SOCIAL BEHAVIOR, COOPERATION AND ECOLOGICAL CONSTRAINTS ON TWO CLOSELY RELATED MICE SPECIES

Outline of PhD Dissertation

Peter Mark Szenczi
Department of Ethology
Biological Institute, Faculty of Science,
Eötvös Loránd University, Hungary

Supervisor
Dr. Vilmos Altbäcker
Department of Ethology
Eötvös Loránd University, Budapest, Hungary

Ph.D. School of Biology
Head of PhD School: Prof. Dr. Anna Erdei

Ph.D. Program of Ethology
Head of Ph.D. Program: Prof. Dr. Ádám Miklósi

- Budapest, 2012 -

INTRODUCTION

Adaptation to different ecological conditions can result not just in markedly different physiology but also in contrasting social behavior (Bronson 1985). Social environment is a fundamental part of the animal's environment, since conspecifics are potential mates and participants in cooperative and competitive interactions. Animals aggregate mainly because of the availability of certain resources or to reduce predation risk (Davies et al. 2012). Formation of groups is expected when the costs of group-living are low or the achieved benefits are high.

Group-living allows the development of complex social behavioral traits like alarm calls (Sherman 1977), food sharing (Benz 1993), helping (Brown 1987), communal breeding (Creel and Creel 1991), establishing dominance order (Bernstein 1981), individual recognition (Wrangham 1983) and mating systems (Emlen and Oring 1977), which further increases the gained benefit. However, there are numerous disadvantages as well; competition is higher, which leads to elevated aggression (Walters and Seyfarth 1986); while dominant individuals may monopolize resources (Wrangham 1981). The risk of infection and the threat posed by parasites are also higher (Brown and Brown 1986). Cooperation among individuals is closely related to the sociality of the animals (Dugatkin 1997).

Cooperation among individuals is an omnipresent phenomenon in nature, from bacteria to primates. Cooperative behaviors appear from fairly simple to highly complicated forms. There are three main explanations on how cooperative behavior can evolve and survive in a population: kin selection (Hamilton 1964), reciprocity (Axelrod and Hamilton 1981; Trivers 1971) and mutual benefit (Lima 1989; Maynard Smith 1983). Mutual benefit models presume situations where there is no temptation to cheat because cooperating always provides the highest payoff regardless of the opponents' behavior.

Aggression plays a major role in the determination of mating systems and social organizations (Trivers 1972). Intraspecific aggression often has a major role in shaping social structure and spatial distribution of conspecifics through territorial behavior connected with competition for space, mates and resources (Grant 1972). The level of agonistic behavior and tolerance between individuals is mostly under the influence of ecological traits and in direct connection with sociality, the presence or absence of social groups, and the breeding system (Armitage 1981; Crowcroft and Rowe 1963; Getz and Carter 1980; Getz et al. 1981; Insel et al. 1995; Livoreil et al. 1993; Patris et al. 2002; Sachser et al. 1999; Shapiro et al. 1986). Mutual tolerance between individuals is key for carrying out cooperative behavior traits, while selective aggression usually directed toward strangers may be very important in maintaining territories and social bonds established between individuals.

Natal dispersal patterns have a strong connection with the levels of sociality (Perrin and Goudet 2001) showed that. It has also been recognized that population structure plays a decisive role in the evolution of cooperation (Nowak and May 1992). Not only because spatial aggregation is necessary for individuals to interact, but because limited dispersal (population viscosity) tends to keep relatives together (Hamilton 1964). Polygynous mammals usually show a male-biased dispersal, while both sexes disperse or dispersal is female-biased in monogamous species (Dobson 1982; Favre et al. 1997; Greenwood 1980; Perrin and Mazalov 2000; Wolff 1993).

For small mammal populations living in temperate and cold climates, especially in northern latitudes, winter is an obvious bottleneck. Over-winter mortality in small mammals is strongly influenced by low ambient temperatures, which leads to a strong selective pressure for the evolution of physiological, anatomical and behavioral adaptations which enhance the probability of survival over the winter. Some of these traits are solitaire responses, affecting only the individual; others are socialistic, requiring more animals to interact. For animals that do not migrate or hibernate, other behavioral strategies, including food hoarding to satisfy nutrient demands (Vander Wall 1990), huddling in communal nests to reduce heat loss (Contreras 1984; Hayes et al. 1992), reduction in winter activity levels to avoid exposure to low temperatures (Jackson et al. 2001) are of special importance.

