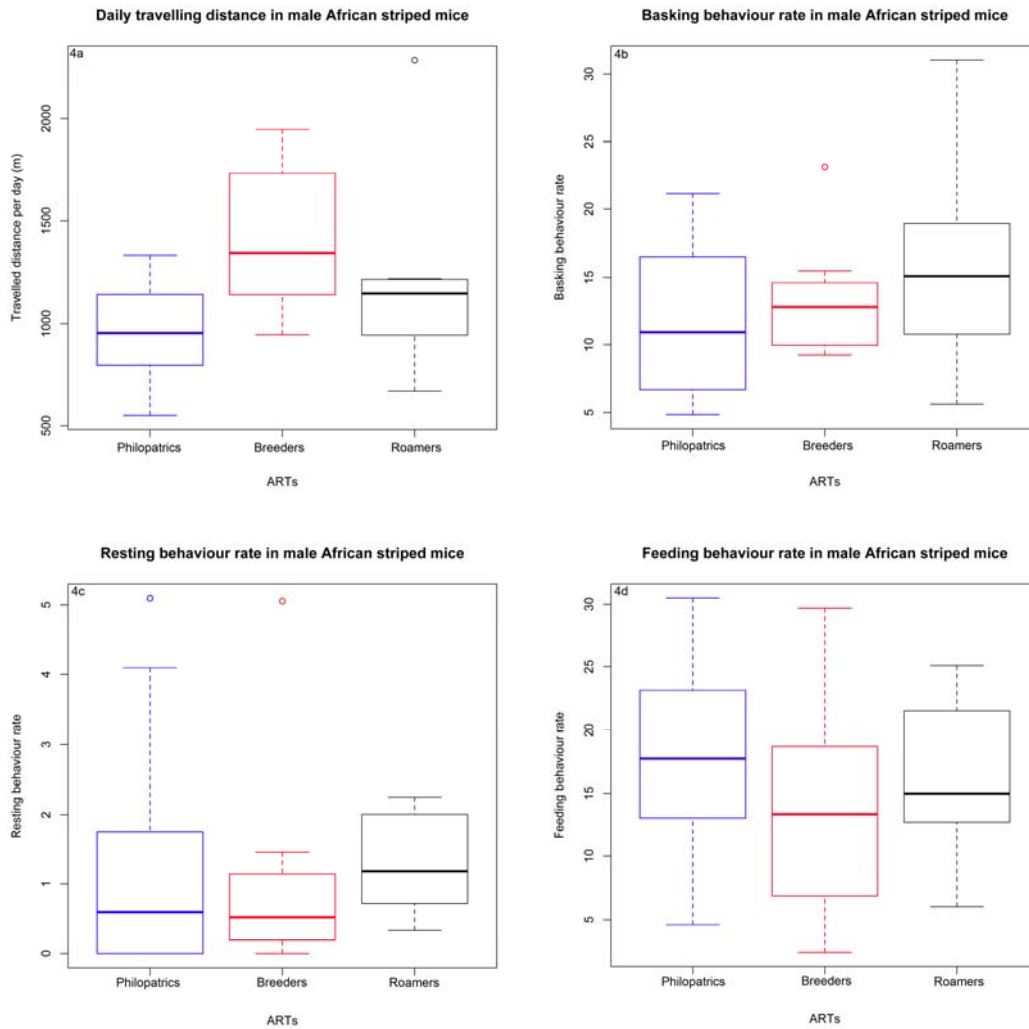


Figure 4: Differences in activity budgets of male striped mice following the three ARTs. ARTs= male alternative reproductive tactics. Median, 1st and 3rd quartile, extreme values and outliers are shown. **4a:** Difference in daily travelled distance between ARTs. Difference between groups was found significant ($P=0.03$) with a significant difference between philopatrics and breeders ($P<0.05$). **4b:** Difference in basking behaviour rate (observed basking/total events outside the nest) between ARTs. There was no significant difference between the three groups ($P=0.6$). **4c:** Difference in resting behaviour rate (observed resting/total events outside the nest) between ARTs. Extreme values and outliers are shown. No significant difference was found ($P=0.4$). **4d:** Difference in feeding behaviour rate (observed feeding/total events outside the nest) between ARTs. No significance was found ($P=0.5$).

3.1.2 Sociopositive behavioural differences

Grooming behaviour

Grooming behaviour differed significantly between the three ARTs (Kruskal-Wallis test, $H_2= 11.827$, $P= 0.002$, Fig. 5a) with philopatrics differing significantly from roamers (Kruskal-Wallis post hoc test, $P< 0.01$). Philopatrics groomed $0.54\pm 0.24/1.4$ times/day ($N=10$), breeders $0.2\pm 0/0.57$ times/day ($N= 10$) and roamers $0\pm 0/0$ times/day ($N= 7$).

Close proximity rate

The time that males of the three ARTs spent in close proximity with other mice differed significantly (Kruskal-Wallis test, $H_2= 11.9$, $P= 0.002$, Fig. 5b). Philopatrics stayed in close proximity with other mice $2\pm 1/3.25$ times/day ($N=10$), breeders $1\pm 0.37/2.75$ times/day, ($N= 10$) and roamers $0\pm 0/0$ times/day ($N= 7$). Significant difference between philopatrics versus roamers (Kruskal-Wallis post hoc test, $P< 0.01$) and breeders versus roamers (Kruskal-Wallis post hoc test, $P< 0.05$) were found.

Body contact rate

The body contact rate between the three ARTs has been found to be significantly different (Kruskal-Wallis test, $H_2= 9.2$, $P= 0.009$, Fig. 5c). Philopatrics and breeders did differ significantly from roamers (Kruskal-Wallis post hoc test, $P< 0.05$ for both the comparisons): breeders did show the highest body contact rate ($0.9\pm 0.34/1.62$ times/day, $N= 10$) followed by philopatrics ($0.7\pm 0.2/1$ times/day, $N= 10$) and roamers as lasts ($0\pm 0/0$ times/day, $N= 7$).

Nest events

A highly significant difference was found in the amount of nest events between the three ARTs (Kruskal-Wallis test, $H_2= 15$, $P= 0.0005$, Fig. 5d). Philopatrics and breeders differ significantly from roamers (Kruskal-Wallis post hoc test, $P< 0.01$ and $P< 0.05$). Philopatrics showed the highest nest behaviour rate ($9.3\pm 6.1/14$ times/day, $N= 10$) followed by breeders ($5.3\pm 1.86/7.1$ times/day, $N= 10$) and roamers as lasts ($0.2\pm 0/0.9$ times/day, $N= 7$).

