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Reproductive strategies and group dynamics in the genus *Acomys*

Ph.D. Thesis

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Annotation:

Reproductive behaviour and aspects of group dynamics in the genus *Acomys* were studied in the respect to the individuals' physical condition, life history traits and social environment. Three of the presented studies reveal the important effect of social environment on the behaviour of group members to the new-coming male and reproductive behaviour of females (sex ratio of the pups and litter size). The other two studies investigate the costs associated with group living and cooperative breeding in Sinai spiny mice and the factors influencing alloparental behaviour. Results of this Ph.D. thesis reveal several aspects of social and reproductive behaviour of group-living mammals and contribute to the understanding of the formation and maintenance of the societies in general.

Declaration (in Czech):

Prohlašuji, že svou dizertační práci jsem vypracovala samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury.

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List of papers and author's contribution

The thesis is based on the following papers:

I. **Čížková B.**, Šumbera R. & Frynta D. (2011). A new member or intruder: how do Sinai spiny mouse (*Acomys dimidiatus*) families respond to a male newcomer? Behaviour 148: 889-908 (IF = 1.657)
Barbora Čížková participated in laboratory work gathering data, statistical analysis, completing the literature sources and writing the manuscript.

II. Nováková M., **Vašáková B.**, Kutalová H., Galeštoková K., Průšová K., Šmilauer P., Šumbera R. & Frynta D. (2010). Secondary sex ratios do not support maternal manipulation: extensive data from laboratory colonies of spiny mice (Muridae: *Acomys*). Behavioral Ecology and Sociobiology 64: 371-379 (IF = 3.209)
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Introduction

1. Group dynamics

Many animal species form some sort of social units, from vast aggregations through mid-sized colonies to smaller familial cooperative groups. Aggregations and colonies consist mostly of unfamiliar and unrelated individuals, gathering predominantly seasonally or for short time on breeding sites, at clumped food resources or during migrations. Familial groups, to the contrary, are more permanent and consist mostly of animals with genetic relationships and dominance hierarchy. Formation of the breeding colonies was recently explained through so-called by-product approach: colonies form as a by-product of individual choice of territory and/or a mate (Wagner et al., 2000). To the contrary, according to the traditional or functional approach, groups form due to certain purpose: e.g. better protection against predators (see below), during migration or due to some ecological constraints.

Proximate factor leading to the formation of family groups in mammals is most often natal philopatry (Solomon, 2003; Ebensperger & Hayes, 2008). Philopatric individuals are sexually maturated offspring that delay or cease dispersal from the natal group, creating than extended families. Natal philopatry occurs in various species of mammals and in variety of social organizations (Woodroffe et al., 1995; Koprowski, 1996; Archie et al., 2006; Lutermann et al., 2006; Tsai & Mann, 2012). Apart from philopatry, group dynamics is affected by processes such as dispersal of single individuals or cohorts. Emigration of several individuals may lead to the complete or partial break-up of the maternal group and separated cohort may then create a daughter group (e.g., Waterman, 2002). Single individuals who decide to leave search for suitable breeding site (territory) and/or breeding opportunity. In the nature, we can sometimes observe unsettled natal dispersers, described as wanderers (e.g., Getz et al., 1993). Those individuals wander through an area, visiting other social groups and benefiting from extra-pair copulations (e.g., Ophir et al., 2008). Alternatively, they may attempt to establish own social group (e.g., Lacey & Wieczorek, 2004). If the chances to do so are low due to e.g. high resource competition or population density, and living conditions for solitaires are unfavourable, they may join established family groups of unrelated conspecifics.

Recruitment of a new, unrelated individual into a social unit is an important part of social dynamics in mammalian species. It has been suggested that dispersal is depended upon the interactions between the members of the natal group and dispersers (e.g., Rosenberry et al. 2001). However, it was documented that dispersal and integration into the unfamiliar group also rely on the behaviour of residents of the new group (e.g., Griesser et al., 2007). In most rodent species, group members are aggressive towards adult newcomers (Crowcroft & Rowe, 1963; Butler, 1980; Adams & Boice, 1989; Blanchard et al., 1988; Brant et al., 1998; Back et al., 2002). Resident breeding male protects its reproductive opportunity and aggressive conflicts between resident and newcomer are frequent (e.g., Back et al., 2002). In most cases, resident male evicts the intruding individual successfully (Blanchard et al., 1988; Palanza et al., 1996). However, on some occasions the newcomer male defeats and replaces the resident (Ewer, 1971; Palanza et al., 1996). To maximize reproductive efforts and avoid costs associated with aggressive conflicts, male dispersers of pine voles *Microtus pinetorum* predominantly join the groups with no male (Solomon et al., 1998). However, elevated aggression of the lactating females of the common house mouse against male newcomers was reported (Palanza et al., 1996), even if dominant females are usually more aggressive against the same sex intruders (Butler, 1980; Parmigiani, 1989). Female aggression towards a female intruder is probably related to competition for breeding opportunities, whereas aggression toward a male newcomer or self-abortion (i.e. the Bruce effect) is the response to the elevated risk of infanticide caused by a strange male (e.g., Stubbe & Janke, 1994).

