



## Differences in social behaviour between group-living and solitary African striped mice, *Rhabdomys pumilio*

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Little is known about the extent to which solitary individuals differ in their social behaviour from group-living ones within the same species. Using the socially flexible African striped mouse, we tested through a series of dyadic encounters in a neutral arena whether group-living mice that later became solitary differed from their philopatric conspecifics. We compared philopatric and solitary mice both before and after dispersal. We predicted striped mice that became solitary would be more aggressive, less amicable and more investigative than individuals that remained group living, and would change their social behaviour after changing from group to solitary living in the same direction (becoming more aggressive, etc.). Dyadic encounters were conducted on 42 group-living individuals and 13 individuals that were first group living and later became solitary. Striped mice that became solitary showed higher levels of aggression and social investigation than their conspecifics that remained group living, differences that were already present before individuals dispersed. Dispersing striped mice showed a negative correlation between amicability and aggression towards opposite-sex individuals, which could be linked to sexual motivation. A second behavioural syndrome in the form of a positive correlation between aggression and social investigation towards same-sex individuals might have indicated that dispersing striped mice were ready to defend their own territory. Our study provides evidence that within the same population and at the same time, individuals that disperse and become solitary differ behaviourally from their group-living conspecifics even before dispersal, and further change their behaviour after dispersal in an evolutionarily adaptive way.

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Animals display a great diversity of social organization, ranging from solitary species to species that form complex societies (Wilson 2000). Solitary and group-living species display distinct social organizations, which are believed to arise as a consequence of differences in social behaviours (Blumstein & Armitage 1998; Lacey 2000). Individuals of solitary species live alone and, apart from when mating, offspring rearing and defending their territory, rarely interact with conspecifics (Lacey & Wierczorek 2003). In contrast, individuals of group-living species remain together for prolonged periods of time, interacting frequently and extensively with one another to a much greater degree than with conspecifics of other groups (Wilson 2000), for example when sharing feeding and nesting sites (Blumstein & Armitage 1998; Solomon 2003). As a consequence, the variety of social behaviours displayed by group-living species exceeds that of solitary species. In addition, social

bonding between adult individuals characterizes group-living birds and mammals, but is usually restricted to mother–offspring bonding in solitary species (Leckman et al. 2005). To understand the evolution of social behaviour it is important to study inter-specific variation in social organization. However, social and solitary species differ in many aspects of ecology, life history traits; and behaviour; thus it is difficult to study a single factor (such as social behaviour) without the problem of confounding effects. To understand how sociality influences social behaviour it would therefore be advantageous to study the behaviour of individuals belonging to a single species that can be either solitary or group living in the same environment.

Socially flexible species give us a unique opportunity to test the behavioural differences between solitary and group-living individuals within the same species and population. In species that have a socially flexible organization, both group- and solitary-living individuals can occur within the same population, at the same time and in the same environment (McGuire & Getz 1998; Schradin et al. 2012). In changing environmental conditions, individuals of socially flexible species are able to switch between alternative social tactics (Oliveira et al. 2008; Schradin et al. 2009a, 2012). By using

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individuals of socially flexible species, we can thus investigate the behavioural differences between solitary and group-living individuals using a single species, which allows us to avoid confounding environmental and phylogenetic factors in interspecies comparisons. Offspring of socially flexible species are typically raised in family groups and have the choice to remain group living when reaching adulthood, for example becoming a philopatric helper, or to disperse and follow a solitary breeding tactic. An individual's dispersal from its natal site to a site where it may breed is one of its most important life history events (Bekoff 1977). The success of natal dispersal might depend on several factors, such as the availability and quality of resources (Emlen 1982; Pruett-Jones & Lewis 1990; Koenig et al. 1992), and the behavioural phenotype of the disperser (Hoset et al. 2011). Several studies have shown that dispersing individuals differ from nondispersers in their behavioural traits (Svendsen 1974; Brandt 1992; Bowler & Benton 2005), particularly in their social behaviours (Koolhaas et al. 1999; Sih et al. 2004a; Rodriguez-Prieto et al. 2011). For example, studies of voles and lemmings have revealed dispersal to be linked with increased aggression, decreased sociability and increased exploration (Myers & Krebs 1971; Ims 1990; Hoset et al. 2011). Furthermore, reactive (i.e. individuals that have a conservation or withdrawal stress response) and less aggressive individuals tend to be more adaptable and show greater behavioural flexibility to new situations than proactive (i.e. individuals that have a fight or flight stress response) and more aggressive individuals (Koolhaas et al. 1999; Sih et al. 2004a). As a consequence, proactive individuals are thought to be more likely to disperse (Rodriguez-Prieto et al. 2011). While there are good indications that dispersing individuals differ behaviourally from nondispersing individuals, not much is known about the extent to which solitary individuals differ behaviourally from group-living ones within the same species. If such differences exist, it would be important to know whether they are a consequence of the new environmental conditions experienced by dispersers or whether they occur independently of the dispersal event and they are thus a result of individuals' different personalities (Hoset et al. 2011).

Personality, defined as individual consistencies in behavioural traits (such as aggression, exploration and sociability) over time and across context, is a phenomenon observed in several species from unicellular organisms to higher vertebrates (Dall et al. 2004; Reale et al. 2007; Bell et al. 2009). Different personality traits are often correlated with each other, in behavioural syndromes (Clark & Ehlinger 1987; Sih et al. 2004b; Bell 2007). For example, aggressive individuals are often also bolder (Reale et al. 2007). Specific personalities, for example high boldness, might underlie good dispersal abilities that lead to lower costs of dispersal and might facilitate settlement in a new environment compared to individuals with a different personality, for example very shy individuals (Clobert et al. 2009). Several studies have shown a link between dispersal tendencies and different behaviours, such as aggression, exploration and sociability, in what is known as a dispersal syndrome (Clark & Ehlinger 1987; Sih et al. 2004b; Bell 2007). Cote et al. (2010b) have shown the existence of a dispersal syndrome linked with sociability, with the most asocial individuals dispersing further away from the natal nest. Thus, studying the behaviour of individuals of socially flexible species before and after a switch from group to solitary living can help us to understand whether individuals within the same species that live solitarily differ consistently in their social behaviour from group-living ones, indicating the existence of a dispersal syndrome.

