Animal Behaviour 84 (2012) 1159–1167

Contents lists available at SciVerse ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

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

Ivana Schoepf [a,b,*], Carsten Schradin [a,b,1]

[a] Department of Animal Behaviour, Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland
[b] School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa

ARTICLE INFO

Article history:
Received 12 February 2012
Initial acceptance 17 April 2012
Final acceptance 8 August 2012
Available online 10 September 2012
MS. number: 12-00115R

Keywords:
African striped mice
aggression
amicability
behavioural syndrome
dispersal
group living
personality
Rhabdomys pumilio
social behaviour
solitary

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.

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 interspecific 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

* Correspondence: I. Schoepf, Department of Animal Behaviour, Institute of Evolutionary Biology and Environmental Studies, University of Zurich-Irchel, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland.
E-mail address: ivana.schoepf@ieu.uzh.ch (I. Schoepf).
[1] *E-mail address:* carsten.schradin@ieu.uzh.ch (C. Schradin).

0003-3472/$38.00
http://dx.doi.org/10.1016/j.anbehav.2012.08.019

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