Adaptation to different habitats plays a more important role than phylogeny in the evolution of behavior and social systems (Carranza 2000; Emlen and Oring 1977). Even between closely related species, differences in behavior, social organizations and mating system can be significant. The mound-building mouse (*Mus spicilegus* Petényi 1882) is endemic to Hungary. This species is believed to be the only one in the *Mus* complex to exhibit a socially monogamous mating system (Baudoin et al. 2005; Patris et al. 2002). They establish a strong social bond between partners (Patris and Baudoin 1998), while both sexes of the adult mice show high level of aggressiveness towards unfamiliars (Patris et al. 2002; Simeonovska-Nikolova 2003; Suchomelova et al. 1998). They form stable male-female associations in experimental groups (Baudoin et al. 2005; Simeonovska-Nikolova 2003) and parents cooperate in the care of their offspring (Patris and Baudoin 2000). The mound-building mouse is also famous for its unique communal overwintering behavior. In the autumn, group of mice hoard seeds and other vegetable material and cover the heap with soil. They spend the winter under the mounds without reproducing. On the next spring they disperse and mate.

Objectives and methods

The mounds under which the mound-building mice overwinter are the primary product of their cooperative behavior. In the first part of this thesis I investigated the role of the mounds in field studies and on artificial mounds. I studied the morphology of the mounds and the nest chambers on several populations across Hungary. I analyzed the compositions of the hoarded plant material and the diet of the mound-building mouse, and the effect of the mounds on the soil's thermal and water characteristics. I determined the number, sex ratio and age of the overwintering mice. I built artificial mounds with varying plant content in semi-natural environment to test their water and thermal insulating properties.

In the second part of this thesis, I investigated the connection between the behavioral bases and ecological constraints of cooperative behavior. I tried to evaluate the contrasting social traits of the mound-building mouse and the house mouse in relation to their different cooperative behavior using laboratory experiments. In comparative tests with the house mouse I investigated the social and aggressive behavior and the natal dispersal of the mound-building mouse. I used the well-established method of neutral cage interaction test to evaluate the development of their aggressive behavior and the role of familiarity on tolerance between individuals. The natal dispersal was tested in apparatuses comprising water basins which the animals had to cross in order to leave the device. Similar procedure was used previously on both house mouse and mound-building mouse.

Results

The morphology of the mounds and their thermal and water insulating capacities under field conditions

By investigating the morphology of the mounds under field conditions we found no differences based on the soil's characteristics. However we found differences in the position of the nest-chamber, as it was significantly deeper in sandy soil. Mounds reduced the thermal variation of the soil beneath, and elevated temperatures were measured in the ground but not in the mounds. There is no evidence that the vegetable material produces heat by rotting. Water content of the soil was also reduced under the mounds, verifying that the mounds have water proofing abilities. That indicated that the mounds may have an insulating role, keeping the nest chamber warm and dry during the winter.

Overwintering success and diet of the mound-building mouse

We excavated whole groups of mice from under their mound during the winter and collected fecal samples. We found no decrease in the average group sizes, which suggests that overwintering under mounds is a successful strategy. By investigating the food composition of the mice's diet, based on their fecal pellets and the plant filling of the mounds, we found no evidence that they consume the hoarded seeds. The vegetable material collected by the mound-building mice for their mound does not completely reflect its availability in the environment. They collect mostly one or two species for mound building. According to my results mice mostly consume and build the mounds using dicots but the species used for the two different roles are not identical but all are parts of common weeds associated with initial successional stages on abandoned land.

Role of the vegetable material layer in the mounds

In a planned experiment we have built artificial mounds with varying plant content, similar to those built by mound-building mice. We have measured temperature change at three levels, at the surface, under the mound and at the nest depth, and investigated their water retaining properties. We showed that the plant fill plays a major role in their thermal insulation and waterproofing properties. Mounds reduced temperature variation of the soil and may protect the nest from absorbing precipitation during the winter.

In comparison with the house mouse the mound building mouse disperse later and show no sexual dimorphism

We compared the natal dispersal behavior of two mice species under laboratory conditions. We used a previously tested device (Gerlach 1996) for measuring dispersal activity. Our results showed, that the natal dispersal of these two species differ: both sexes of the mound-building mice dispersed later, than the house mice, where a difference between sexes also occur: house mice males dispersed earlier than females. The mound-building mice showed no sexual dimorphism in this behavior. The observed dispersal pattern in the mound-building mouse is in agreement both with its socially monogamous mating system (Baudoin et al. 2005; Patris et al. 2002) and their communal overwintering.