The socially flexible African striped mouse is one species that allows comparisons between group- and solitary-living individuals within the same population. In the Succulent Karoo of South Africa, striped mice normally form communally breeding groups

consisting of one breeding male, two to four breeding females and their philopatric offspring (Schradin & Pillay 2004). However, if population density is low during the breeding season, philopatric mice leave their natal group, disperse and start solitary breeding; in doing so, they switch from group living to solitary living (Schradin et al. 2010a; Schoepf & Schradin 2012). We studied whether the change from group to solitary living is associated with changes in social behaviour. In particular, we tested: (1) whether individuals that later become solitary differed in their behaviour from individuals that remained group living before dispersal and whether these differences were present between solitary and dispersing individuals of the same litter; (2) whether individuals differed behaviourally before and after switching from group to solitary living; (3) whether individuals that remained group living differed behaviourally before and after other group members dispersed; (4) whether within each tactic (solitary and group-living individuals) behaviour remained consistent before and after dispersal, indicating personality; and (5) whether different behaviours (e.g. aggression, amicability and social investigation) would be correlated in different behavioural syndromes that would be specific to either group-living or solitary individuals. We predicted individuals that would disperse and become solitary would be more aggressive, less amicable and more investigative than individuals staying in their natal group. Because group size, and thus within-group competition, declined after individuals dispersed, we tested whether individuals that remained in their natal group changed their behaviour after the dispersal of other group members. We predicted behavioural differences between group-living and solitary mice would already be present before dispersal, that is, that mice that would later disperse would already be less social before switching to solitary living. Finally, we predicted behaviours would be consistently different between group-living and solitary individuals (i.e. solitary mice would be consistently more aggressive than group-living mice) and would be correlated in behavioural syndromes that would reflect the specific tactic adopted (i.e. aggression would be positively correlated with social investigation in solitary individuals but not in group-living individuals).

## METHODS

### *Study Area and Animals*

Data were collected during the breeding season from August to November in 2007–2010, when dispersal typically occurs and striped mice might switch from group living to solitary living (Schradin et al. 2010a; Schoepf & Schradin 2012). The study was conducted on a field site located on the farm Klein Goegap (29°42.30'S, 18°02.95'E) near the town of Springbok in South Africa. All the striped mice within the study area were identified and their social tactics (solitary or group living) determined using a combination of trapping, radiotracking and behavioural observations (Schradin et al. 2010a; Schoepf & Schradin 2012). Striped mice were trapped at their nest, sexed, weighed and marked permanently with ear tags (National Band and Tag Co., Newport, KY, U.S.A.). Additionally, each individual received a specific temporary mark, which was applied using a nontoxic hair dye (Inecto Rapido, Pinetown, South Africa) and allowed for easy individual recognition during behavioural observations. Trapping and marking methods were identical to those used by Schradin et al. (2010b). All adult breeders and four philopatric mice (two females and two males) of each studied group were fitted with radiocollars (Holohil, Carp, Ontario, Canada; 1.2–4.5 g; in total 126 males and 166 females). Radiocollars always weighed less than 8% of a mouse's body mass (mostly less than 5%), with the lightest collars (1.2 g) fitted on the smallest juveniles (20 g). No individuals that weighed less than 20 g

received a radiocollar and all radiocollars were removed after 10 weeks of radiotracking. We did not find any indication that radiocollars caused increased mortality, and there is no indication that striped mice carrying radiotransmitters have increased stress hormone levels (Schradin 2008). Striped mice were radiotracked to determine home ranges and composition of sleeping groups at night (Schradin & Pillay 2005a, 2006). Striped mice that shared the same nest at night on more than 75% of occasions were regarded as group living whereas those that slept alone on more than 75% of occasions were regarded as solitary living; no values occurred in between (i.e. there were no individuals that displayed intermediate scores; for more details see Schoepf & Schradin 2012). All striped mice used were from a field experiment in which we experimentally reduced population density by removing individuals from additional groups (not considered here), demonstrating that decreased population density induces dispersal and, in several mice, a switch from a group-living to a solitary-living tactic (Schoepf & Schradin 2012).

### Behavioural Phenotyping

Striped mice are diurnal, with their peak activity periods in the early morning and late evening (Schradin & Pillay 2004). Striped mice were trapped in the early morning directly at their nests soon after they emerged. Each mouse was kept in its own trap and transported 3 km to our research station for testing. Once at the station, they were transferred to a Perspex cage (38 × 22 cm and 15 cm high) provided with bedding (straw), water (*ad libitum*) and food (five sunflower seeds). Mice were allowed to settle for 10 min in the test room. All tests were performed in a neutral arena made out of wood chip (80 × 65 cm and 94 cm high, with a partition in the middle). Each stimulus and focal mouse was introduced to the arena and allowed to settle for 5 min before the partition was removed. The presentation arena was cleaned each time before a new encounter took place using diluted Dettol Antiseptic Liquid (Reckitt Benckiser Pharmaceuticals Ltd., Elandsfontein, South Africa) and water. Each focal individual went sequentially through three successive tests: (1) pup encounter (5 min); (2) opposite-sex encounter (10 min); and (3) same-sex encounter (10 min). Stimuli mice (pup, opposite and same sex) were obtained from a captive colony, which is permanently maintained at the research station. All the pups used in the tests were less than 10 days old (i.e. pre-weaned), as striped mice cannot distinguish between their own and strange pups that are younger than 10 days old (Pillay 2000). Adult stimulus animals were always lighter than the focal animal, as body mass is known to have a positive influence on the outcome of aggressive encounters (Schradin 2004) and we wanted the focal mouse to initiate encounters. At the end of each test, mice were returned to their cages where they were allowed to rest for 5 min. A different stimulus mouse was used for each test. We recorded the behaviour of focal mice by direct observations. Three different categories of behaviour were scored: (1) amicable behaviours (i.e. grooming, huddling and licking); (2) social investigation (i.e. sniffing); and (3) aggression (i.e. chasing, standing upright for fighting and threat displays). The frequency of the behaviours was recorded using focal animal sampling (Martin & Bateson 1993). Most of the agonistic encounters observed involved chasing and threat displays. However, in a few cases (<4% of all tests performed) encounters had to be interrupted because of high levels of aggression. Tests were immediately terminated as soon as (1) pups were pushed and (2) older individuals started wrestling (before any biting could occur). In this way we ensured that none of the individuals used in the tests received any physical injuries. As we could not know beforehand which individual was going to become solitary, before dispersal we tested most of the philopatric individuals