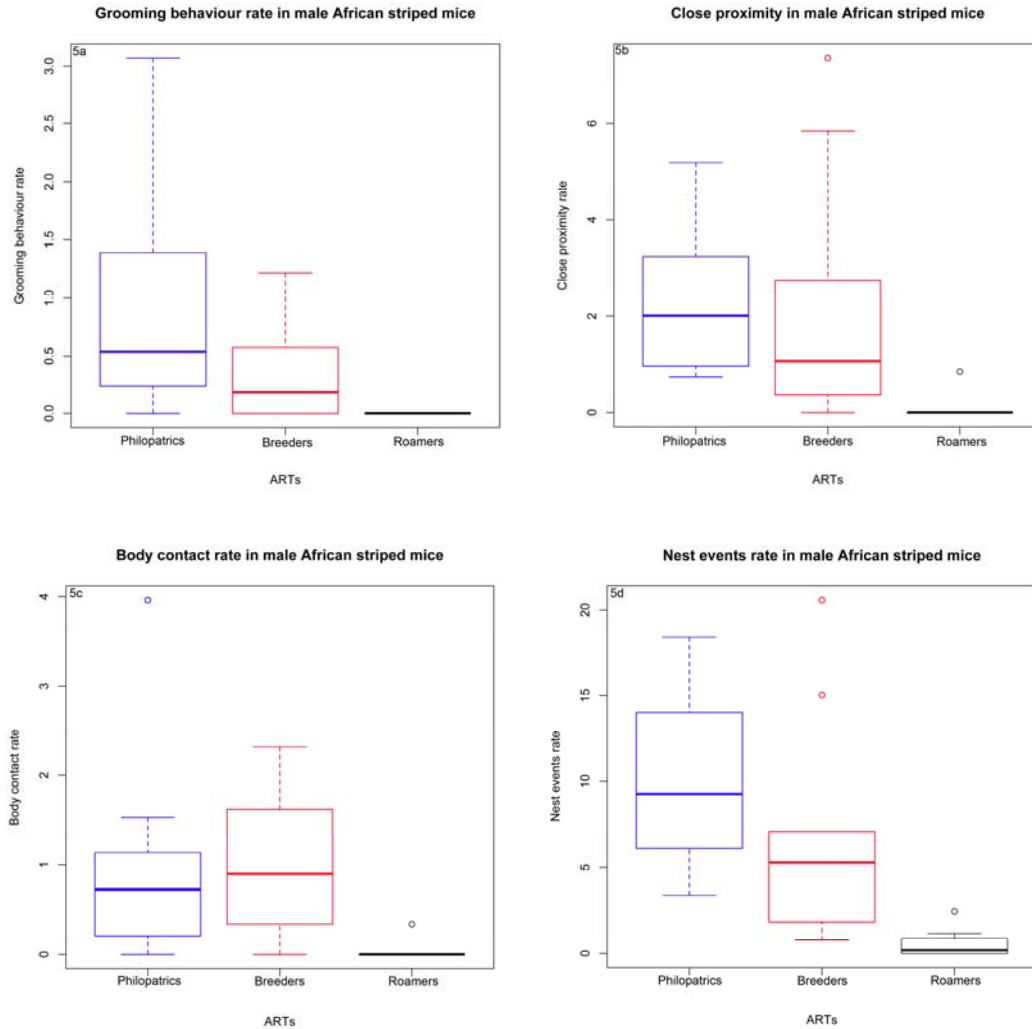


Fig. 5: Difference in sociopositive behaviours of male striped mice following the three ARTs. ARTs= male alternative reproductive tactics. Median, 1st and 3rd quartile, extreme values and outliers are shown. **5a:** Difference in grooming behaviour rate (observed grooming/total events outside the nest) between ARTs. A significant difference was found between the three groups ($P= 0.002$) with philopatrics differing significantly from roamers ($P< 0.01$). **5b:** Difference in close proximity rate (observed close proximity/total events outside the nest) between ARTs. A high significant difference between the three groups has been found ($P= 0.002$) with philopatrics and breeders differing significantly from roamers ($P< 0.01$ and $P< 0.05$). **5c:** Difference in body contact rate (body contact observed/total events outside the nest) between ARTs. A significant difference between the three groups has been found ($P= 0.009$), with philopatrics and breeders differing significantly from roamers ($P< 0.05$). **5d:** Difference in nest events rate (nest events observed/total events) between ARTs. A significant difference between groups was found ($P= 0.0005$): philopatrics and breeders differed significantly from roamers ($P< 0.01$ and $P< 0.05$).

3.1.3 Socionegative behavioural differences

Avoidance in case of encounters with other individuals

Difference in avoiding rate between the three ARTs was found to be highly significant (Kruskal-Wallis test, $H_2= 12.5$, $P= 0.002$, Fig. 6a). Philopatrics showed

no avoidance behaviour ($0\pm 0/0$ times/day, $N=10$) and did differ significantly from roamers (Kruskal Wallis post hoc test, $P < 0.05$), which showed avoidance $0.37\pm 0.12/0.44$ times/day, ($N=7$). Breeders avoided encountered individuals $0\pm 0/0$ times/day ($N=10$), showing thus no avoidance behaviour either.

Chasing rate

A highly significant difference in chasing rate has been found between the three ARTs (Kruskal-Wallis test, $H_2 = 12.4$, $P = 0.002$, Fig. 6b). Although from the graph we can observe a difference between medians among all the three groups, just philopatrics versus breeders have been found to differ significantly using the Kruskal-Wallis post hoc test ($P < 0.01$). The P value between chasing rate of breeders and roamers (Kruskal-Wallis post hoc test, $P = 0.06$) was found to be not significant. Breeders chased other individuals $0.37\pm 0.2/0.5$ times/day ($N = 10$) and are the ones that chased most, philopatrics the least ($0\pm 0/0$ times/day, $N = 10$). Roamers chased other mice $0\pm 0/0.09$ times/day ($N = 7$).

Aggression experienced rate

The rate of aggressions experienced differed significantly between the three ARTs (Kruskal-Wallis test, $H_2 = 8.2$, $P = 0.02$, Fig. 6c). Although this significant result, the P value of the post hoc test resulted slightly bigger than the conventional 0.05. Roamers ($0.6\pm 0.2/0.85$ aggressions experienced/day, $N = 7$) did experience more aggressions than breeders ($0\pm 0/0.19$ times/day, $N = 10$) and philopatrics ($0\pm 0/0.21$ times/day, $N = 10$; Kruskal-Wallis post hoc test, $P = 0.057$ and $P = 0.051$).

