SHORT COMMUNICATION

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

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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*.

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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

Introduction

Within-population variance in litter size is typically large and may be viewed either as an unavoidable consequence of stochastic processes (i.e., combination probabilities of fertilization and/or implantation success and/or embryonic survival) or as a manifestation of individual strategies of females adjusting their reproductive investment according to actual body condition and/or external circumstances (cf. discussion concerning clutch size in birds; Both et al. 1998; Tinbergen and Both 1999; Tinbergen and Sanz 2004).

Taxa producing small litters tend to evolve invariant or nearly invariant litter size (e.g., ungulates, primates, bats; cf. invariant clutch size in some bird and reptile groups; Bennett and Owens 2002; Kratochvíl and Frynta 2006). Otherwise, an increment of even a single newborn affects maternal investment dramatically. It may have considerable fitness consequences for both the mother and offspring, especially in taxa with a precocial developmental strategy and high maternal investment per newborn. This is the case of some rodent species, e.g., guinea pigs (Kasparian et al. 2005) and spiny mice (Kam et al. 2006).

The distribution patterns of developmental time (from conception to eye opening) scaled to maternal body size

among rodent families suggest a high level of evolutionary conservatism. A long ontogenetic development associated with precociality is typical for Hystricomorpha and possibly represents the plesiomorphic character state in rodents (Burda 1989).

Spiny mice of the genus *Acomys* may serve as an example of putatively derived precociality in rodents. This group possesses an exceptional life history among the family Muridae. In contrast to many other muroid rodents, spiny mice produce after an extended gestation period (36–42 days) only small litters consisting of relatively large (the mean litter weight at birth represents 20–25% of maternal weight; Dieterlen 1961) and well-developed precocial newborns (Brunjes 1990). Maternal investment is therefore extremely biased in favor of the prenatal period and consequently is largely determined by litter size itself.

Spiny mice are small, rock-dwelling rodents inhabiting deserts, semideserts, and savannas (i.e., areas with high spatiotemporal variation in resource availability) in Africa and the Middle East. In spite of their earlier systematic placement, they are more related to gerbils than to true murids belonging to the subfamily Murinae, which are represented by rats and house mice (Michaux et al. 2001; Steppan et al. 2004). Spiny mice, even those recently captured in the field, exhibit no behavioral signs of stress under standard laboratory conditions and breed well. Therefore, *A. dimidiatus* or *A. cahirinus* are widely used as an experimental model in both physiological and behavioral studies (e.g., Shafrir 2000; Haim et al. 2006; Pinter-Wollman et al. 2006; Nováková et al. 2008).

Spiny mice are social animals that should be kept in families consisting of an adult male, multiple females, and their descendants (Young 1976), which mimics their wild social system. Their societies are not anonymous, and individual recognition was demonstrated unequivocally (Porter et al. 1986). In groups consisting of related individuals, communal care for the young comprising allosuckling is frequent; however, mothers are able to recognize their own offspring (Porter et al. 1980). Interestingly, male sires participate in parental care and clearly discriminate between own and alien young (Makin and Porter 1984). Our data from laboratory colonies suggest that adolescent males are driven away by the territorial male, while females are tolerated. Occasionally such conflicts may result in apparent social tension within the whole group and immediate suspension of reproduction. In affected groups, mice start to bite each other. As the tails are most vulnerable, this aggression results in frequent tail losses, a phenomenon also reported from natural populations (Shargal et al. 1999).

We analyzed the data on litter size collected in captive colonies of spiny mice belonging to four closely related species/populations of the *cahirinus-dimidiatus* clade (Barome et al. 1998, 2000; Volobouev et al. 2007; Frynta et al. 2010) to determine the effects of maternal life history variables and social composition of the breeding groups on litter size. We tested the hypothesis that litter size is strongly dependent on maternal body size because maternal size and amount of body reserves strongly limit litter size in these rodents with large size of newborns and heavy prenatal maternal investment. We also hypothesized that in this social rodent possessing biparental and communal parental care, presence of additional group members enhances rather than precludes production of larger litters.