belonging to experimental groups (for more details see Schoepf & Schradin 2012). Behavioural tests were conducted on a total of 42 focal mice (females:  $N = 18$ ; males:  $N = 24$ ) before focal mice dispersed and became solitary. All focal mice were philopatric. Six focal mice that remained group living (females:  $N = 2$ ; males:  $N = 4$ ) and 13 focal mice that became solitary (females:  $N = 7$ ; males:  $N = 6$ ) were tested a second time after dispersal and tactic change. All behavioural tests were carried out in the early morning. At the end of each test, captive mice were immediately returned to the captive colony. Captive mice were later used for other behavioural studies (not considered here). Wild mice were taken back to the field and released in the same spot where they had been captured once all three tests were performed. All mice (captive and wild) were returned in good condition. The study obtained ethical clearance from the University of the Witwatersrand (AESC: 2007/38/04).

### Data Analysis

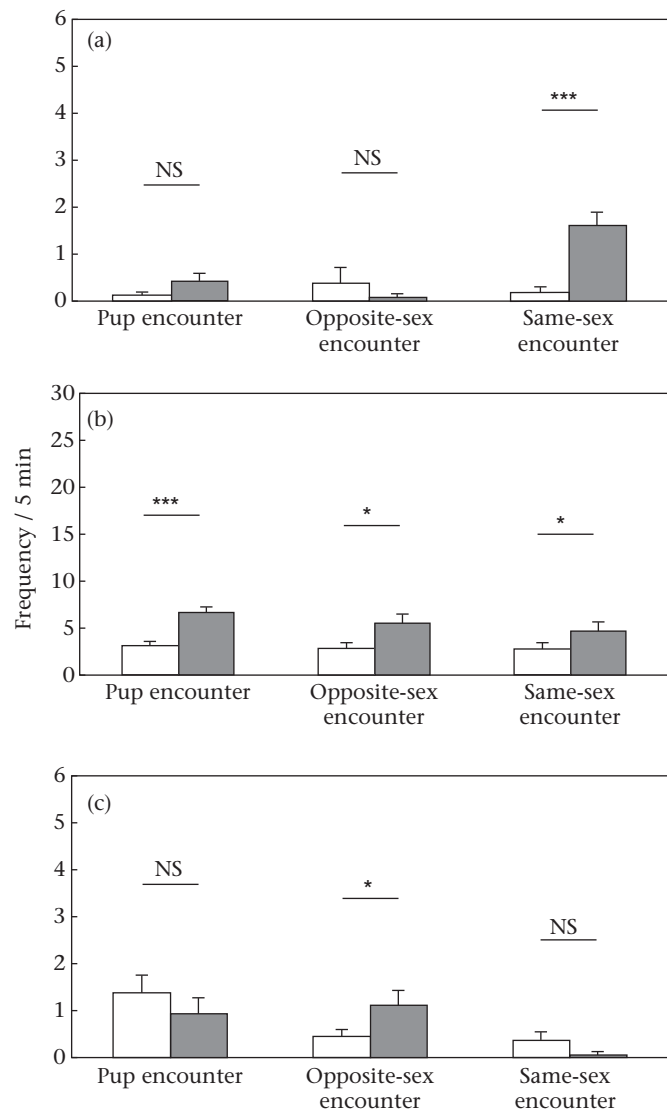
Data analysis was performed using the R statistical software version 2.11.0 (The R Foundation for Statistical Computing, Vienna, Austria, <http://www.r-project.org>). Exact  $P$  value calculations were performed on all tests to correct for small sample sizes. We used a Mann–Whitney  $U$  test to test the prediction that individuals that would become solitary ( $N = 16$ ) differed in their behavioural traits from individuals that remained group living ( $N = 36$ ). Paired Wilcoxon signed-ranks tests were used to assess behavioural changes within the same individual, particularly the predictions that (1) a change in tactic from group living to solitary would lead to changes in aggression, social investigation and amicability (solitary individuals before and after tactic change:  $N = 13$ ), and (2) dispersal of group members would trigger a behavioural change in those individuals that remained at their nest (group living before and after individuals dispersed:  $N = 6$ ). We assessed the behavioural consistency of the traits by calculating Kendall's  $W$  coefficient of concordance. With this test we measured consistency in rank scores of behavioural traits among group-living and solitary mice before and after dispersal (after Hoset *et al.* 2011). We checked for the existence of a behavioural syndrome by performing pairwise Spearman rank correlations ( $r_s$ ) between the different behavioural traits.  $P$  values of multiple comparisons tests for personalities and behavioural syndromes were adjusted using the Benjamini–Hochberg method (Benjamini & Hochberg 1995), which allowed us to control for both type I and II errors. Several factors such as body mass and sex have been shown to influence behavioural traits. For example, several studies on small mammals have found aggressive behaviour to be influenced by sex (Boonstra 1978; Ebensperger 1998; Andreassen & Gundersen 2006). Age, body weight and reproductive condition are known to have an effect on the tactic adopted in striped mice (Schradin *et al.* 2009a; Schoepf & Schradin 2012), and thus we used generalized linear mixed models (GLMM) fitted with a Poisson distribution to test for the effects of sociality (group living or solitary), dispersal (before or after), sex, weight (g), type of individual presented (pup, opposite sex or same sex), age and reproductive status (mature or immature) on each behavioural trait as dependent variable (aggression, social investigation or amicability) and sociality (group living or solitary). Individual identity was included in each model as a random factor as individuals were measured repeatedly in the three tests. Each GLMM was fitted by Laplace approximation and had a sample size of  $N = 252$ . Individual identity was defined as a random factor and we selected the best model by a stepwise backward procedure (following Crawley 2007). We used a linear mixed-effect model (LMM) to compare the behaviour of group-living versus solitary striped mice that were from the same communal litter (raised at