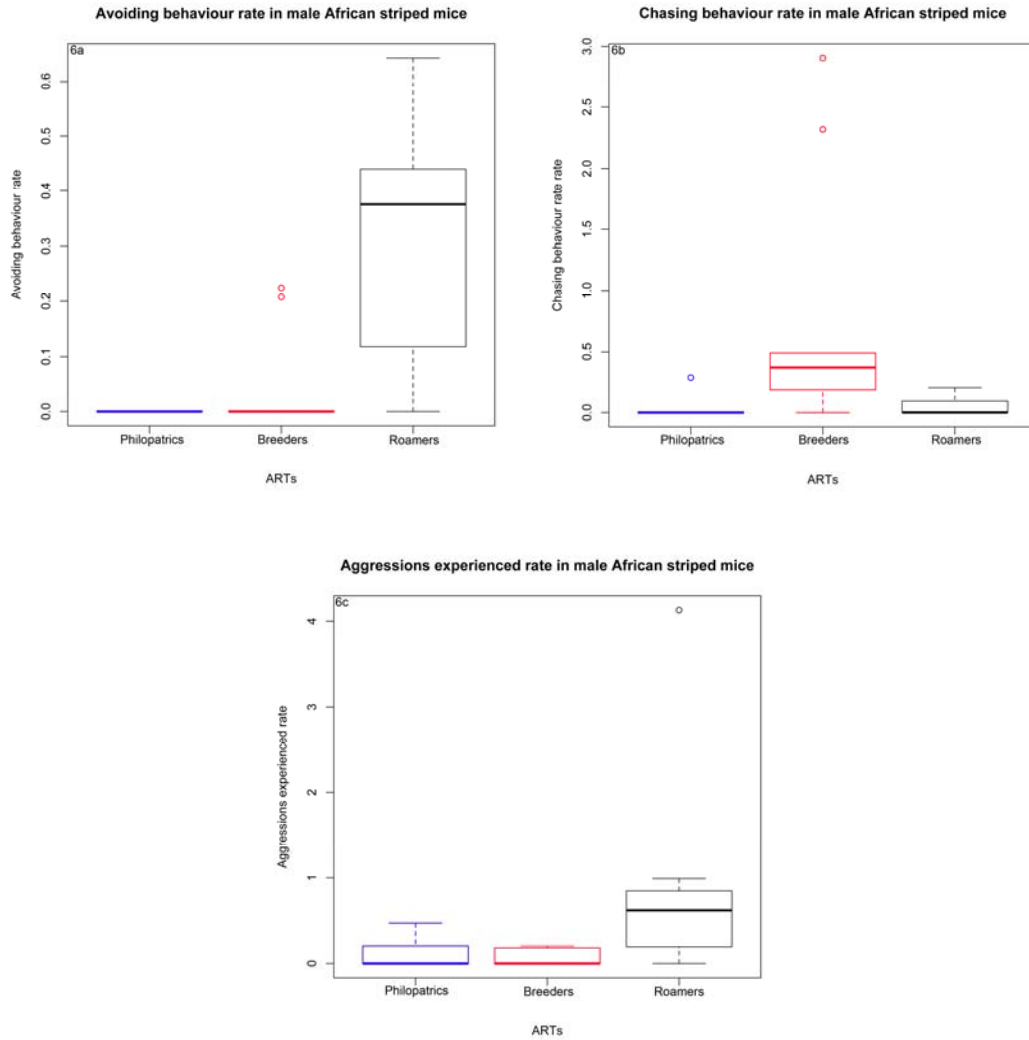


Fig. 6: Differences in socionegative behaviours in mice following the three ARTs. ARTs= male alternative reproductive tactics. Median, 1st and 3rd quartile, extreme values and outliers are shown. **6a:** Difference in avoiding rate (avoidance observed/total events outside the nest) between ARTs. There was significant difference between the three groups ($P= 0.002$) with philopatrics differing significantly from roamers ($P < 0.05$). **6b:** Difference in chasing behaviour rate (chasing observed/total events outside the nest) between ARTs. The three groups differ significantly ($P= 0.002$), with philopatrics showing a significantly lower chasing rate than breeders ($P < 0.01$) and breeders chasing more than roamers ($P= 0.06$). **6c:** Difference in aggressions experienced rate (aggressions experienced observed/total events outside the nest) between ARTs. The three groups differ significantly one to another ($P= 0.02$), with roamers experiencing more aggressions than philopatrics ($P= 0.051$) and breeders ($P= 0.057$).

3.2 Behavioural data from arena experiments

I tested the weight difference between each focal-individual and stimulus-individual pair in order control that all the data had continuity. No significant difference was found (Mann Whitney U test, $U= 26$, $P= 0.7$, breeders weight was

$5 \pm 2/7$ g, $N= 12$; roamers weight was $7 \pm 3/7$ g, $N= 5$), meaning that all the pairs that I tested had a similar difference in weight and thus generate comparable data.

3.2.1 Avoidance and approaching showed by roamers and breeders

No significant difference has been found in avoidance during contests between wild breeders-captive breeders pairs ($0.085 \pm 0/0.3$ times/sec, $N=12$) and with wild roamers-captive breeders pairs ($0.07 \pm 0/0.07$ times/sec, $N=5$; Mann Whitney U test, $U= 42.5$, $P= 0.2$, Fig. 7a).

Wild breeders showed a higher approaching rate then wild roamers when confronted with captive breeders (Mann Whitney U test, $U= 51$, $P= 0.03$, Fig. 7b); breeders approached the stimulus mouse $0.32 \pm 0.07/0.45$ times/sec ($N= 12$) whereas roamers $0 \pm 0/0.2$ times/sec ($N= 5$).

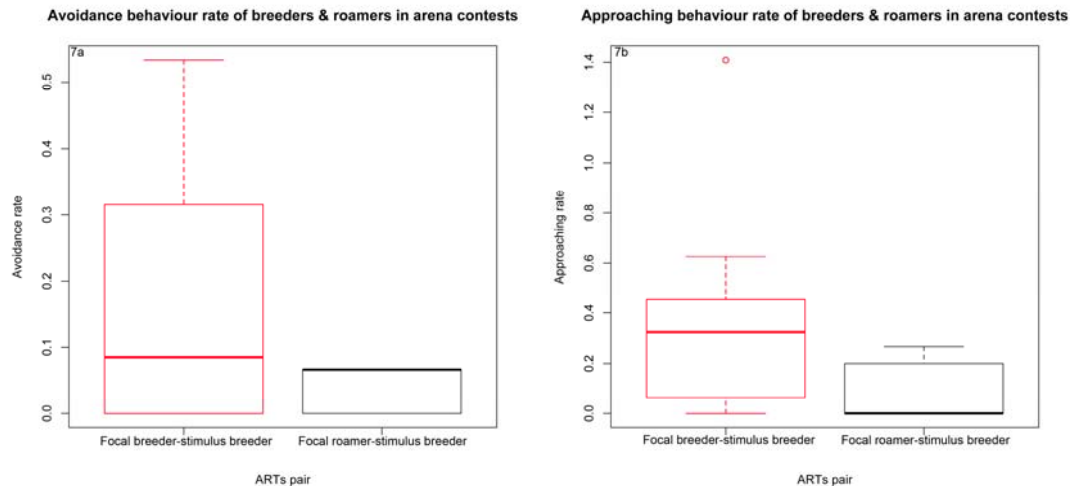


Fig. 7: Avoidance and approaching behaviour rate between wild breeders and roamer males towards captive breeders. ARTs pair= male alternative reproductive tactic pairs. Median, 1st and 3rd quartile, extreme values and outliers are shown. **7a:** Difference in avoidance rate (avoidance observed/duration of the experiment in sec) in arena contests ARTs pair. No significant difference has been found ($P= 0.2$). **7b:** Difference in approaching rate (observed approaching/duration of the experiment in sec) in arena contests between ARTs pairs. The two pair groups differ significantly ($P= 0.03$).

3.2.2 Aggressions initiated and aggressions experienced by focal roamers and breeders

Breeders ($0.023 \pm 0.016 / 0.036$ initiated aggressions/sec, $N = 12$) showed a significantly higher rate of initiated aggressions than wild roamers ($0 \pm 0 / 0$ times/sec, $N = 5$) in encounters with captive breeders (Mann Whitney U test, $U = 57$, $P = 0.005$, Fig. 8).

No significant difference was found between this two ARTs pair in aggressions experienced rate (Mann Whitney U test, $U = 26$, $P = 0.5$, Fig. 17 in Appendix). Just two individuals did experience aggressions in the arena experiments, one for each group (representing outliers data): wild breeders experienced aggressions with a rate of $0 \pm 0 / 0.0$ times/sec ($N = 12$) and wild roamers experienced aggressions with a rate of $0 \pm 0 / 0$ times/sec ($N = 5$).

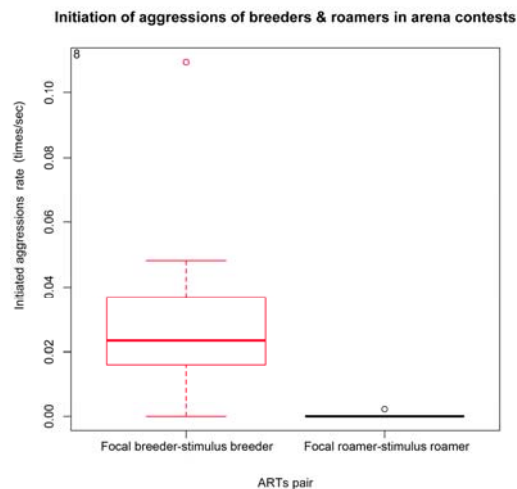


Fig. 8: Difference in initiation of aggressive behaviour (observed aggressions initiated/duration of the experiment) in arena contests between ARTs pairs in arena contests. ARTs pair= male alternative reproductive tactic pairs. Median, 1st and 3rd quartile, extreme values and outliers are shown. A significant difference was found between wild breeders and wild roamers ($P = 0.005$).