Nevertheless, “immigrants” may settle in the new group, usually gaining some of the low-ranking position in the hierarchy (e.g., Andrzejewski et al., 1963; Griesser et al., 2007). In cooperative species, successful integration into the new group may also depend on the group size and its composition; small groups rather accept new member because they need additional helper(s) (e.g., Schaffner & French, 1997).

2. Reproductive strategies of cooperative breeders

Search and comparison of the costs and benefits associated with group living is crucial to understand mechanisms of evolution of animal societies. Among the most highlighted costs for the particular individual living in group belong: delayed or complete suppression of reproduction (e.g. Saltzman et al., 2009; Pettitt & Waterman, 2011), transmission of diseases and parasites (e.g. Altizer et al., 2003), higher competition for resources (e.g. Scott & Lockard, 2006) and increased conspicuousness in large groups (e.g. Ioannou & Krause, 2008). However, evolution of group living predicts that the benefits of individuals must outweigh the costs (e.g. Emlen, 1994; Hatchwell & Komdeur, 2000). Overriding benefits resulting from group living may be the driving force of animal cohesion; e.g. improved defence against the predators (e.g. Graw & Manson, 2007; Edwards & Waterman, 2011), more effective searching for food or hunting (e.g. Creel & Creel, 1995), social thermoregulation (e.g. Willis & Brigham, 2007) and cooperative breeding (e.g. Clutton-Brock et al., 2001). Impact of the latter on individual fitness has been intensively studied throughout the animal kingdom primarily due to unequal distribution of benefits between participating individuals (Emlen, 1994; Solomon & French, 1997; Hatchwell & Komdeur, 2000).

Cooperative breeding in mammals occurs in two forms according to the level of reproductive skew. Groups with low reproductive skew contain several breeding individuals (plural breeders), while only one reproductively active pair usually occurs in groups with high reproductive skew (singular breeders). Other group members usually help with rearing of the young (Krebs & Davies, 1997; Earley & Dugatkin, 2010). Such assistance may include feeding of the pups, warming them, grooming, carrying, or simply taking care of them (babysitting), while their mother forages (Riedman, 1982; Solomon & French, 1997). Helpers often stay in the group at the expense of their own reproduction, which may be suppressed by dominant individuals through several mechanisms, such as behavioural (e.g. Asa & Valdespino, 1998) or physiological suppression (e.g. Creel et al., 1992), monopolization of the resources crucial for breeding (shelter, food) (e.g. Nichols et al., 2012), killing of subordinates’ pups and eviction from the group (e.g. Clutton-Brock et al., 1998; Young et al., 2006).

Despite the above described costs for helpers, staying at a group is often more beneficial than leaving. Dispersal is often connected with higher mortality due to increased risk of predation and stress and/or energy depletion (e.g. Greenwood, 1980). On the other hand, if the restrictions in group impose fitness costs that outweigh the benefits, helpers are driven to leave their natal area. In such case, dominant pair should rather loose strict control over reproduction and concede some breeding events to subordinates creating then plural breeders that at least to some extent, share the reproduction evenly (Creel & Waser, 1991; Cant, 2000; Packer & Pusey, 1985). Sometimes, sharing of reproduction may result in communal breeding (e.g. Boyce & Boyce, 1988; Pilastro, 1992; Blumstein & Armitage, 1999; Schradin & Pillay, 2004).

2.1. Communal nesting, nursing and retrieving

Proximate factor leading to the formation of family groups in rodents and communal nests are delayed dispersal, as mentioned above (Solomon, 2003). In several species, philopatry occurs predominantly due to limited availability of crucial resources such as food, shelters, mates and nesting sites, their saturation and/or distribution (Jarvis et al. 1994; Johnson et al., 2002; Clutton-Brock & Lukas, 2012). For instance, high local population density leads to philopatry in most rodent species (Lambin & Krebs, 1991; Wolff 1992; Lacey & Wieczorek, 2004; Randall et al., 2005; Lucia et al., 2008). On the other hand, occurrence of communal nests is not associated with availability of breeding sites in fat dormice *Glis glis* (Pilastro et al., 1994).