the same time in the same group) before dispersal. Each LMM had one of the behaviours as the response variable; dispersal status (will disperse and will not disperse), sex and the type of individual presented were the fixed factors, and individual ID and Group were the random factors. Data for GLMM and LMM were tested for normality using the Shapiro–Wilk normality test. Data are presented as mean frequency/5 min  $\pm$  SE.

## RESULTS

### *Behaviour of Dispersing and Nondispersing Mice Before Dispersal*

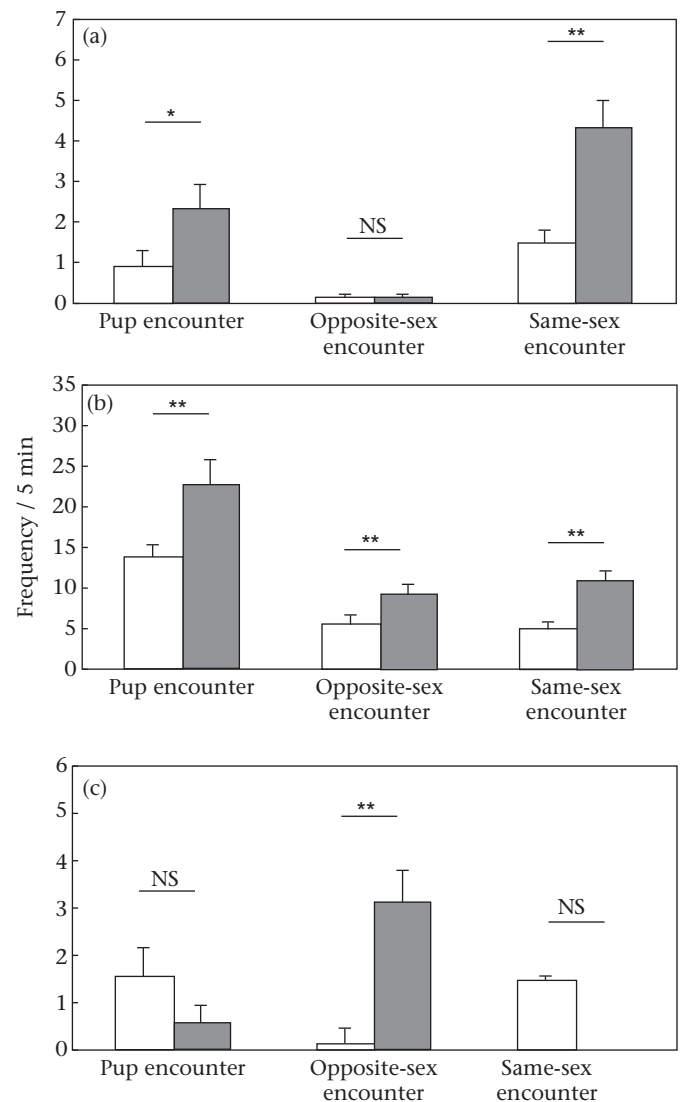
Dispersing striped mice were significantly more aggressive towards same-sex individuals than nondispersing mice ( $W = 48$ ,  $P < 0.001$ ; Fig. 1a), but not towards pups ( $P = 0.051$ ; Fig. 1a) nor towards opposite-sex individuals ( $W = 205$ ,  $P = 0.73$ ; Fig. 1a). Dispersing mice displayed significantly more social investigation than nondispersing mice in all three trials: pup encounters



**Figure 1.** Behavioural differences between striped mice that remained group living (in white,  $N = 28$ ) and that became solitary (in grey,  $N = 14$ ), before dispersal took place. Striped mice were presented with pups, same-sex or opposite-sex individuals in a neutral test arena. (a) Aggression, (b) social investigation and (c) amicable behaviours. \* $P < 0.05$ ; \*\*\* $P < 0.001$ . Data are presented as mean frequency/5 min  $\pm$  SE.

( $W = 62$ ,  $P < 0.001$ ; Fig. 1b), opposite-sex encounters ( $W = 102$ ,  $P = 0.012$ ; Fig. 2b) and same-sex encounters ( $W = 118$ ,  $P = 0.037$ ; Fig. 2b). Dispersing mice showed significantly more amicable behaviours than nondispersing mice during opposite-sex encounters ( $W = 121.5$ ,  $P = 0.026$ ; Fig. 1c), but not during pup encounters ( $W = 193.5$ ,  $P = 0.95$ ; Fig. 1c) nor during same-sex encounters ( $W = 227$ ,  $P = 0.21$ ; Fig. 1c).