Materials and methods

Studied animals

Our laboratory colonies of spiny mice were of the following origin: *A. cahirinus*, founder animals were caught in 1995 in the Abu Simbel archeological site, southern Egypt (22° 22′ N, 31° 38′ E); *A. cilicicus*, east of Silifke, southern Turkey (36° 26′ N, 34° 06′ E), obtained in 1993; *A.* sp., Zagros, SW Iran (28° 56′ N, 52° 32′ E), caught in 2002; and *A. dimidiatus*, laboratory strain, Prague Zoo, Czech Republic (the stock imported in the early 1970s from the Bronx Zoo, NY; probably originated from Israel or Sinai). Molecular phylogenetic analysis based on mitochondrial control region sequences in these colonies revealed that all the studied populations/species belong to the *cahirinus-dimidiatus* group of the genus *Acomys*. The former two populations/species belong to the clade of *A. cahirinus* sensu lato inhabiting North Africa and the Eastern Mediterranean (Crete, Cyprus, and the Kilikian coast in Anatolia), while the latter two belong to the *A. dimidiatus* sensu lato clade ranging from Sinai, throughout the Arabian Peninsula, and along the coast of the Gulf of Oman from Iran to Pakistan. The specific/subspecific status of the Iranian population, referred to here as *A.* sp., requires further clarification (Frynta et al. 2010).

The animals were kept in terrariums (60×50×40 cm or 70×60×40 cm) or in rodent plastic cages (VELAZ T4, Czech Republic; 55×32×18 cm) under standard laboratory conditions. Wood shavings were used as bedding material; a clay flowerpot with a lateral opening served as a shelter; and tree branches for climbing and gnawing were provided as environmental enrichment. The light schedule in the animal housing room corresponded to the outdoor light cycle. Food (standard diet for rats and mice, ST1, VELAZ, Czech Republic, occasionally supplemented with a mixture of grains, dry bread, apples, and herb leaves) and water were available ad libitum.

Spiny mice were kept in family groups consisting of two closely related females (full or half siblings), one non-relative male, and their descendants. The groups were

established from founding animals about 3 months of age (maturing age) and then allowed to breed freely for several months. Manipulation of group structure only occurred in the case of male-to-male aggression between the male founder and his mature male offspring (if so, young males were removed). The experimental groups were regularly checked (either daily or every other day); each litter was recorded and sexed immediately after its detection; and the putative mother was identified.

The following life history and social variables were measured: maternal parity (range, 1–11), maternal age in days (range, 52–990 days), postpartum conception (the litter was considered as conceived postpartum when delivered before day 41 after the previous one; categorical variable), number of adult males actually present in the group (aged 90 days or older; range, 1–22), number of adult females (aged 90 days or older; range, 1–20), number of breeding females in the group (i.e., those that already gave birth; range, 1–11), maternal status (first breeding founder, second breeding founder, their daughters; categorical variable), number of immature males (aged under 90 days; range, 0–13), and of immature females (aged under 90 days; range, 0–17). In addition, maternal body weight in grams (range, 25–79.7 g; mean values were 43, 57, 50, and 56 g for *A. cahirinus*, *A. cilicicus*, *A. dimidiatus*, and *A. sp.*, respectively) after parturition was included in the particular analyses of individual species. Maternal age and body weight were log-transformed. Litter sex ratio was not included, as the analyses had revealed no consistent relationship of this variable with litter size (Nováková et al. 2010).

Only the records containing a complete set of required explanatory variables were further analyzed. In total, these were 1,809 (1,569 when maternal body weight was also included) litter size records, i.e., 1,037 (968) for *A. cahirinus*, 186 (49) for *A. cilicicus*, 414 (414) for *A. dimidiatus*, and 172 (138) for *A.* sp.

Statistical analysis

Statistical models were estimated, tested, and visualized using the R statistical package (version 2.11.1). The significance and size of the effects of explanatory variables were estimated using generalized mixed-effect models (GLMM) using package *lme4*, with a quasi-likelihood approach based on the Poisson distribution, and using maternal identity as a random factor. The size of the litter as a response variable excludes, however, zero values, so estimates based on the Poisson distribution could be biased. We have therefore validated the estimates of regression coefficients obtained in GLMM using a generalized linear model (GLM) using zero-truncated ("positive") Poisson distribution, fitted using the package VGAM. Regression

coefficients from GLMM that fall into 95% confidence interval of the coefficients estimated using the GLM model were deemed unbiased. This indirect approach was chosen because random maternal effect cannot be fitted in combination with the zero-truncated Poisson distribution, and thus, the inferred type-I errors would underestimate the true ones.