It was already mentioned that communal rearing of the pups includes grooming, thermoregulation, pup defence against predators, retrieving and nursing of alien pups (e.g., Hayes, 2000). Retrieving and nursing are considered to be the most costly forms of alloparental behaviour. Nursing requires increased food intake for the female and affects her subsequent reproductive success (e.g., Clutton-Brock et al., 1989). Retrieving of the pups to the nest restricts female's movement and increases predation risk (e.g., Gilchrist, 2004). However, benefits resulting for individuals participating in those activities should outweigh the costs. Nevertheless, communal nursing often occurs in species with large litters and sometimes is considered to be a by-product of communal nesting and group living generally (e.g., Manning et al., 1995). In larger litters, containing age-matched pups, discrimination of own pups may be too difficult especially in less experienced females and chasing away the alien pups may be more energetically costly than nursing them (e.g., Packer et al., 1992). Retrieving of alien pups may imply even higher costs than nursing due to increased risk of predation. Thus, while allo-nursing may be result of misdirect parental care, retrieving of alien pups should be more directed. However, in some species females retrieve (and nurse) alien pups indiscriminately even though they are able to recognize own pups (e.g., Jesseau et al., 2008). On the contrary, in other species females nurse strange pups but do not retrieve them (e.g., Eberle & Kappeler, 2006). Thus, joining in alloparental care that is associated with increased costs may also depend upon other social factors.

Individuals participating in cooperative breeding may suffer apparent costs (see above). Potential costs associated with cooperative breeding may be reduced by helping the relative conspecifics and thus enhance indirect fitness (Hamilton, 1964). Due to philopatric tendencies, social units (and/or communal nests) consist predominantly of close kin in many rodent species (e.g. Pilastro et al., 1994; Dobson et al., 2000; Lacey & Wieczorek, 2004). Several studies documented, that overall reproductive success of kin co-nesting females is higher than in non-kin ones (König, 1993; 1994b; Schultz & Lore, 1993; Dobson et al., 2000; Mappes et al., 1995). In some rodent species, familiarity between nestmates also plays a role; it reduces aggression and enhances formation of female alliances (D'Amato 1993; Schultz & Lore, 1993; König, 1994b). It is also one of the important mechanisms in the process of recognition (e.g. Penn & Frommen, 2010), which is inseparable part of successful kin-selected cooperation.

Reproductive success of communally nesting females is usually measured by number of born and weaned pups, their mortality and further survival. Communally breeding females of house mice *Mus domesticus* have higher reproductive success than solitarily or singly nesting females (Sayler & Salmon, 1969; König, 1993; 1994a; Manning et al., 1995). Higher survival rate for yearling females born and reared by group-living individuals has been found also in other rodents (Blumstein & Armitage, 1998; Lacey, 2004). These results indicate that communal care of pups is beneficial for their survival. On the other hand, communal nesting might be a by-product of group living in species, where number of nesting individuals does not affect reproductive success, such as white footed and deer mice *Peromyscus maniculatus* and *P. leucopus*, great gerbils *Rhombomys opimus* or degus

Octodon degus (e.g. Wolff, 1994; Randall et al., 2005; Ebensperger et al., 2007). Alternatively, the benefits of cooperative breeding may be exhibited in different form than traditionally measured reproductive success; e.g. decreased energy cost during lactation, higher amount of time spent by foraging and other activities. In many rodent species, however, solitary nesting seems to be better option than communal at least in terms of short-term reproductive success (Boyce & Boyce, 1988; Schultz & Lore, 1993; Blumstein & Armitage, 1998; Gerlach & Bartmann, 2002; Lacey, 2004; Smorkatchewa & Orlova, 2011). Yet, communal nests in these species occur in nature, probably due to some ecological constraints and benefits of grouping (see above).

2.2. The effect of litter size

One of the important criterions of the reproductive success in cooperative and non-cooperative breeders is litter size. This is apparent especially in polycotous species where the reproductive effort is often higher than in monocotous ones. Litter size affects future breeding success in females, postnatal maternal care and subsequent offspring quantity and quality (Mendl, 1988; König, 1994a; Neuhaus, 2000; Bales et al., 2002; Oksanen et al., 2002).