3.2.3 Latency time and duration of experiments

Latency time of encounters between breeders ($28.2 \pm 3.6 / 103.8$ s, $N = 12$) was significantly shorter than between wild roamers and captive breeders ($900 \pm 900 / 900$ s, $N = 5$; Mann Whitney U test, $U = 9$, $P = 0.03$, Fig. 9a). Another

significant result has been found between the total duration of the experiment in wild breeders-captive breeders encounters ($507 \pm 229.8/790.5$ s, $N= 12$) and wild roamers-captive breeders encounters ($900 \pm 900/900$ s, $N= 5$). The experiment lasted significantly less when testing the first pairs' group (Mann Whitney U test, $U= 5$, $P= 0.007$, Fig. 9b). Encounters with wild roamers did never need to be stopped before the expected time, while encounters with breeders needed to be stopped longer before the end of the experiment.

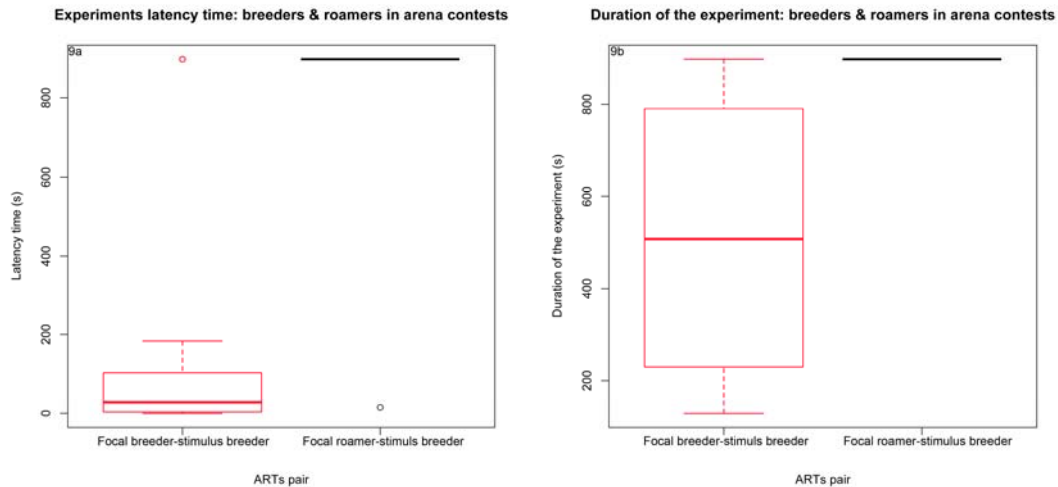


Fig. 9: Latency time and total duration of the experiment. ARTs pair= male alternative reproductive tactic pairs. Median, 1st and 3rd quartile, extreme values and outliers are shown. **9a:** Difference in latency time (sec) between male ARTs pair. Difference between the two group pairs was found significant ($P= 0.03$). **9b:** Difference in duration time (sec) of the experiment between ARTs pair. Difference in duration of the experiment has been found out to be significant ($P= 0.007$).

3.3 Home range sizes and overlapping areas

No significant difference was found between home range sizes of the two ARTs (Mann Whitney U test, $U= 25$, $P= 1$, Fig. 10a). Breeders showed a home range size of $0.25 \pm 0.22/0.31$ ha ($N= 7$) whereas roamers of $0.22 \pm 0.2/0.36$ ha ($N= 7$).

A significant difference was found in overlapping areas between breeders and roamers (Mann Whitney U test, $U= 28$, $P = 0.001$, Fig. 10b and Fig 13 in Appendix), where roamers ($25 \pm 11.8/28.9$ % of overlapped areas, $N= 7$) did have a bigger overlapping percentage of their home range areas shared with other mice than breeders ($17.8 \pm 14.8/24.3$ % of overlapped areas, $N= 7$).

Roamers did not show any significant difference between overlapping times with other roamers home ranges or breeders home ranges (Mann Whitney U test, $U=30.5$, $P=0.47$, Fig. 10c). They overlapped breeders home range sizes $2\pm 1/3$ times and $2\pm 0.5/2$ with other roamers home ranges ($N=7$).

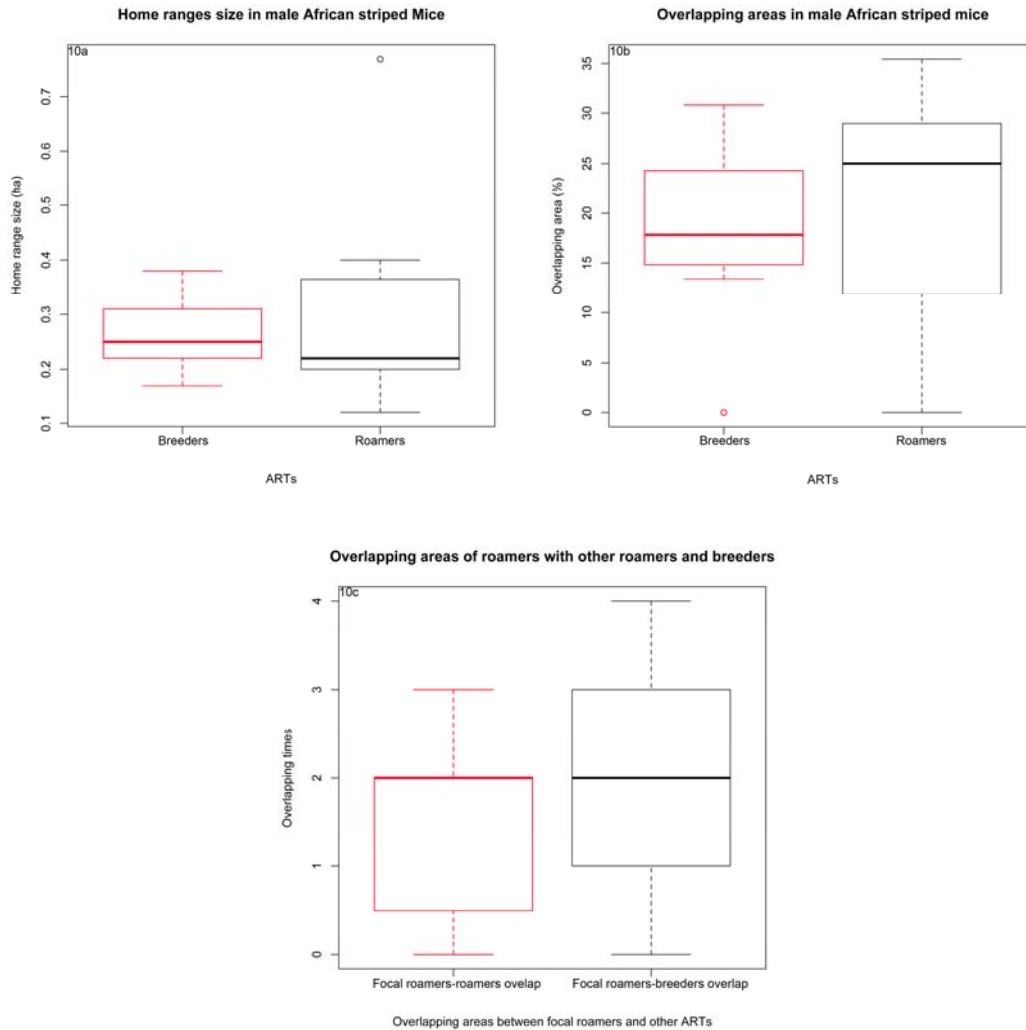


Fig. 10: Home ranges size and overlapping areas in African striped mice. ARTs = male alternative reproductive tactics. Median, 1st and 3rd quartile, extreme values and outliers are shown. **10a:** Difference in home range sizes (ha) between ARTs. No significant difference has been found ($P=1$). **10b:** Difference in overlapping areas (%) in ARTs. Difference was significant ($P=0.001$). **10c:** Overlapping areas of roamers with other roamers and breeders, showed as overlapping times. Median, 1st and 3rd quartile and extreme values are shown. No significant difference has been found ($P=0.47$).