The mound-building mouse show elevated level of aggression, but remains tolerant with familiar individuals

To study how social system and cooperation reflects on social behavior, dyadic social interaction tests in neutral cages were performed on 21, 60 and 120 days old house mice and mound-building mice. Each individual was tested against a sibling and an unfamiliar individual at all three ages. Our results showed that social behavior and its development differed between the species and sexes. When facing a stranger, both sexes of the mound-building mouse were more aggressive than house mouse. The familiarity of the opponent was more important to mound-building mouse than to house mouse. Despite their elevated level of aggression mound-building mouse remained less agonistic against their sibling, indicating that either kinship or early social experiences elicit tolerance. Our study suggests that the social system of mice is reflected in their behavioral patterns, and the two contrasting species studied may provide a useful model of behavioral development.

Conclusions

In this thesis I demonstrated, that the mounds of the mound-building mouse are integral parts of their overwintering behavior. With field studies and experiments under seminatural conditions I demonstrated that the mounds have thermal and water insulating capacities which may contribute to the successful overwintering of this species. Contrary to the common belief, I found no evidence that the mice consume the hoarded plant material. The use of mounds enhances the probability of surviving through winter, so it seems that the benefit of the mounds during the winter exceeds the costs of the delayed reproduction, which was demonstrated by other research teams.

The aggressive behavior and natal dispersal of the mound-building mouse reflect the needs of the communal overwintering and the monogamous mating system. The observed tolerance among siblings and the elevated level of aggression against unfamiliars is essential in the maintaining of the communally overwintering groups. Limited aggression and dispersal keeps siblings together, which makes cooperatively building the mounds easier and evolutionary more profitable.

The unique overwintering strategy and the monogamous mating system make the mound-building mouse a good model for ethological studies. Revealing the genetic structure of the overwintering social groups and comparative experiments with more related species would provide valuabe information on the behavioral bases of cooperation and the ecological constraints shaping social systems.

References

Armitage KB (1981) Sociality as a life-history tactic of ground-squirrels. Oecologia 48 (1):36-49.

Axelrod R, Hamilton WD (1981) The Evolution of Cooperation. Science 211 (4489):1390-1396.

Baudoin C, Busquet N, Dobson FS, Gheusi G, Feron C, Durand JL, Heth G, Patris B, Todrank J (2005) Male-female associations and female olfactory neurogenesis with pair bonding in *Mus spicilegus*. Biological Journal of the Linnean Society 84 (3):323-334.

Benz JJ (1993) Food-elicited vocalizations in golden lion tamarins: design features for representational communication. Animal Behaviour 45 (3):443.

Bernstein IS (1981) Dominance - the baby and the bathwater. Behavioral and Brain Sciences 4 (3):419-429.

Bronson FH (1985) Mammalian reproduction: an ecological perspective. Biology of Reproduction 32 (1):1-26.

Brown CR, Brown MB (1986) Ectoparasitism as a cost of coloniality in cliff swallows (*Hirundo pyrrhonota*). Ecology 67 (5):1206-1218.

Brown JL (1987) Helping and communal breeding in birds. Princeton University Press, Princeton

Carranza J (ed) (2000) Environmental effects on the evolution of mating systems in endotherms. Vertebrate Mating Systems. World Scientific Pub Co Inc, Erice, Italy

Contreras LC (1984) Bioenergetics of Huddling - Test of a Psycho-Physiological Hypothesis. Journal of Mammalogy 65 (2):256-262.

Creel SR, Creel NM (1991) Energetics, reproductive suppression and obligate communal breeding in carnivores. Behavioral Ecology and Sociobiology 28 (4):263-270.

Crowcroft P, Rowe FP (1963) Social organization and territorial behaviour in the wild house mouse (*Mus musculus* L.). Proceedings of the Zoological Society of London 140 (3):517-531.

Davies NB, Krebs JR, West SA (2012) An introduction to behavioural ecology. Wiley-Blackwell, Oxford

Dobson FS (1982) Competition for mates and predominant juvenile male dispersal in mammals. Animal Behaviour 30 (Nov):1183-1192.

Dugatkin LA (1997) Cooperation among animals: an evolutionary perspective. Oxford University Press, New York

Emlen ST, Oring LW (1977) Ecology, sexual selection, and evolution of mating systems. Science 197 (4300):215-223.

Favre L, Balloux F, Goudet J, Perrin N (1997) Female-biased dispersal in the monogamous mammal Crocidura russula: Evidence from field data and microsatellite patterns. Proceedings of the Royal Society of London Series B-Biological Sciences 264 (1378):127-132.

Gerlach G (1996) Emigration mechanisms in feral house mice: a laboratory investigation of the influence of social structure, population density, and aggression. Behavioral Ecology and Sociobiology 39 (3):159-170.

Getz LL, Carter CS (1980) Social organization in *Microtus ochrogaster* populations. Biologist 62 (1-4):56-69.