Although higher litter size may imply higher reproductive success, it is often associated to the increased costs (e.g., Oksanen et al., 2002). Manipulative experiments with litter size showed that females with enlarged litters decreased in body mass, delayed subsequent breeding event due to prolonged lactation and have higher mortality during nursing in some cases (Koskela, 1998; Huber et al., 1999; Oksanen et al., 2002). With increasing litter size, amount of maternal investment decreases per individual, thus leading to the production of the pups of “lower quality”. For example, pups from larger litters exhibit lower weight at birth and/or weaning, or higher mortality (König, 1988; Mendl, 1988; Koskela, 1998; Humphries & Boutin, 2000; Guerra & Nunes, 2001; Oksanen et al., 2002). Pups with higher birth weight (i.e. born in smaller litters) are also less susceptible to diseases than pups with lower weights (e.g., Oksanen et al., 2003). Even though females of house mice with enlarged litters increase their milk production, energy content of the milk did not enhance equally (e.g., König et al., 1988; Kenagy et al., 1990). Higher mortality rates were, on the other hand, observed also in very small litters (e.g. one pup) in polycotous species (Mendl, 1988; Sikes, 1995; Cantoni & Brown, 1997). Rearing only one pup may be so costly, that females let the pup die and prepare for next reproduction (e.g., Cantoni & Brown, 1997). Alternatively, high mortality of small litters may be caused by decreased thermoregulation (e.g., Mendl, 1988).

Influence of the litter size on pup survival and quality has already been mentioned. However, litter size is also affected by many various factors. For example, litter size is limited by mothers' body size; females with larger body mass often give birth to larger litters (e.g., Tuomi, 1980; König, 1993; Campbell & Slade, 1995; Rödel et al., 2008). Dominance status of the mother also plays a role in several species; low-ranking females have smaller litters (e.g., Rödel et al., 2008). Scheibler et al. (2005) even documented negative correlation between litter size and family size. Reproductive experience (number of delivered litters) has also great impact on litter size (e.g., Innes & Millar, 1990; Kai et al., 1995; Tkadlec & Krejčová, 2001). Due to increased costs associated with large litters, mothers may adjust litter size by infanticide or just letting several pups die (e.g., Mendl, 1988; Poigner et al., 2000). In this way, females may invest energy and resources to wean less pups of higher "quality". However, in species with precocial pups, the prenatal investment is too high (Kam et al., 2006) and killing of pups after birth may be too costly for these species. Better option for species with high prenatal investment may be cooperative breeding with benefits of gaining helper.

2.3 Sex ratio adjustment in cooperative breeders

Direct fitness of the breeding individuals in cooperative groups is also affected by the number of the helpers in the group (e.g., Russell et al., 2003). If the assistance of the helping individual is essential for the survival of breeders' offspring and their reproductive efforts, breeders should try to enhance the number of the helpers in the group. If only one sex is helpful, cooperative breeders should overproduce the helping sex (Griffin et al., 2005).

According to the helper repayment hypothesis (e.g., Emlen et al., 1996) sex helping with rearing of the breeders' offspring become less costly to produce and partially repay the costs associated with its production. Fisher's principle of equal investment in the sexes then predicts the production of helping sex because it is less costly (Fisher, 1930). Moreover, production of the helpers pays off only in the case that their contribution to the breeders' fitness outweighs the direct fitness loss connected with the production of the helpers (Koenig & Walters, 1999). For example in Alpine marmots (*Marmota marmota*), the species with social thermoregulation during winter hibernation, increased number of subordinate males enhances the juvenile survival (Allainé et al., 2000). Indeed, the sex ratio at birth and weaning across the Alpine marmots population is biased in favour of the males. Nevertheless, even in cooperative species with clearly defined contribution of the helpers, sex ratio is not consistent in the whole population. Several studies show that greater sex ratio adjustment is connected to the extent of the benefits provided by the helpers and the number of the helpers in the group (e.g., Penn & Weissing, 2000; Griffin et al., 2005).

Although these factors seem to be crucial in the sex ratio adjustment, several other factors may play a role. For instance, females should produce an excess of the more profitable sex in accord to their own phenotypic condition (Trivers & Willard, 1973). If mothers vary in their condition, the helping sex may not be always the profitable one. Alternatively, production of the helping sex may be dependent upon the environmental conditions. For example in Seychelles warblers (*Acrocephalus sechellensis*), sex ratio is biased in favour of helping sex only in territories of high quality (Komdeur 1996; Komdeur et al., 1997). Some studies considered also life-history traits of the breeders and social factors such as dominance status, population density, group size, and group composition that may affect sex ratio adjustment (e.g., Emlen et al., 1986; Lambin, 1994; Russell et al., 2003; Scheibler et al., 2005).

Research on reproductive strategies and group dynamics of the social species significantly contributes to the understanding of the social relationships within societies and mechanisms of their formation, maintenance and perishing. Higher reproductive success associated with enhanced survival in communal dens may be the driving force of evolution of sociality in many mammalian species. However, reproductive success may be affected by many social and life history factors, such as kinship and familiarity between co-nesting females, litter size and sex ratio. Thus, revealing of the factors that influence reproductive behaviour and group dynamics in social mammals may elucidate to what purpose sociality serves.