Mice raised in the same litter differed significantly in their aggression levels depending on whether they later dispersed or remained group living (LMM:  $t = -2.26$ ,  $P = 0.04$ ) and on the sex of the stimulus mouse presented (dispersing striped mice were more aggressive towards same-sex individuals;  $t = 2.15$ ,  $P = 0.03$ ), but not the sex of the focal individual ( $t = -0.41$ ,  $P = 0.68$ ). Amicability and social exploration in individuals that were raised in the same litter were not significantly influenced by dispersal status (amicability:  $t = -0.63$ ,  $P = 0.53$ ; social exploration:  $t = -0.21$ ,  $P = 0.84$ ), sex (amicability:  $t = 0.87$ ,  $P = 0.39$ ; social exploration:  $t = 0.68$ ,



**Figure 2.** Behavioural changes in striped mice that became solitary. Striped mice ( $N = 13$ ) were tested twice, before (in white) and after (in grey) dispersal. Data presented are paired. Mice were presented with pups, same-sex or opposite-sex individuals in a neutral test arena. (a) Aggression, (b) social investigation and (c) amicable behaviours. \*\* $P < 0.01$ . Data are presented as mean frequency/5 min  $\pm$  SE.

$P = 0.51$ ) or the type of individual presented (amicability:  $t = -1.69$ ,  $P = 0.09$ ; social exploration:  $t = 1.06$ ,  $P = 0.29$ ).

#### Behavioural Changes in Mice That Became Solitary

After dispersal, striped mice showed significantly more aggressive behaviour towards pups (Wilcoxon signed-ranks test:  $V = 21$ ,  $N = 13$ ,  $P = 0.034$ ; Fig. 2a) and towards same-sex individuals ( $V = 78$ ,  $N = 13$ ,  $P = 0.002$ ; Fig. 2a) than before dispersal. This was not the case for aggressive behaviour shown towards opposite-sex individuals ( $V = 10.5$ ,  $N = 13$ ,  $P > 0.99$ ; Fig. 2a). After becoming solitary, striped mice showed significantly higher frequencies of social investigating behaviour in all three tests: pup encounter ( $V = 87.5$ ,  $N = 13$ ,  $P = 0.004$ ; Fig. 2b), opposite-sex encounter ( $V = 90$ ,  $N = 13$ ,  $P = 0.002$ ; Fig. 2b) and same-sex encounter ( $V = 91$ ,  $N = 13$ ,  $P = 0.002$ ; Fig. 2b). Striped mice showed significantly more amicable behaviours towards members of the opposite sex after they became solitary ( $V = 65$ ,  $N = 13$ ,  $P = 0.005$ ; Fig. 2c), but not towards mice of the same sex ( $V = 0$ ,  $N = 13$ ,  $P = 0.35$ ; Fig. 2c) nor towards pups ( $V = 6$ ,  $N = 13$ ,  $P = 0.19$ ; Fig. 2c).

#### Behaviour of Group-living Mice After Group Member Dispersal

Group-living individuals did not show any significant changes in aggressive behaviour towards pups (before dispersal of group members:  $0.00 \pm 0.00$ ; after dispersal of group members:  $0.76 \pm 0.48$ ; Wilcoxon signed-ranks test:  $V = 6$ ,  $N = 6$ ,  $P = 0.17$ ), towards members of the opposite sex (before dispersal of group members:  $0.00 \pm 0.00$ ; after dispersal of group members:  $0.33 \pm 0.33$ ;  $V = 1$ ,  $N = 6$ ,  $P > 0.99$ ) and towards same-sex individuals (before dispersal of group members:  $0.99 \pm 0.45$ ; after dispersal of group members:  $1.50 \pm 1.09$ ;  $V = 7$ ,  $N = 6$ ,  $P = 0.58$ ). Group-living individuals did not differ in their social investigation before and after dispersal of group members during pup encounters (before dispersal of group members:  $1.50 \pm 0.81$ ; after dispersal of group members:  $2.92 \pm 0.93$ ;  $V = 14$ ,  $N = 6$ ,  $P = 0.10$ ), during opposite-sex encounters (before dispersal of group members:  $4.83 \pm 2.06$ ; after dispersal of group members:  $8.33 \pm 2.97$ ;  $V = 16$ ,  $N = 6$ ,  $P = 0.29$ ) and during same-sex encounters (before dispersal of group members:  $6.96 \pm 3.57$ ; after dispersal of group members:  $8.48 \pm 4.46$ ;  $V = 10$ ,  $N = 6$ ,  $P = 0.59$ ). Furthermore, we did not find any significant difference in amicable behaviours of group-living individuals before and after individuals dispersed for pup encounters (before dispersal of group members:  $0.67 \pm 0.49$ ; after dispersal of group members:  $0.17 \pm 0.17$ ;  $V = 0$ ,  $N = 6$ ,  $P > 0.99$ ); opposite-sex encounters (before dispersal of group members:  $1.67 \pm 1.05$ ; after dispersal of group members:  $1.50 \pm 0.81$ ;  $V = 3$ ,  $N = 6$ ,  $P > 0.99$ ) and same-sex encounters (before dispersal of group members:  $0.50 \pm 0.67$ ; after dispersal of group members:  $1.00 \pm 0.68$ ;  $V = 3$ ,  $N = 6$ ,  $P = 0.37$ ).

#### Consistency in Behavioural Traits Before and After Dispersal

Before and after dispersal, individuals that would later become solitary showed consistency in aggressive behaviour towards pups and same-sex individuals, in social investigation during their encounters with pups, opposite-sex individuals and same-sex individuals and in amicable behaviour towards opposite-sex individuals (Table 1). However, they did not show significant consistency in their aggressiveness towards individuals of the opposite sex or in their amicability towards pups or individuals of the same sex (Table 1).

Before and after dispersal of group members, individuals that remained group living did not show consistency in any of the

behaviours recorded (aggression, social investigation and amicability; Table 1).