Getz LL, Carter CS, Gavish L (1981) The mating system of the Prairie vole (*Microtus ochrogaster*): field and laboratory evidence for pair-bonding. Behavioral Ecology and Sociobiology 8 (3):189-194.

Grant PR (1972) Interspecific competition among rodents. Annual Review of Ecology and Systematics 3:79-106.

Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour 28 (4):1140-1162.

Hamilton WD (1964) The genetical evolution of social behavior. Journal of Theoretical Biology 7:1-52.

Hayes JP, Speakman JR, Racey PA (1992) The contributions of local heating and reducing exposed surface area to the energetic benefits of huddling by short-tailed field voles (Microtus agrestis). Physiological Zoology 65 (4):742-762.

Insel TR, Preston S, Winslow JT (1995) Mating in the monogamous male: behavioral consequences. Physiology & Behavior 57 (4):615-627.

Jackson DM, Trayhurn P, Speakman JR (2001) Associations between energetics and over-winter survival in the short-tailed field vole *Microtus agrestis*. Journal of Animal Ecology 70 (4):633-640.

Lima SL (1989) Iterated prisoner's dilemma: an approach to evolutionarily stable cooperation. The American Naturalist 134 (5):828-834.

Livoreil B, Gouat P, Baudoin C (1993) A comparative study of social behaviour of two sympatric ground squirrels (*Spermophilus spilosoma, S. mexicanus*). Ethology 93 (3):236-246.

Maynard Smith J (1983) Game theory and the evolution of cooperation. In: Bendall DS (ed) Evolution from molecules to men Cambridge University Press, Cambridge, pp 445-456

Nowak MA, May RM (1992) Evolutionary games and spatial chaos. Nature 359 (6398):826-829.

Patris B, Baudoin C (1998) Female sexual preferences differ in *Mus spicilegus* and *Mus musculus domesticus*: the role of familiarization and sexual experience. Animal Behaviour 56:1465-1470.

Patris B, Baudoin C (2000) A comparative study of parental care between two rodent species: implications for the mating system of the mound-building mouse *Mus spicilegus*. Behavioural Processes 51 (1-3):35-43.

Patris B, Gouat P, Jacquot C, Christophe N, Baudoin C (2002) Agonistic and sociable behaviors in the mound-building mice, *Mus spicilegus*: A comparative study with *Mus musculus domesticus*. Aggressive Behavior 28 (1):75-84.

Perrin N, Mazalov V (2000) Local competition, inbreeding, and the evolution of sex biased dispersal. The American Naturalist 155:116-127.

Perrin N, Goudet J (2001) Inbreeding, kinship, and the evolution of natal dispersal. In: Clobert J, Danchin E, Dhondt AA, Nichols JD (eds) Dispersal: individual, population and community. Oxford University Press, Oxford, pp 127-146

Sachser N, Schwarz-Weig E, Keil A, Epplen JT (1999) Behavioural strategies, testis size, and reproductive success in two caviomorph rodents with different mating systems. Behaviour 136:1203-1217.

Shapiro LE, Austin D, Ward SE, Dewsbury DA (1986) Familiarity and female mate choice in two species of voles (*Microtus ochrogaster* and *Microtus montanus*). Animal Behaviour 34:90-97.

Sherman PW (1977) Nepotism and the evolution of alarm calls. Science 197 (4310):1246-1253.

Simeonovska-Nikolova DM (2003) Social relationships and social structure of the mound-building mouse (*Mus spicilegus*) in intraspecific cage groups. Acta Ethologica 6:39-45.

Suchomelova E, Munclinger P, Frynta D (1998) New evidence of pseudosexual behaviour and female aggression in mice: neutral cage interactions in *Mus spicilegus* and *Mus spretus* (Rodentia : Muridae). Folia Zoologica 47 (4):241-247.

Trivers RL (1971) The evolution of reciprocal altruism. The Quarterly Review of Biology 46 (1):35-57.

Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) Sexual selection and the descent of man. Aldine, Chicago, pp 136-176

Vander Wall SBV (1990) Food hoarding in animals. University of Chicago Press, Chicago

Walters JR, Seyfarth RM (1986) Conflict and cooperation. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW (eds) Primate societies. University of Chicago Press, pp 306-317

Wolff JO (1993) What is the role of adults in mammalian juvenile dispersal? Oikos 68 (1):173-176.

Wrangham RW (1981) Drinking competition in vervet monkeys. Animal Behaviour 29:904-910.

Wrangham RW (1983) Social relationships in comparative perspective. In: Hinde R (ed) Primate social relationships: an integrated approach. Oxford: Blackwell, pp 325-334