3. Genus Acomys as a model species

Spiny mice are highly social rodents, living in family groups in rocky areas, arid woodlands, semi-deserts and/or savannahs of the Middle East and Northern Africa (Nowak, 1999). Most of the species are primarily nocturnal and omnivorous, but see Shargal et al. (2000). Their activity peaks in the early morning and at dusk. These small rodents do not build nests; they use rocky crevices and other rodents' burrow as a shelter. In the arid environments with low resources, group-living individuals may benefit from social thermoregulation and communal care of pups in the families (e.g., Porter et al., 1980).

The Sinai spiny mice (*Acomys dimidiatus*) was previously considered a subspecies of the Cairo spiny mice (*A. cahirinus*) and even synonymised with it, but it is now considered a distinct species according to Musser & Carleton (2005) and Volobouev et al. (2007). Natural social structure of the Sinai spiny mice is unknown, but Cairo spiny mice live in small family groups composed of a dominant male, several breeding females and their offspring (Delany & Happold, 1979; Grzimek, 2003). Due to similarity in biology of the both species and our observation from the captivity (living in large groups and communal nesting), it is likely that Sinai spiny mice have similar social system to that of Cairo spiny mice in the wild. The body mass of adult Sinai spiny mice range from 45 to 60 g (Frynta et al., 2011). Reproduction is continual and females have postpartum oestrous (Čížková, unpubl. data). If fertilization is not successful, copulation re-occurs in 9 to 11 days, similar to Cairo spiny mice (Peitz, 1981). After long gestation period contrary to other muroid rodents, females Sinai spiny mice deliver small litters with one to six precocial pups (Frynta et al., 2011). Pups are weaned at 3-4 weeks of age and reach sexual maturity at about two months.

Sinai spiny mice are a suitable model species for studying reproductive behaviour and group dynamics owing to their high level of sociality and cooperative behaviour. Despite extensive knowledge on the physiology and recognition abilities of the genus *Acomys* (predominantly Cairo spiny mice) (e.g., Kam & Degen, 1993; Degen et al., 2009; Porter, 1988), studies on their social behaviour are rare. However, aspects of cooperative behaviour during parturition in Cairo spiny mouse was firstly described by Dieterlen (1962). Mostly reproductively experienced females or males of Cairo spiny mice assist in delivery by grabbing the half-expelled foetus facilitating the delivery and licking it. Assistance of the males is not so surprising knowing that males exhibit high level of paternal care; they huddle with the pups, groom and lick them (Makin & Porter, 1984). According to our observation, Sinai spiny mice always nest communally, gathering the pups in one nest (Čížková, unpubl. data). Communally nesting Cairo spiny mice participate in nursing and retrieving of the alien pups (Porter et al., 1980; Porter & Doane, 1978). Porter & Doane (1978) reported that cooperative care is affected by the dominance hierarchy; dominant females nurse own pups and those from subordinate female trying to chase her away by aggressive behaviour. These studies indicate that group living and cooperation is typical in spiny mice. However, the factors affecting cooperative breeding and sociality in these species are mostly unknown. Similarly, information on other aspects of reproductive behaviour such as factors affecting litter size or sex ratio is still lacking.

Although spiny mice breed easily in captivity, studies on social relationships among group members and overall group dynamics of the families are mostly lacking. Porter (1976) shows that females are more dominant than males in their home ranges. However, studies on dominance relationships, recruitment of the group members and their dispersal in established families are lacking. Anecdotal observation on captive animals (e.g., breeding males chase young males; young males are more aggressive to each other after removal of the breeding male) indicates that male is the dispersive sex in Sinai spine mice. Due to harsh living condition (arid regions), we may suppose that dispersing males may attempt to join an established family group of unrelated conspecifics.

Aim of the PhD. thesis

Aim of this PhD. thesis is to clarify various aspects of the reproductive and social behaviour of the group-living spiny mice species and gain information on the factors influencing formation and maintenance of the mammalian societies and contribution to the evolution of sociality in general. Specific objectives of the PhD. thesis are following:

1) Determination of the effects of the life history and intra-social parameters on the ability of the male newcomer to successfully integrate into the established family group in Sinai spiny mice.
2) Revealing ability of the mothers to regulate the sex ratio of the pups by analysis of the effect of the mother condition and social environment in four species of the genus *Acomys*.
3) Assessment of the influence of the life history and social parameters on the litter size in four species of the genus *Acomys*.
4) Determination of the costs and benefits of communal and single nesting, and analysis of the effect of kinship and familiarity between co-nesting females on the reproductive success of the females.
5) Assessment of the contribution of the communally nesting females in alloparental behaviour in dependency on the kinship and familiarity of the females and other social factors.