3.4 Hormones and behaviours

No significant difference was found between roamers and breeders for plasma corticosterone levels (Mann Whitney U test, $U = 23$, $P = 0.5$, Fig. 11a). Roamers had $304.7 \pm 249.7/532.5$ ml/g and breeders had $289.25 \pm 177.3/416.4$ ml/g of plasma corticosterone.

No significant difference was found for plasma testosterone levels between breeders and roamers (Mann Whitney U test, $U = 42$, $P = 0.2$, Fig. 11b). Roamers had $0.54 \pm 0.5/0.62$ ml/g ($N = 5$) and breeders had $0.92 \pm 0.65/1.5$ ml/g ($N = 12$) of plasma testosterone.

Testosterone levels of individuals (roamers and breeders combined together) correlated significantly and negatively with their corticosterone level (Fig. 12a) with $r_s = -0.66$ and $P = 0.005$ (Spearman correlation test). There was a trend for a correlation between aggressions and testosterone ($r_s = 0.48$ and $P = 0.051$, Spearman correlation test, Fig. 12b).



Fig. 11: Levels of corticosterone and testosterone in plasma of African striped mice. ARTs = male alternative reproductive tactics. Median, 1st and 3rd quartile, extreme values and outliers are shown. **11a:** Corticosterone level (g/ml) in plasma of male African striped mice. No significant difference has been found ($P = 0.5$). **11b:** Testosterone level (g/ml) in plasma of male African striped mice. Difference between tactics was not significant ($P = 0.2$).

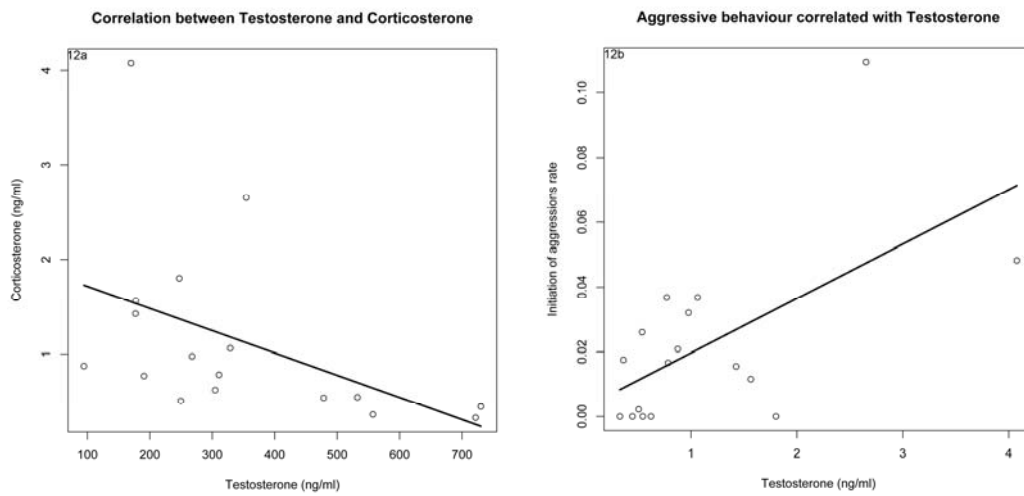


Fig. 12: Correlations using hormone levels in African striped mice. 12a: Correlation between testosterone and corticosterone of African striped mice. Levels are shown for roamers and breeders, $r_s = -0.66$ and $P = 0.005$. **12b:** Aggressive behaviour of African striped mice correlated with plasma testosterone level. Data are combined for roamers and breeders, $r_s = 0.45$ and $P = 0.067$. Initiation of aggression rate is calculated as aggression initiated observed/ total duration of the experiment (s).

4 Discussion

I found differences in activity budgets and social behaviours between the three ARTs in striped mice, which indicate trade-offs between following a particular tactic and investing time in determinate behaviours.

4.1 Behaviours

Philopatrics are the ones that showed significantly more sociopositive behaviours compared to the other two tactics. They showed higher levels of sociopositive interactions such as grooming, body contact and close proximity than roamers and breeders and they also showed the tendency to spend more time in the nest than the other mice. Even though they did always differ significantly from roamer individuals, it was not always the case with breeders. Breeders and philopatrics are both group living mice: that might be a reason why I did not find significant differences between them concerning sociopositive interactions. Philopatrics are thought not to reproduce in their own natal group especially due to avoidance of inbreeding depression (Pillay, 2002; Schradin and Pillay, 2005a) and reproductive suppression by the breeder. However, as shown in subordinate male meerkats as well (Young, 2007), philopatric striped mice might try to copulate with neighbouring females if they get the chance (Schradin *et al.*, 2010b). Reproduction is thus constrained but not impossible to happen. Philopatrics are young individuals and they might still need to stay near to their parents and their brothers due to different causes. In fact, despite the reproductive costs involved (Emlen, 1994), philopatry has been shown to comport several benefits such as thermoregulation and enhanced survival through group defense (Emlen, 1994; Schradin and Pillay, 2004b). Thus, the best tactic for young striped mice is probably to stay with their family group as philopatric individuals, enjoying benefits that the group life comports and try to gain body condition until the following breeding season and then finally switch tactic. As shown in Scantlebury *et al.* (2008) for Cape ground squirrels, the safety of the natal group increases the chances of philopatric individuals to reach the breeding season at an older stage and thus increases mating success as well. Accordingly, they might need to collaborate with other individuals of the family

in order to remain with them and be accepted, collaborating in building the nest, guard it and rear pups (Schradin and Pillay, 2004b).

Breeders also showed sociopositive behaviours towards mice of their group (either females or offspring). A likely reason for it is that they have to interact positively with their own offspring in order to provide parental care helping their harem in rearing pups. As shown in the study of Schradin and Pillay (2005c), providing parental care, breeder males increase the survival of their litter and thus they optimize their own fitness success. The same results have been shown from others studies with rodents (Cantoni and Brown, 1997; Wright and Brown, 2000). Showing paternal care can also help males to be accepted by females as advantageous mating partners as already suggested by Schradin and Pillay (2004b). At the same time it might be important for territorial breeders to show amicable behaviour directly towards their females, to gain access to them, reproduce and sire offspring (Schradin *et al.*, 2009b). Amicable behaviours have been suggested to aim to reproduction in other rodent species, the vlei rat, *Otomys irroratus* (Pillay, 1997) and the Algerian mouse from the South of France, *Mus spretus* (Cassaing and Isaac, 2007).