Because the information about maternal body weight was available only for a subset of observations (see above), model selection was performed in parallel on the full dataset, but excluding maternal weight variable, and on the subset of observations with maternal weight values. In either case, the full model was fitted first and then refitted as final only with explanatory variables suggested as significant in the full model. The significance of explanatory variables was estimated separately for both the full and final models using the likelihood-ratio test (LRT), comparing such models with alternative ones, where the tested variable was dropped. Effects of explanatory variables selected into individual models were visualized using the *effects* package.

Ethical note The experiments were performed in accordance with Czech law implementing all the corresponding EU regulations and were approved by the Institutional Animal Care and Use Committee.

Results

We analyzed the effects of ten fixed factors on litter size using GLMM procedures. Initially, we performed separate analyses for each species/population; except for *A. dimidiatus*, we proceeded with both models, including and excluding maternal body weight as a factor. We further provide only significant results of the final reduced models (Table 1). The numbers of immature females and males had significant positive effect on litter size in *A. dimidiatus* (P= 0.0275, P=0.019, respectively); the former factor appeared marginally significant also in *A. cilicicus* (P=0.0619). Postpartum conception had positive significant effect in the case of *A. cahirinus* (P=0.0391); however, this effect disappeared when maternal body weight was included in the model. Maternal body weight had significant positive effect on litter size both in *A. cahirinus* and *A.* sp. (P= 0.0016, P=0.0102, respectively).

When the data for individual populations were pooled into a single GLMM model, postpartum conception (P= 0.0124; Fig. 1), number of immature females (P=0.0003; Fig. 2), and species (P<0.0001; Fig. 3) significantly contributed to litter size. When maternal body weight was included into the model, the effect of this variable appeared

Table 1 Explanatory variables selected as affecting the litter size in four species/populations of *Acomys*

	Estimate	Std. error	χ^2	DF	P value
Models not including maternal body weight					
A. cahirinus					
Postpartum conception	0.0982	0.0413	4.26	1	0.0391
A. cilicicus					
Number of immature females	0.0308	0.0174	3.49	1	0.0619
A. sp.					
Not significant					
Pooled dataset					
Postpartum conception	0.0859	0.0322	6.25	1	0.0124
Number of immature females	0.0256	0.0066	13.06	1	0.0003
Species	0.0778	0.0497	81.73	3	<0.0001
Models including maternal body weight					
A. cahirinus					
Maternal body weight	0.4908	0.1357	9.96	1	0.0016
A. cilicicus					
Not significant					
A. dimidiatus					
Number of immature females	0.0354	0.0178	4.86	1	0.0275
Number of immature males	0.0412	0.0194	5.50	1	0.019
A. sp.					
Maternal body weight	1.4382	0.4552	6.60	1	0.0102
Pooled dataset					
Maternal body weight	0.4457	0.1196	12.25	1	0.0005
Number of immature females	0.0200	0.0070	7.13	1	0.0076
Species	0.0941	0.0930	64.44	3	<0.0001

Coefficient estimates affect the log-transformed litter size, so exponential function must be applied to them to see multiplicative effects of the variable. The last three columns (χ^2, DF, and P value) summarize the results of variable-wise LRT, displaying respectively the value of the test statistic, degrees of freedom, and estimated probability of type-I error

significant (P=0.0005; Fig. 4), while that of postpartum conception disappeared. The effects of number of immature females (P=0.0076) and species (P<0.0001) remained nearly unchanged. Further testing revealed no need for inclusion of the interaction between species and any of the explanatory variables.