#### Behavioural Syndrome

For mice that were going to become solitary we found a negative correlation between aggression and amicability towards pups before dispersal took place, with the most aggressive mice being the least amicable towards pups (Table 2). However, this relationship did not persist after dispersal (Table 2). After dispersal, striped mice never showed amicable behaviours towards same-sex individuals, making calculations of correlation coefficients impossible. We found a positive correlation between social investigation and aggression for same-sex encounters in solitary mice after dispersal (Table 2).

For mice that would remain group living, we found a positive correlation between social investigation and amicability for pup encounters and opposite-sex encounters before and after dispersal, suggesting that the most investigative individuals were also the most amicable when they were presented with a pup or an individual of the opposite sex. We also found a positive correlation between social investigation and aggression in group-living mice before dispersal during same-sex encounters.

#### Factors Affecting An Individual's Behaviour

Aggressive behaviour was significantly influenced by the body mass of the focal mice (heavier individuals were more aggressive;  $Z = 4.35$ ,  $P < 0.001$ ), its sociality (solitary mice were more aggressive than group-living mice;  $Z = 3.59$ ,  $P < 0.001$ ), whether it had dispersed (mice became more aggressive after dispersal;  $Z = 2.76$ ,  $P = 0.006$ ), its age (older mice were more aggressive;  $Z = 2.64$ ,  $P = 0.008$ ) and its reproductive status (sexually mature individuals were more aggressive;  $Z = 2.46$ ,  $P = 0.014$ ). The interactions between dispersal and age ( $Z = -2.31$ ,  $P = 0.021$ ), between dispersal and reproductive status ( $Z = -2.19$ ,  $P = 0.028$ ) and between age and reproductive status ( $Z = -2.33$ ,  $P = 0.020$ ) all positively influenced aggression. Older and sexually mature individuals that became solitary tended to be more aggressive than

**Table 1**  
Consistency in behavioural traits of group-living and solitary mice before and after dispersal

		N	W	$\chi^2$	P
<b>Solitary</b>					
Pup encounter	Aggression	13	0.46	6	0.04*
	Social investigation	13	0.72	9.3	0.008*
	Amicable behaviour	13	0.27	3.57	0.17
Opposite-sex encounter	Aggression	13	0	0	0.99
	Social investigation	13	0.72	9.3	0.007*
	Amicable behaviour	13	0.57	7.4	0.02*
Same-sex encounter	Aggression	13	0.92	12	0.004*
	Social investigation	13	1	13	0.004*
	Amicable behaviour	13	0.15	2	0.56
<b>Group</b>					
Pup encounter	Aggression	6	0.5	3	0.25
	Social investigation	6	0.3	1.8	0.37
	Amicable behaviour	6	0.17	1	0.99
Opposite-sex encounter	Aggression	6	0.17	1	0.99
	Social investigation	6	0.44	2.7	0.22
	Amicable behaviour	6	0.06	0.3	0.99
Same-sex encounter	Aggression	6	0	0	0.99
	Social investigation	6	0	0	0.99
	Amicable behaviour	6	0.33	2	0.5

Consistency in behavioural traits was calculated using Kendall's  $W$  coefficient (after Hoset et al. 2011). Asterisks denote significant results.  $P$  values were adjusted using the Benjamini–Hochberg method.

**Table 2**  
Behavioural syndrome in group-living and solitary mice before and after dispersal

		Before dispersal			After dispersal		
		<i>N</i>	<i>r<sub>S</sub></i>	<i>P</i>	<i>N</i>	<i>r<sub>S</sub></i>	<i>P</i>
<b>Solitary</b>							
Pup encounter	Amicability–Investigation	16	–0.38	0.38	21	–0.01	0.99
	Aggression–Investigation	16	0.41	0.33	21	–0.09	0.99
	Aggression–Amicability	16	–0.72	0.027	21	–0.26	0.87
Opposite-sex encounter	Amicability–Investigation	16	0.46	0.25	21	0.3	0.84
	Aggression–Investigation	16	–0.2	0.92	21	0.12	0.99
	Aggression–Amicability	16	–0.49	0.25	21	–0.51	0.13
Same-sex encounter	Amicability–Investigation	16	–0.23	0.78	21	NA	NA
	Aggression–Investigation	16	0.47	0.25	21	0.69	0.006*
	Aggression–Amicability	16	–0.54	0.25	21	NA	NA
<b>Group</b>							
Pup encounter	Amicability–Investigation	36	0.56	0.003	11	0.78	0.05*
	Aggression–Investigation	36	0.13	0.99	11	–0.52	0.49
	Aggression–Amicability	36	–0.17	0.99	11	–0.47	0.54
Opposite-sex encounter	Amicability–Investigation	36	0.7	0.002	11	0.85	0.02*
	Aggression–Investigation	36	0.15	0.99	11	–0.25	0.99
	Aggression–Amicability	36	0.07	0.99	11	–0.27	0.99
Same-sex encounter	Amicability–Investigation	36	0.35	0.18	11	0.22	0.99
	Aggression–Investigation	36	0.51	0.009	11	0.51	0.49
	Aggression–Amicability	36	–0.06	0.99	11	–0.15	0.99

Spearman correlation coefficients between two behavioural traits indicating behavioural syndromes are shown. Asterisks denote significant correlations. NA: all data obtained for amicability towards same-sex individuals were 0; thus it was not possible to calculate a correlation coefficient or a *P* value for these interactions. *P* values were adjusted using the Benjamini–Hochberg method.

younger and immature individuals that remained group living. The sex of the focal mice ( $Z = -1.29$ ,  $P = 0.197$ ) and the stimulus mouse ( $Z = 1.27$ ;  $P = 0.203$ ) did not influence aggression.