In spite of their significant sociopositive behaviour, breeders were also the tactic group with the highest aggressiveness level. They did chase individuals (in the field) and in particular strangers (in the artificial arena and in the field, personal observation). Besides, they did experience very little aggressions in the field. On the other hand, philopatric did not show a high level of aggressiveness, probably due to the fact that they do not have access to the control of a harem, they do not need to be aggressive in order to maintain the monopoly and mate. Breeders are actively defending their territory and their harem from strangers that could intrude in their area, trying to steal fertilization (Schradin *et al.*, 2010b) or kill the pups. Presentation experiments in the arena did show the same result. Encounters between couple of breeders were significantly shorter than encounters between breeders and roamers and did have a shorter latency time as well, indicating a faster aggressive reaction by breeders. I observed lots of aggressive encounters in the arena but I did not in the field. At the same time, I found a higher approaching behaviour showed by breeders in the artificial arena and a higher avoidance showed by roamers in the field. The results about

avoidance in the field are difficult to interpret, as I could not record if the encounters between mice were happening between relatives (coming from the same group) or stranger mice: I thus cannot say whether group living mice were avoiding relatives or strangers. Nevertheless, as roamers are not living group mice, the results suggest that they experienced encounter and then chose to run away. All these results combined together suggest that roamers actively tried to avoid encounters with breeders. Breeders are heavier than roamers (Schradin *et al.*, 2009b), thus in a fight roamers would be more likely injured. An encounter is therefore too risky and costly for roamers (females are thought to be aggressive towards strangers as well; Schradin, 2006).

Even if the arena contest is a good experimental design to understand several behavioural mechanisms, it still remains unnatural. In the field, roamers have the possibility to escape or prevent the encounter simply avoiding breeders: as I observed they rarely get involved in fights. In the arena escape is not possible: there is no room that allows roamers to run away. That is probably why in most cases I could observe roamers just standing in a corner, perhaps trying to send some kind of submissive signals to the breeder. Consequently in the arena, roamers did manage not to be attacked by breeders. Supporting my findings, avoidance and submissive behaviours towards territory owners are also shown by intruders of another rodent species (*Calomys musculus*) regarding mating tactic (Steinmann *et al.*, 2009).

A further observation coming from my experiments is that captive breeders are not as aggressive as wild breeders. Even though they have a female and they are the reproductive males, they are not pushed under the same stressful life as wild breeders are. They have no experience about intruders and territories, therefore they probably do not have any need to be much aggressive. That could be why I just observed once a wild breeder to be attacked by a captive one, even though captive breeders had in all cases a similar or a bigger weight than wild breeders. In the future it would be interesting to test wild breeders versus wild roamers in the arena, in order to see if roamers will still manage to avoid the attack or not.

4.2 Activity budgets and home ranges

I did not find significant differences in activity budgets such as feeding, resting and basking between the three male ARTs. Breeders are the ones that showed the highest travelling distance but this was due to movements inside their own territories (possibly patrolling the territory to check for intruders) rather than home range size. In fact, I did not find any difference between home range sizes of breeders and roamers. While not being significant, I found a trend for philopatrics to travel less and feed more than the others. In other words, this scenario sees philopatric investing their energies more in survival rather than reproduction (Schradin and Pillay, 2004b). They might try to increase the probability to reach the next year and start the new breeding season in good conditions (Scantlebury *et al.*, 2008), which will allow them to become roamers or breeders. Besides, they might still not know the territory very well and travelling further towards the boundaries of the group territory could imply too dangerous encounters with older and stranger mice (most of the aggressive interaction have been observed there, Schradin and Pillay, 2004b). Furthermore, the risk of dying because of predation might increase significantly when offspring travel outside their natal territory, as shown for red squirrels (*Tamiasciurus hudsonicus*) in the study of Larsen and Boutin (1994). These might be reasons limiting their travelling distance. Thus, for philopatrics survival plays the most important role and probably they are not influenced by environmental conditions (such as food availability) in the same way breeders and roamers are, given that their chance to reproduce is low: in all cases for them the most important activity is feeding, whether the availability is high or not. Would be interesting to try to test this suggestion in further studies, trying to understand in which way for instance variation in food availability influences behaviours of the three ARTs.

Oppositely breeders and roamers do reproduce and environmental condition might play a more important role. For example during the breeding season 2009, differently from the years 2003-2008 (Schradin *et al.*, 2009b), home range sizes of breeders and roamers did not differ significantly and seems to be smaller than the previous years for both tactics. Besides, no significant difference was found

between tactics in feeding, basking and resting. It might be important to repeat focal-animal observations in order to get a bigger sample size.

During the breeding season 2009 we had several days with rainfall (personal observation) and thus a high food amount and flowers were present all over the field site. The overall good food presence might have led to smaller home ranges (Ostfeld, 1990). Another plausible explanation for the smaller size of home ranges could be the high population density that we had during the breeding season 2009 (Schradin *et al.*, 2010a). Furthermore, the high intruder pressure by neighbouring males, which can be likely at a high population density, has been negatively correlated with home range sizes in male bushbuck, *Tragelaphus scriptus* (Wronski and Plath, 2006). However, this still does not explain why I did not find significant differences between home range sizes of roamers and breeders. Probably it would be better to augment the GPS points per day and per individual used to build home ranges in order to get a more precise view.

Roamers did show significantly bigger overlapping areas than breeders: this suggests that roamers actively intrude in other mice' territory whereas breeders do it in a significantly smaller way. They thus enter in breeders' territories or they overlap ranging span of other roamers. I did not find any significant preference from roamers to intrude either in roamers or breeders home ranges, however, I can infer a trend to intrude more in breeders territory and I predict a significant result if the experiment will be repeated with a bigger sample size. Roamers have to intrude in breeders territories because this is the only place where they could find females and try to mate (Schradin and Pillay 2004b). The roamer's tactic is therefore a very complex one and seems to require a high equilibrium between intrude in territories of breeder males (reproduction) and at the same time trying to avoid risky encounter with them (survival).

Breeders invested the same amount of time than the other ARTs in activity budgets. Due to their high aggressiveness and dominance they have to be in good body condition (Schradin and Lamprecht, 2002) and thus activity budgets that provide energy such as feeding, resting and basking are important for them (Scantlebury *et al.*, 2008). Moreover, during their daily activity they did travel more than the others, possibly because they had to cover and travel around all

their territories patrolling (Schradin 2006) in order to defend their females, which usually do not forage in groups (Schradin and Pillay, 2004b) and to provide territorial defense (Schradin, 2004). Besides, they returned to the nest often during the day, probably in order to defend offspring from infanticide as occurs in other animal species as well (Kiyota and Okamura, 2005). They thus invest in reproduction and defense of their own territory, most likely forced by the high intrusive rate of roamers and neighbouring males, confirmed by the study of Schradin *et al.* (2010b).

4.3 Testosterone and corticosterone plasma levels

No significant difference was found between breeders and roamers in their hormones levels (analysis of further data collected in the breeding season 2009 showed the same results, personal communication of Carsten Schradin). There was a negative correlation between testosterone and corticosterone of individuals and the trend showed testosterone to be linked more closely with aggressiveness of mice than with tactic, although we do not have to forget that this correlation resulted to be non-significant. Thus, I did not find any evidence that suggest androgen levels to play a role in the differentiation of ARTs in the African stripe mouse regarding aggressiveness. This is in conflict with previous results (Schradin *et al.*, 2009b) where breeders have been found to present lower testosterone plasma level than roamers. This contradictory result suggests that hormone levels in striped mice could be regulated and influenced by very complex mechanisms. The energy allocation in one mating tactic rather than another could presumably play an important role such as already mentioned in the Introduction section for gray-cheeked mangabeye, teleost fishes and African elephants (Arlet *et al.*, 2009; Arterbery *et al.*, 2010; Rasmussen *et al.*, 2008) but other factors such as changes in the environment, the amount of food available and the population density might influence hormones levels of mice. Indeed, all this factors are leading to competition for food, females and territories and might thus influence physiology (hormone levels) and behaviours. However, studies as the one of Baird and Hews (2007) with male collared lizards (*Crotaphytus collaris*) did also not find significant differences in androgen levels between ARTs. Besides, we do not have to forget that striped mice in the Succulent Karoo

have to face a very complex habitat, a semi desert, which can present very extreme and quick environmental changes (Schradin, 2008) and furthermore that hormonal levels might be affected by non-hormonal factors such as body weight and age (Carlson *et al.*, 2004; Carlson *et al.*, 2005). As already pointed in other studies (Carlson *et al.*, 2004; Carlson *et al.*, 2005; Schradin and Anzenberger 1999) trying to understand if and how hormones are underlying behaviours, and in this case ARTs, is thus very difficult. Further investigations are therefore needed in this topic, which could lead to new interesting and surprisingly findings about different mechanisms, which combined together control androgen levels in striped mice.