Discussion

The positive association between litter size and maternal body weight found in the entire dataset as well as in two particular sets (*A.* sp. and *A. cahirinus*) of the breeding records is not surprising in animals exhibiting such a heavy maternal investment in the progeny (Kam et al. 2006). In many other mammals, a positive association between litter size and maternal body size has also been repeatedly reported (e.g., Zejda 1966; Tuomi 1980; Myers and Master 1983 and the references herein). As thoroughly documented in laboratory mice, this close association typical for unselected populations is caused by high correlation between body size and ovulation rate. Nevertheless, this does not restrict a relative independent change in these traits above the population level, as both of the traits are
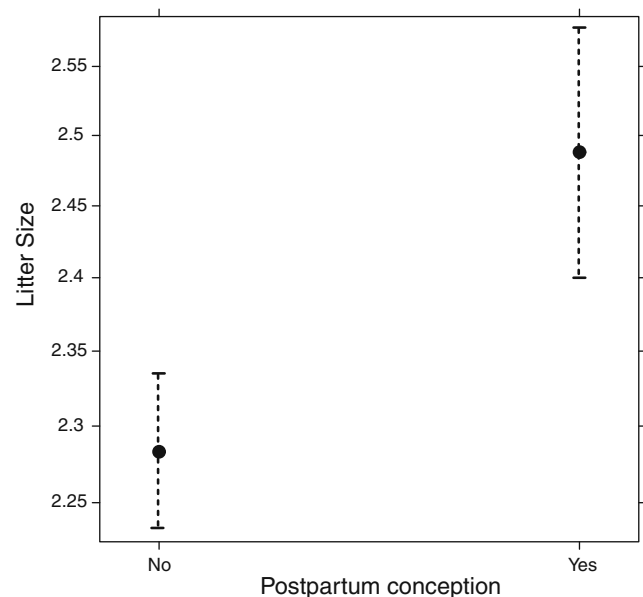

Fig. 1 The effect of postpartum conception on litter size in laboratory colonies of four species/populations of the genus *Acomys*. Data are given as means and 95% confidence intervals
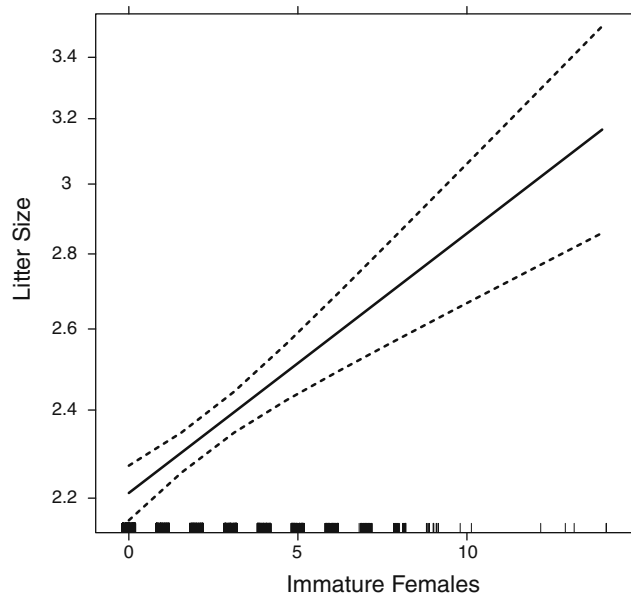
Fig. 2 The effect of the number of immature females on litter size in four species/populations of the genus *Acomys*. Data are given as means and 95% confidence intervals

Fig. 4 The effect of maternal body weight on litter size in four species/populations of the genus *Acomys*. Data are given as means and 95% confidence intervals

determined by specific genes (alleles, QTLs) and thus easily respond to selective forces (for review, see Bünger et al. 2005).