Summary of the results and conclusions

According to our **study I (Čížková et al., 2011)**, the settlement of dispersing male of Sinai spiny mice relies mainly on the actual reproductive situation in the group. Presence of the pregnant or lactating females caused increased aggression toward new-coming male from the family members. If the resident breeding male was present, he was the initiator of the most aggressive contacts toward newcomer. Nevertheless, even in the absence of the resident male, the settlement of the newcomer was no easier due to high aggression from the breeding females and young adult males (sexually matured offspring). Comparison of the situations in the families before arrival of the newcomer, immediately and one month after it shows that after all newcomer male is able to settle in the new group; number of aggressive and non-aggressive contacts of the family members to the newcomer before and one month after addition was similarly low. Our study indicates that acceptance of the new-coming male into the established family does not rely only on the composition of the group (absence or presence of the breeding male), but also on the actual reproductive state of the breeding females.

Similarly, composition of the group and actual social environment has the main effect on the sex ratio of spiny mice and litter size in **study II and III (Nováková et al., 2010; Frynta et al., 2011)**. Sex ratio in four species of spiny mice is affected by number of immature males, number of immature females and number of breeding males. Nevertheless, the results are not consistent for all four studied species (*Acomys dimidiatus, A. cahirinus, A. cilicicus and A. sp.*) and the same factor show even opposite effect in separate analyses of particular species. No significant effect of the factors associated with condition of the mother (e.g., age, social status, parity and postpartum oestrous) and sex ratio close to 1:1 (only *Acomys sp.* showed female-biased sex ratio) may be connected to the long period of breeding in laboratory (see stable) environment. Spiny mice are used to live in pretty harsh and unpredictable environment with seasonally unavailable resources. Thus, they may regulate their breeding (e.g., sex ratio, litter size) only in accord with actually unfavourable environment.

Besides social environment (number of immature females) results of **study III (Frynta et al., 2011)** also revealed the significant effect of maternal condition (body weight) on the litter size. Heavier females (i.e., in better body condition) have larger litters. Positive effect of immature females on the litter size may correspond to the advantages of the cooperative breeding. Spiny mice are known for communal nursing, assistance in delivery (see above) and huddling of the whole group that indicates social thermoregulation. Thus, larger group size with more assisting females has positive effect on reproductive success.

On the contrary, results of **study IV (Čížková & Šumbera, in prep)** indicate that in terms of reproductive success, monogamy is more beneficial for females than communality; monogamously nesting females had higher production of the pups than those nesting communally. In the case of communally nesting females, kinship and familiarity between females play a role; the lowest reproductive success was observed in non-kin unfamiliar females. The dominance status (defined according the weight of the mother and production of the pups) in co-nesting females also has a significant effect on the reproductive success; subordinate females have higher mortality of the pups and smaller litters. However, communal nesting, kinship and familiarity have no beneficial effect on weight gain of pups. Despite some costs associated to communal breeding, group living in Sinai spiny mice may be beneficial in terms of social thermoregulation or other features of cooperative behaviour (e.g., assistance in delivery).

These conclusions are consistent with **study V (Tučková et al., in prep)**. Results of this study indicate that communal nursing and retrieving alien pups is a by-product of communal nesting and group living generally. Co-nesting females nurse and retrieve alien pups predominantly if they lack breeding experience and/or their litters are age-matched. This may indicate low ability of pup recognition in some situations. We suppose that Sinai spiny mice are able to discriminate between own and alien pups if the costs associated with certain behaviour are too high. This suggestion corresponds with other results of this study: females rather nurse than retrieve alien pups and have a tendency to retrieve own pup faster than the alien one.

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Study I

Čížková B., Šumbera R. & Frynta D. (2011). A new member or intruder: how do Sinai spiny mouse (*Acomys dimidiatus*) families respond to a male newcomer? Behaviour 148: 889-908

A new member or an intruder: how do Sinai spiny mouse (*Acomys dimidiatus*) families respond to a male newcomer?

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Summary

Recruitment of unrelated individuals into a group plays an important role in the social life of the group living animals. The main goal of our study was to analyze the reactions of established, breeding families of the Sinai spiny mouse, *Acomys dimidiatus* (Muridae, Rodentia), a social species with precocial pups, to male newcomers in the presence and the absence of a breeding resident male. We compared the behaviour of family members of different sex or age to the presence of a new male. The number of non-aggressive and aggressive interactions with the focal male (resident/newcomer male) was recorded during three periods: before, during and one month after the addition of the newcomer. Only a few aggressive and/or non-aggressive types of contacts occurred before and one month after the addition of the new male. During the experiment, both types of contacts arose, but the results were highly variable. Increased aggressive behaviour of the family toward the intruder was explained mainly by the presence of pregnant or lactating females, which suggests that aggression towards a male newcomer is associated with the reproductive status of females. This phenomenon is most likely connected with the counter-infanticide strategy.