5 Conclusion

I found a general confirmation of my hypotheses: male ARTs in African striped mice differ from each other behaviourally.

Philopatric individuals seem to mainly invest in their survival; they are probably benefiting from living with their family group, delaying onset of breeding to the next breeding season, when they will have higher probability for high reproductive success by becoming a breeder. They might have to show high sociopositive behaviours in order to be accepted in the group and at the same time they invest their time in gaining energy (feeding, travelling less, etc.).

Roamers are in a middle stage, they are big enough to compete for reproduction but given that they are still lighter than breeder males their only possibility to mate is to leave the group, live as solitary and intrude in breeders' territory trying to steal copulations. They are thus probably subjected to a trade-off between gain matings (intruding in territories) and stay alive, showing avoidance or submissive behaviours to avoid risky encounters with breeders. They also fight to become breeding males (and achieve an increased mating success) in the case a breeding position becomes vacant, therefore activity budgets aiming to increase their body condition (such as feeding) might be important for them.

Breeders are the heaviest males and usually the oldest ones, they have thus better body conditions. They keep the monopoly of a female harem and as a result their reproduction is better assured but just as long as they can maintain this monopoly. To do so, they show amicable behaviour towards their females and offspring probably in order to gain access to mating partners and increasing the survival of their own pups. Besides, they are aggressive towards strangers, especially neighbouring males and roamers, which could sneak fertilizations. They defend their territory travelling inside of it and retouring to the nest often during the day probably to defend pups. Furthermore, they might need to maintain their good body conditions showing considerable feeding behaviour to support aggressive encounters and optimize their fitness.

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8 Appendix

8.1 Personal note

During my experience in the field, I did some thinking and observations that might be useful for future similar projects.

First of all, I think it would be really interesting to follow the same focal-mouse more than twice a day. This could lead to important data about spatial utilization of mice i.e., if they have some specific patterns regarding their daily movements, especially when researching on patrolling behaviour of breeders. I observed some breeder males to visit and roaming always around the same areas, and sometimes even repeating the same pathway (observations coming from focal-animal observations and daily radio-tracking). I also noticed that some breeders were visiting same areas especially when a roamer was present in that specific zone. Is it possible that breeders know very well where roamers are inhabiting, and thus are more alert and active on those areas? My sample size about focal-animals was too little (just 2 GPS tracks per individual) to lead to a powerful analysis. As I already suggested in the Conclusion section of my thesis, augmenting the sample size of the mice followed will lead to more data about the overlapping areas of mice. I predict roamers to actively intrude in breeders territory either than roamers one.

I kindly recommend avoiding performing behavioural observations in very hot days (up to 35°C) because mice will just stay hidden in the bushes.

As last, as far as possible, it will be better to choose not to follow mice inhabiting the long grass areas present in Goegap, because observations through the long grass are almost impossible.

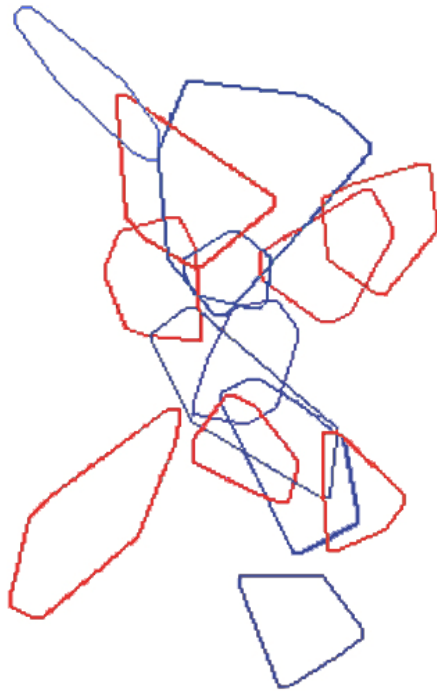
8.2 Focal-animal observations

Table 2: Individuals of focal-animals observations (breeding season 2009)

Individual ID	Date of 1 st observation	ART	Remarks
4553	6-Oct-2009	Roamer	
4643	3-Oct-2009	Roamer	
4823	21-Sep-2009	Roamer	
4681	1-Oct-2009	Roamer	
4811	24-Oct-2009	Roamer	Bachelor group, excluded from analysis
4751	22-Oct-2009	Roamer	Bachelor group, excluded from analysis
4711	29-Sep-2009	Roamer	Not scrotal, excluded from analysis
4657	26-Sep-2009	Roamer	
4743	24-Sep-2009	Roamer	
6225	19-Oct-2009	Roamer	
4803	3-Sep-2009	Breeder	
4825	20-Aug-2009	Breeder	
4815	1-Sep-2009	Breeder	
4387	27-Aug-2009	Breeder	
4611	24-Aug-2009	Breeder	
4501	29-Aug-2009	Breeder	
4391	18-Sep-2009	Breeder	
4913	12-Sep-2009	Breeder	
4759	7-Sep-2009	Breeder	
4395	25-Sep-2009	Breeder	
5007	2-Nov-2009	Philopatric	
4925	25-Oct-2009	Philopatric	
5001	5-Nov-2009	Philopatric	
5003	3-Nov-2009	Philopatric	
4999	16-Nov-2009	Philopatric	
5089	21-Nov-2009	Philopatric	
5177	19-Nov-2009	Philopatric	
5047	13-Nov-2009	Philopatric	
5163	16-Nov-2009	Philopatric	
5057	6-Nov-2009	Philopatric	

Table 3: List of recorded behaviours

Category	Behaviour	Description
Socionegative interactions	Chasing	One mouse running after another mouse and the other escaping
	Biting	One mouse touching another mouse with its teeth
	Fighting	Two mice standing on their hind legs and touching each other with their forelegs
	Being chased	One mouse running away when another mouse chases him
	Avoidance	One mouse moves away if another mouse comes in its proximity
Sociopositive interactions	Grooming	One mouse touching the other mouse's body with the nose and cleaning it
	Body contact	One mouse sitting next to another mouse and touching it
	Close proximity	One mouse sitting less than one mouse length from the next individual
	In nest	Mouse observed to be in the nest
	Proximity	Mouse observed to be in the same bush with another individual
Activity budgets	Feeding	Feeding on seeds, plants, flowers or insects
	Basking	Mouse sitting in the sun, no movements
	Mating attempts	Male trying to mount a female
	Resting	Mouse sitting in the shade, no movements
	Sniffing	One mouse touching another mouse with its nose
	In nest form another group	When being in another group's nest
	In bush	When hidden in a shrub that was not its nest
	Auto grooming	Cleaning itself
Travelling	Mouse moving from bush to bush, without feeding or showing any social interactions	



Breeders ID	Roamers ID
4387	4553
4391	4643
4611	4657
4759	4681
4803	4743
4815	4823
4913	6225

Fig. 13: Home ranges overlap of roamers and breeders in the Succulent Karoo of South Africa. Roamers (blue lines) did have significant bigger overlapping areas than breeders (red lines), although no significant difference has been found between home ranges sizes.