Among other factors we examined, only the number of immature females has consistent effects on litter size both in two particular analyses and the analysis of pooled species/populations. We interpret this finding as the effect of continuous reproduction reflecting positive social settings within the breeding group in social spiny mice. It fits
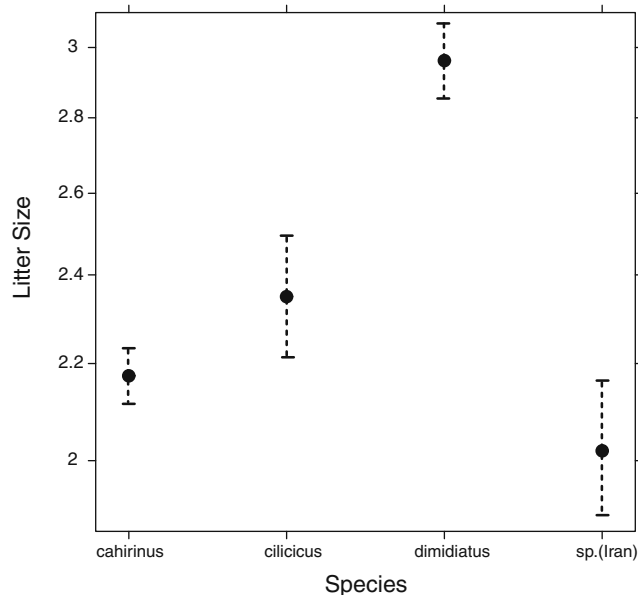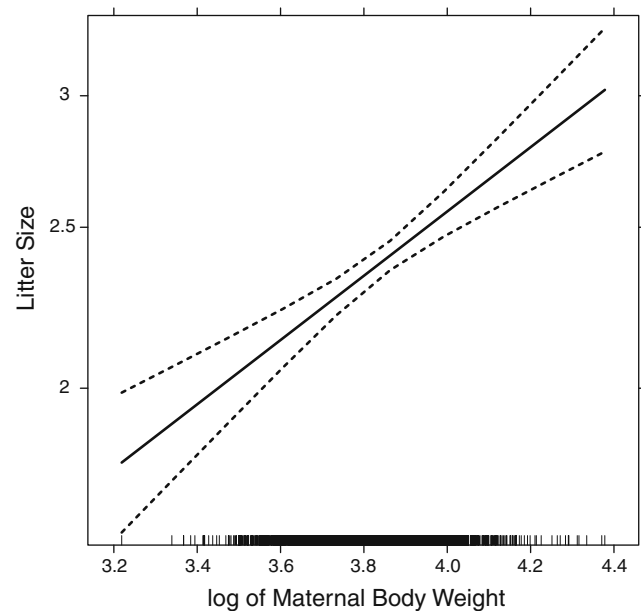

Fig. 3 Means and 95% confidence intervals for litter size in studied species/populations of the genus *Acomys*: *A. cahirinus*, *A. cilicicus*, *A. dimidiatus*, and *A.* sp. (Iran)

our finding that the levels of stress hormones (fecal glucocorticoid metabolites) differ between the breeding groups in *A. cahirinus* (Nováková et al. 2008). In contrast, Scheibler et al. (2005) reported a negative effect of family size on litter size in Mongolian gerbils (*Meriones unguiculatus*). Therefore, our results do not confirm the intuitive expectation that large size of the family group interferes with reproduction. Regular occurrence of such social phenomena as paternal care (Dieterlen 1962; Makin and Porter 1984), communal nursing (Porter and Doane 1978), and social thermoregulation (note that spiny mice do not build their own burrows and nests) makes large family size advantageous in spiny mice.

The other factors that appeared significant in at least one of our particular analyses of litter size, i.e., postpartum conception and number of immature males, reflect the continuous reproductive activity of the female. Postpartum conception had fairly positive effects on litter size (especially in *A. cahirinus*) when maternal body weight was not controlled; thus, concurrent lactation did not reduce litter size. This may be attributed to the higher body weight of females with postpartum conception that reflects their specific physiological settings and/or presence of body reserves required for continuous reproduction.

The absence of the effect of parity on litter size is somewhat surprising as such a relationship has been frequently reported in rodents (e.g., *Myodes glareolus*, Clarke 1985; Innes and Millar 1990; *M. unguiculatus*, Kai et al. 1995; *Microtus arvalis*, Tkadlec and Krejčová 2001). One may argue that we included parity as a continuous predictor, and the effects may be bimodal. Nevertheless,

detailed inspection of our data did not uncover any markedly shaped relationship. The same is true for maternal age which usually belongs to the most successful predictors of rodent litter size (e.g., in *Apodemus sylvaticus*, Žižková and Frynta 1996; *Peromyscus leucopus*, Havelka and Millar 2004).

In conclusion, variation in litter size within populations of spiny mice kept under laboratory conditions may be partially explained by maternal weight and factors reflecting hospitable social environment of the breeding unit. Nevertheless, manipulative experiments are needed to prove our results based on the correlative approach.

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