Social investigation was significantly influenced by the body mass of the focal mice (heavier individuals were more investigative;  $Z = 3.34$ ,  $P = 0.001$ ), its sociality (solitary individuals were more investigative;  $Z = 3.60$ ,  $P < 0.001$ ) and its sex (males were more investigative than females;  $Z = 2.76$ ,  $P = 0.006$ ). The interactions between body mass and sociality ( $Z = -3.74$ ,  $P < 0.001$ ), between body mass and the stimulus mouse ( $Z = -2.98$ ,  $P = 0.003$ ), between sociality and age ( $Z = 2.99$ ,  $P = 0.003$ ), between dispersal and sex ( $Z = -2.64$ ,  $P = 0.008$ ), between dispersal and the type of stimulus mouse ( $Z = -2.71$ ,  $P = 0.007$ ), between sex and the stimulus mouse ( $Z = -2.00$ ,  $P = 0.045$ ) and between sex and age ( $Z = -2.37$ ,  $P = 0.018$ ) negatively influenced social investigation. Older and heavier females that became solitary were more socially investigative towards pups, whereas older and heavier males that became solitary were more socially investigative towards opposite-sex and same-sex individuals. Dispersal ( $Z = -0.68$ ,  $P = 0.496$ ), stimulus mouse ( $Z = -0.92$ ,  $P = 0.359$ ), age ( $Z = -1.82$ ,  $P = 0.068$ ) and reproductive status ( $Z = -0.25$ ,  $P = 0.801$ ) did not influence social investigation significantly.

Amicability was significantly influenced by sex (males were significantly more amicable than females;  $Z = 2.61$ ,  $P = 0.009$ ), age (younger individuals were more amicable;  $Z = -2.04$ ,  $P = 0.042$ ), whether the focal mice had dispersed (individuals were more amicable before dispersal;  $Z = -4.13$ ,  $P < 0.001$ ) and by the type of stimulus mouse presented (focal individuals behaved more amicably according to which mouse was presented to them; in particular they were more sociable to opposite-sex individuals;  $Z = -3.02$ ,  $P = 0.003$ ). We found significant interactions between sociality and the type of stimulus mouse ( $Z = -2.54$ ,  $P = 0.011$ ) and between dispersal and the type of stimulus mouse ( $Z = 2.01$ ,  $P = 0.045$ ). Individuals that became solitary were more amicable towards opposite-sex individuals than individuals that remained group living. Sociality ( $Z = 1.95$ ,  $P = 0.051$ ), body mass ( $Z = 1.16$ ,  $P = 0.248$ ) and reproductive status ( $Z = -0.43$ ,  $P = 0.665$ ) did not significantly influence amicability.

## DISCUSSION

Group-living striped mice that dispersed and became solitary changed their behaviour, becoming more aggressive and more investigative. These striped mice already differed in their behaviours from mice that remained group living before they dispersed, being more aggressive and more investigative. Our study suggests that striped mice are able to adjust their behaviour according to what tactic they follow. This adjustment might occur already before switching tactics or alternatively may result from a predisposition.

Group-living individuals that later became solitary were more aggressive and more investigative than individuals that remained group living. Previous studies demonstrated that more aggressive individuals are more likely to disperse (Myers & Krebs 1971; Kaplan et al. 1995; Howell et al. 2007). Our results also corroborate the findings of previous studies, which suggested that the tendency to show more exploratory behaviour may develop even before dispersal occurs (Holekamp 1986; Cote et al. 2010a; Hoset et al. 2011). In group-living species, competition over space and resources is often intense and dominant individuals often reproductively suppress or even evict subordinates (Blumstein & Armitage 1999; Pocock et al. 2005; Saltzman et al. 2006). In striped mice, there is no indication of eviction events, but there is good indication of reproductive suppression of philopatric males by the male breeder (Schradin et al. 2009b) and strong reproductive competition between females (Schradin et al. 2010b). In many species dispersal and onset of solitary living is a tactic to avoid competition and harassment by dominant group members (Andreassen & Gundersen 2006; Le Galliard 2006; Le Galliard et al. 2007). Important differences in dispersal-related behaviours, especially in aggression, already existed in striped mice before dispersal. This was even the case for the comparison between individuals that had experienced the same environment when growing up, that is, individuals that were raised in the same communal litter (mice that later dispersed were more aggressive than their litter siblings that remained in the family group).

Striped mice of both sexes can follow three alternative reproductive tactics: (1) remain as nonbreeding philopatric mice within the natal group; (2) disperse and become solitary males or solitary breeding females; or (3) become breeding individuals in a group, which is the natal group in the case of females or a new group in the case of males (Schradin & Pillay 2003; Schradin 2004). Several studies have found an association between exploration and dispersal (Holekamp 1986; Belthoff & Dufty 1998; Dingemans et al. 2003). Accordingly, we found that striped mice became more investigative after they switched from group to solitary living. It has been suggested that individuals that are more explorative may be able to gather more information from their surroundings (Guillette et al. 2009; Rodriguez-Prieto et al. 2011). Such information gathering may ultimately allow individuals to assess risks more rapidly (Crusio 2001; Tebbich et al. 2009), which can be an advantage when venturing into an unknown environment (Dall et al. 2005; Rodriguez-Prieto et al. 2011). In all these studies exploration was assessed via open field tests, while we measured social investigation during dyadic encounters. We suggest that an individual that is able to gather social information faster might also be able to react more promptly to competitors or potentially suitable mates that live close to or intrude on to their territory.

Striped mice that became solitary behaved more aggressively to same-sex individuals and pups, but were more amicable to individuals of the opposite sex. Dispersing striped mice are thought to be searching for mating opportunities (Schradin et al. 2010a), and thus should be more wary of mice of the same sex, which represent a particular threat as they are reproductive competitors. Hence, males are expected to be more wary of other males as they

represent mating competitors, whereas females are expected to be more wary of other females as they compete for access to breeding territories. Reproductive competition can be high among group-living striped mice, as a single breeding male monopolizes several communally breeding females (Schradin et al. 2009c) and suppresses adult male offspring living in the group (Schradin et al. 2009c; Schoepf & Schradin 2012). Breeding females show intra-sexual aggression and infanticide towards the pups of other females (Schradin et al. 2010a). Striped mice of both sexes that become solitary have been shown to be more reproductively successful than group-living philopatric mice (Schoepf & Schradin 2012), success that may stem from their enhanced amicable behaviour towards opposite-sex individuals.