Table 4: P-values summary of activity budgets

Activity budget	P-Value (Kruskal Wallis)	P-Value (Kruskal-Wallis post hoc test)		
		Breeders-Roamers	Breeders-Philopatrics	Philopatrics-Roamers
Daily traveled distance	0.02*	>0.05	< 0.05 *	> 0.05
Basking behaviour	0.6	-	-	-
Resting behaviour	0.4	-	-	-
Feeding behaviour	0.5	-	-	-

Note: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 5: P-values summary of sociopositive behaviours

Sociopositive behaviour	P-Value (Kruskal Wallis)	P-Value (Kruskal-Wallis post hoc test)		
		Breeders-Roamers	Breeders-Philopatrics	Philopatrics-Roamers
Grooming behaviour	0.002*	>0.05	>0.05	<0.01**
Close proximity rate	0.002*	<0.05*	>0.05	<0.01**
Body contact rate	0.009*	<0.05*	>0.05	<0.05*
Nest events	0.0005*	<0.05*	>0.05	<0.01**

Note: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 6: P-values summary of socionegative behaviours

Socionegative behaviour	P-Value (Kruskal Wallis)	P-Value (Kruskal-Wallis post hoc test)		
		Breeders-Roamers	Breeders-Philopatrics	Philopatrics-Roamers
Avoiding rate	0.002**	>0.05	>0.05	< 0.05*
Chasing rate	0.002**	0.06	< 0.01**	>0.05
Aggressions experienced rate	0.02**	0.057	>0.05	0.051

Note: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

8.3 Presentation experiments

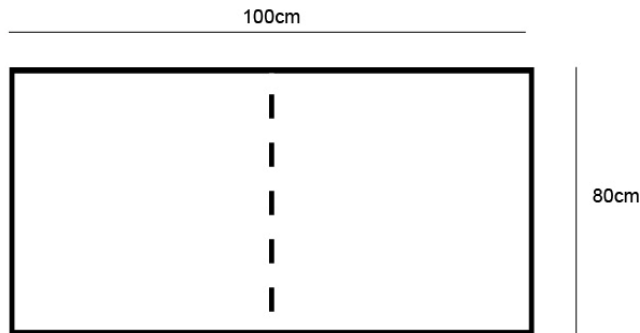


Fig.14: Over view of the arena box. The slashed line represents the removable partition

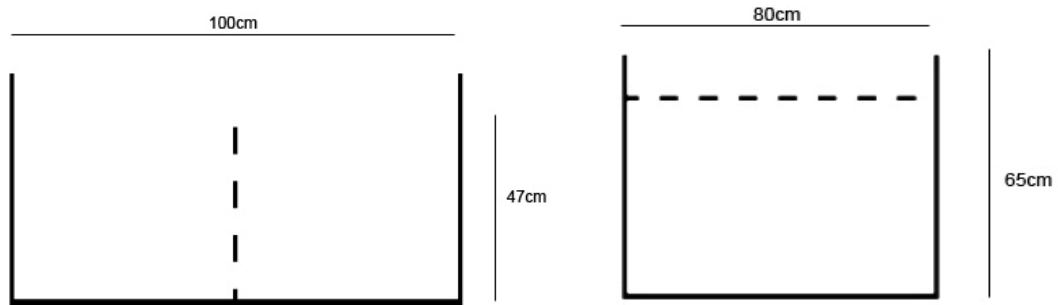


Fig. 15: Side view (left picture) and side view from the front (right picture) of the arena box. Dashed lines represent the removable partition.

Table 7: Individuals of the presentation experiments (breeding season 2009)

Individual ID	Date of experiments	ART	Remarks
4429	5-Oct-09	Breeder	
4501	11-Sep-09	Breeder	
4391	19-Sep-09	Breeder	
4769	22-Sep-09	Breeder	
4395	27-Sep-09	Breeder	
4815	2-Oct-09	Breeder	
4913	3-Oct-09	Breeder	
4759	3-Oct-09	Breeder	
4387	20-Oct-09	Breeder	
4611	23-Oct-09	Breeder	
4803	27-Oct-09	Breeder	No interactions during the test
4825	14-Oct-09	Breeder	
4811	14-Oct-09	Roamer	Bachelor group, excluded from analysis
4553	22-Sep-09	Roamer	No interactions during the test
4751	14-Oct-09	Roamer	Bachelor group, excluded from analysis
4743	8-Nov-13	Roamer	No interactions during the test
4643	10-Nov-13	Roamer	
5059	31-Nov-09	Roamer	No interactions during the test
6225	15-Nov-13	Roamer	
4711	14-Oct-09	Roamer	Not scrotal, excluded form analysis

Table 8: List of recorded behaviours

Category	Behaviour	Description
Sociopositive interactions	Grooming	One mouse touching the other mouse body with the nose and cleaning it
	Body contact	One mouse sitting next to another mouse and touching it
	Approaching	Moving in the direction of the other individual
Socionegative interactions (aggressiveness)	Chasing	One mouse running after another mouse and the other escaping
	Fighting	Mice standing on their hind legs and touching each other with their forelegs
Others	Auto grooming	Cleaning itself
	Sniffing	One mouse touching another mouse with its nose
	Neutral behaviours	No interactions at all
	Submissive behaviours	One mouse sitting far away from the other mouse

Table 9: P-values summary of the arena experiments

From the arena experiment	Median		P-Value (Mann Whitney U)
	Breeders	Roamers	
Avoiding rate	0.085	0.07	0.2
Approaching rate	0.3	0	0.03*
Aggressions initiated	1.4	0	0.005**
Aggressions experienced	0	0	0.5
Latency time (s)	28.2	900	0.03*
Duration of the experiment (s)	512.9	900	0.007**

Note: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

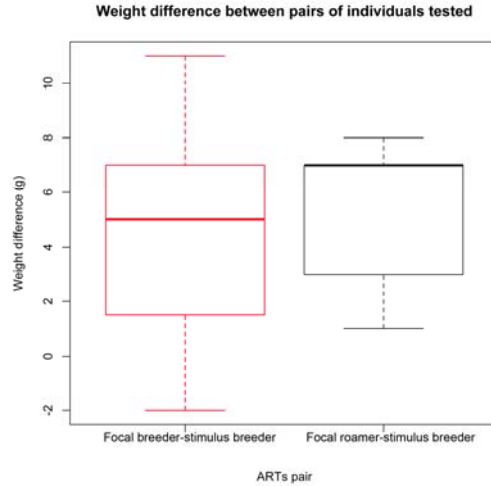


Fig. 16: Weight difference between pairs of individuals tested in presentation experiments. ARTs= male alternative reproductive tactics. Median, 1st and 3rd quartile, extreme values and outliers are shown. No significant difference has been found between the two pairs group ($P= 0.7$).

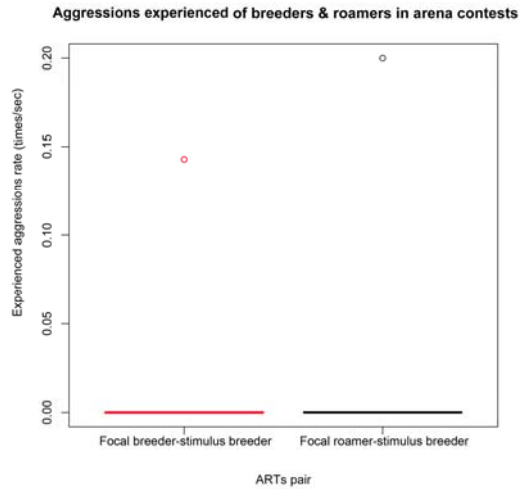


Fig. 17: Difference in experienced aggressions (observed aggressive behaviour experienced/duration of the experiment) between ARTs pairs in arena contests. ARTs pair= male alternative reproductive tactic pairs. Median, 1st and 3rd quartile and outliers are shown. No significant difference has been found ($P= 0.5$).