Keywords: Sinai spiny mouse, family dynamics, immigration, social behaviour, aggression, *Acomys*, familiarity.

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Study II

Nováková M., **Vašáková B.**, Kutalová H., Galeštoková K., Průšová K., Šmilauer P., Šumbera R. & Frynta D. (2010). Secondary sex ratios do not support maternal manipulation: extensive data from laboratory colonies of spiny mice (Muridae: *Acomys*). Behavioral Ecology and Sociobiology 64: 371-379

Behav Ecol Sociobiol (2010) 64:371–379
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ORIGINAL PAPER

Secondary sex ratios do not support maternal manipulation: extensive data from laboratory colonies of spiny mice (Muridae: *Acomys*)

Marcela Nováková · Barbora Vašáková · Hana Kutalová · Katarina Galeštoková · Klára Průšová · Petr Šmilauer · Radim Šumbera · Daniel Frynta

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Abstract Spiny mice of the genus *Acomys* (Muridae) represent a very suitable mammalian model for studying factors influencing the secondary sex ratio (SSR). The maternal effort in these rodents is extremely biased in favour of the prenatal period and, therefore, maternal manipulation of the SSR is potentially more advantageous. We studied the SSR in four populations/species of spiny mice kept in family groups consisting of two closely related females, one non-relative male and their descendants. The groups were established from founding animals aged about 3 months (maturing age) and were allowed to breed freely for several months. Each litter was sexed after birth, and relevant data were thoroughly recorded. Altogether, data were collected on 1684 litters: 189 of *Acomys sp.* from Iran, 203 of *A. cilicicus*, 875 of *A. cahirinus*, and 417 of *A. dimidiatus*. We recorded the sex of 4048 newborns of which 1995 were males and 2053 were females. The overall sex ratio was close to 1:1 (49.2%). Generalized linear mixed models and/or generalized linear models were constructed to evaluate the effect of four life history and eight social variables on the sex ratio. No consistent effects of these variables on the sex ratio were found and, interestingly, none of the variables associated with maternal life history had any effect on the sex ratio. Three factors associated with group composition (i.e. the number of immature males, the number of immature females and the number of breeding females) did have significant effects on the sex ratio, but these effects were not consistent across the studied species. In conclusion, our evaluation of this large dataset revealed that the sex ratio in spiny mice is surprisingly stable.

Keywords Parental effort · Rodents · Sex allocation · Sex ratio · Social behaviour

Communicated by G.Wilkinson

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Study III

Frynta D., Fraňková M., **Čížková B.**, Skarlandtová H., Galeštoková K., Průšová K., Šmilauer P. & Šumbera R. (2011). Social and life history correlates of litter size in captive colonies of precocial spiny mice (*Acomys*). Acta Theriologica 56: 289-295

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SHORT COMMUNICATION

Social and life history correlates of litter size in captive colonies of precocial spiny mice (*Acomys*)

Daniel Frynta · Marcela Fraňková · Barbora Čížková · Hana Skarlandtová · Katarina Galeštoková · Klára Průšová · Petr Šmilauer · Radim Šumbera

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Abstract Litter size is an important component of life history contributing to reproductive success in many animals. Among muroid rodents, spiny mice of the genus *Acomys* are exceptional because they produce large precocial offspring after a long gestation. We analyzed data on 1,809 litters from laboratory colonies of spiny mice from the *cahirinus-dimidiatus* group: *Acomys cahirinus*, *Acomys cilicicus*, *Acomys* sp. (Iran), and *Acomys dimidiatus*. Generalized mixed-effect models revealed that litter size increased with maternal body weight and/or number of immature females present in the family group. Thus, both maternal body reserves and presence of immature descendants demonstrating previous reproductive success enhance further reproduction in this social rodent.

Keywords *Acomys* · Rodents · Litter size · Maternal investment · Precocial life history

Communicated by: Jan M. Wójcik

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Study IV

Čížková B. & Šumbera R. (in prep). Costs and benefits of communal breeding in Sinai spiny mouse (*Acomys dimidiatus*): Effect of relatedness and familiarity.

This study will be submitted in a few months in Animal Behaviour.