Individuals with particular personality types might find dispersal to be less costly than others and thus may be more successful in settling in a new environment (Clobert et al. 2009). Several studies have demonstrated dispersers to differ from non-dispersers in their personality traits; for example, Cote & Clobert (2007) showed that dispersing common lizards, *Lacerta vivipara*, are less sociable than nondispersing individuals. Duckworth & Badyaev (2007) showed that highly aggressive western bluebirds, *Sialia mexicana*, are more successful at dispersing. Striped mice that became solitary changed their behaviour, but in a consistent manner. In particular, we found that the most aggressive, the most investigative and the least amicable mice were still the most aggressive, the most investigative and the least amicable after they changed their tactic. That dispersing mice differed in behaviour from philopatric mice, and that their behaviour was consistent, implies an important role of personality in the decision to disperse or to remain philopatric. An interesting question would be whether differences in personality traits that influence dispersal probabilities influence fitness. In another publication using data from the same field experiment we demonstrated that striped mice that became solitary were more reproductively successful than striped mice that remained group living (see Schoepf & Schradin 2012 for more details), indicating that under these environmental conditions differences in personality traits might in fact influence fitness.

In our study we found behavioural syndromes in striped mice that would/did become solitary, syndromes that were not detectable in our small sample of striped mice that remained group living. A behavioural syndrome consisting of a negative correlation between amicability and aggression was found for the pup encounter test before dispersal, but not after dispersal. A second behavioural syndrome was observed after dispersal for same-sex individuals and consisted of a positive correlation between aggression and investigation. Dispersing striped mice might be more sexually motivated than striped mice that remained group living, and sexual motivation might be the proximate cause of dispersal. By dispersing, striped mice are able to escape reproductive suppression and are thus finally able to reproduce (Schoepf & Schradin 2012).

Individuals that live within a family group may be affected both by their parents' and by their siblings' behaviour (Dingemanse et al. 2003). Thus, when some group members disperse, this might affect the behaviour of the group members that stay behind. After dispersal of other striped mice, group-living philopatric individuals possibly experienced a less crowded environment and thus had more access to limited resources, such as food, in their territory. However, in our study group-living philopatric striped mice did not change their behaviour significantly after other group members left the group, but a larger sample size would be needed to make a firm conclusion.

Several factors, such as age, weight or reproductive maturity, may affect the behaviour of an individual. For example, several studies on small mammals have found aggressive behaviour to be influenced by sex (Boonstra 1978; Ebensperger 1998; Andreassen &

Gundersen 2006). Age has been demonstrated to be an important factor affecting sociability, for example in root voles, *Microtus oeconomus*, which show an increase in asocial behaviour with age (Hoset et al. 2011). In our study, we found that striped mice that were heavier, older and had reached sexual maturity were more aggressive. Striped mice switch between tactics depending on their body mass and age: as philopatric mice become older and heavier, they tend to leave the nest and adopt a solitary strategy, with their social status likely to be maintained by aggressive interactions (Schradin & Pillay 2005b; Schradin et al. 2009c) as heavier individuals are more likely to win competitive encounters against lighter individuals (Schradin 2004). Reproductive competition has been shown to be the main factor driving striped mice to become solitary with individuals that become solitary being sexually mature more often than individuals that remain philopatric (Schoepf & Schradin 2012). We found solitary heavier individuals to be more socially investigative, and males to be more socially investigative than females, which can be interpreted as their willingness to assess more rapidly whether a strange individual is a potential competitor or a potential mate, because striped mice males are normally the dispersing sex (Solmsen et al. 2011). Philopatric mice choose either to disperse or to remain group living according to when they are born during the breeding season (Schradin et al. 2010a). Individuals that are born early have more chances of finding a suitable area to move into than individuals that are born late as conditions in the field quickly deteriorate as the season progresses. Thus solitary roamers are often also older than males that remain group living. Sex also had an effect on amicability, with males being less amicable than females and older individuals being less sociable than younger individuals. Dispersal of striped mice typically takes place during the breeding season when food is abundant (Schradin & Pillay 2005a). Males and females might both disperse and become solitary. By the end of the breeding season, roaming males often become group living by joining a solitary breeding female and her offspring (Schradin et al. 2010a). However, in contrast to males, females have never been observed joining other groups of females. Striped mice were more sociable towards opposite-sex individuals than towards pups or same-sex individuals. Competition for mating partners and space is expected to be stronger between individuals of the same sex (Le Galliard 2006), and striped mice of both sexes compete fiercely with other individuals of the same sex (Schradin 2004), and are expected to be less tolerant and thus less sociable towards individuals of the same sex than they are towards individuals of the opposite sex that might always represent a potential mate instead.

Few other studies have examined the potential link between specific behaviours, such as aggression, social investigation and amicable behaviour, and their repercussion on the social tactic of an individual. Our results indicate that solitary striped mice differ in behavioural traits from group-living striped mice, and these behavioural differences are already present before the solitary tactic is adopted. Behavioural traits such as exploration, aggression and amicability may influence the chances of individuals succeeding in a new environment and they may ultimately determine its reproductive success. It would be interesting to study whether closely related species that differ in sociality (solitary versus group living) differ in the same personality traits as do solitary and group-living striped mice. The decision to disperse and become solitary seemed to be driven by increased aggressive behaviour towards same-sex individuals and increased amicable behaviours towards opposite-sex individuals, both being indicators of sexual motivation. Our study provides evidence not only that individuals that disperse and become solitary differ behaviourally from their group-living counterparts, but also that these differences are already present even before the dispersal event.

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