Costs and benefits of communal breeding in Sinai spiny mouse (*Acomys dimidiatus*): Effect of relatedness and familiarity

Barbora Čížková and Radim Šumbera

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Abstract

In group living mammals, communal breeding may provide apparent advantages to the participating individuals, but it could be also connected with some remarkable costs. In our study we compared reproductive success (number of pups born and weaned, number of litters, litter size, mortality of the pups and pups weight gain) of singly (female and male) and communally (two females and male) nesting females of Sinai spiny mice (*Acomys dimidiatus*). We analyzed their reproductive success also with respect to the kinship and familiarity and supposed dominance between communally nesting females. We also investigated influence of several other factors on female's reproductive success. Mortality of the pups and litter size were influenced by mother's identity group age and family identity in all females. Heavier females had larger litters. We found that singly nesting females gave birth and weaned a higher number of pups and delivered more and larger litters, whereas pups weight gain and mortality were comparable between the single and communal females. In communally breeding females, kinship, familiarity and dominance between females marginally affected reproductive success; the lowest reproductive success was observed in non-kin unfamiliar females and subordinate females. Thus, we assume that communal breeding in this species may be only a by-product of group living due to the enhanced costs of reproductive success related probably to competition between co-nesting females. It seems that advantages of Sinai Spiny mice sociality are probably associated with other forms of cooperation (e.g., social thermoregulation).

Keywords: spiny mice, communal breeding, kinship, familiarity, reproductive success

Study V

Tučková V., Šumbera R. & **Čížková B**. (in prep). Alloparental behaviour in Sinai spiny mice *Acomys dimidiatus*: The case of misdirect parental care?

This study will be submitted in a few months in Behavioural Ecology and Sociobiology.

Alloparental behaviour in Sinai spiny mice *Acomys dimidiatus*: The case of misdirect parental care?

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Abstract

Communal breeding, when reproducing females share a nest and take care of their pups mutually, occurs in several mammalian species. According to the kin selection theory, alloparental behaviour should appear predominantly between related conspecifics. However, familiarity between females, a prerequisite for reciprocal altruism, plays also a role. The aim of our study was to analyse the effect of the kinship and familiarity on the occurrence of two types of alloparental care (nursing of pups and retrieving them to the nest) in cooperatively breeding Sinai spiny mice *Acomys dimidiatus*. In addition, the effect of other social factors influencing alloparental care was tested. The kinship and familiarity had no significant effect on the alloparental care. Nursing of alien pups depended on the reproductive experience of females measured as a number of weaned litters and the age difference between litters of both females. Less experienced females nursed alien pups more often than experienced ones. With increasing age difference between litters, females nursed preferentially their own pups. Similarly, retrieving of alien pup was affected by the age disparity between litters; with increased difference, the females retrieved rather own pup. These results indicate that occurrence of alloparental care in Sinai spiny mouse is probably more related to the difficulties of the pup recognition in communal nests and misdirected parental care than kin selection strategy. However, females Sinai spiny mice rather nursed alien pups than retrieved them. It indicates higher energy expenditure associated with retrieving and ability to recognize own pups if the costs associated with alloparental behaviour is too high.

Keywords: spiny mice, alloparental behaviour, nursing, retrieving, pup recognition

Curriculum vitae

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Higher education

2001-2004	Bc. study at the Faculty of Science, University of South Bohemia, České Budějovice; field study: zoology; Bc. thesis: Social interactions in *Acomys dimidiatus* and *A. cilicicus*
2004-2006	M.Sc. study at the Faculty of Science, University of South Bohemia, České Budějovice; field study: zoology; M.Sc. thesis: Effect of simulated immigration on the social behaviour in Sinai spiny mice (*Acomys dimidiatus*)
Since 2007	PhD. study at the Faculty of Science, University of South Bohemia, České Budějovice; field study: zoology; PhD. thesis: Reproductive strategies and group dynamics in the genus *Acomys*

Research interest

Behavioural ecology and ethology of mammals

Projects and stay abroad

Finished:

2005 one month PPP DAAD scholarship at the University of Duisburg-Essen in Germany

2008 Reproductive strategy and the effect of the presence of the social partner on the reproductive success of Sinai spiny mice (*Acomys dimidiatus*), supported by GAJU (39_2007_P-PřF); result: Čížková et al., 2011

2011 three weeks PPP DAAD scholarship at the University of Duisburg-Essen in Germany

Teaching experience

Practices in Ethology (2008), Practices in Vertebrate Zoology (2008), Fieldwork Practices (2008, 2009), Keeping of Mammals (2008, 2010), Summer School of Behavioural Methods (2009), Behavioural Ecology (2011)

List of publications

Čížková B., Šumbera R. & Frynta D. (2011). A new member or an intruder: how do Sinai spiny mouse (*Acomys dimidiatus*) families respond to a male newcomer? Behaviour 148(8): 889-908

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