ANIMAL BEHAVIOUR, 2001, **62**, 965–972
doi:10.1006/anbe.2001.1833, available online at http://www.idealibrary.com on IDEAL®

Intra- and interspecific variation in vigilance and foraging of two gerbillid rodents, *Rhombomys opimus* and *Psammomys obesus*: the effect of social environment

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*(Received 27 March 2001; initial acceptance 16 May 2001;
final acceptance 8 July 2001; MS. number: 6885)*

We studied time budgets in two closely related and ecologically similar gerbillids to test the effect of group size on vigilance and foraging in adult females. *Psammomys obesus* is strictly solitary, while *Rhombomys opimus* is mainly social. We compared time budgets of (1) solitary *P. obesus* females, (2) solitary *R. opimus* females and (3) *R. opimus* females living in male–female pairs. Solitary *R. opimus* females spent more time underground, more time in low-cost vigilant postures, moved more, hoarded food more and fed above ground less than paired females. However, females of both categories spent similar time in high-cost upright postures. These results conform mainly to the group size effect hypothesis, while the high level of high-cost vigilance in paired females can be attributed to within-group vigilance, masking the group size effect. Solitary females of *P. obesus* and *R. opimus* showed similar time budget patterns; however, *P. obesus* allocated more time to high-cost vigilance and less time to feeding. In general, differences in time budgets between heterospecific females of the same social status (solitary or paired) were less pronounced than differences between conspecifics of different status. Thus, variation in activity patterns of females can be largely explained by different social conditions rather than by species affiliation. We discuss the results in terms of predation avoidance strategies in solitary and social species.

Avoidance of predation is one of the main ultimate factors responsible for the evolution of group living in animals (Alexander 1974; Krebs & Davies 1993, but see Janson 2000). Living in groups has been repeatedly reported to reduce per capita vigilance, allowing more time for individual foraging (the group size effect, see Elgar 1989 and Quenette 1990 for reviews, but see Catterall et al. 1992; Treves 2000). The main explanation of the group size effect on the vigilance/foraging trade-off is based on the group vigilance and individual risk hypotheses (Roberts 1996). The former assumes collective detection of a predator and suggests that as group size increases an individual forager can devote less time to vigilance, saving time for feeding and/or benefit from the increased probability of predator detection (Roberts 1996). The individual risk hypothesis suggests that the probability of being encountered, attacked and captured by a predator decreases as the number in the group increases (Hamilton 1971; Foster & Treherne 1981; Inman & Krebs 1987; Schradin 2000). Thus, animals reduce their risk of predation by being social and may (but not always, see Roberts 1996) allocate more time to foraging at the cost of reduced vigilance.

The fat sand rat, *Psammomys obesus* Cretzschmar, 1828, and the great gerbil, *Rhombomys opimus* Lichtenshtein, 1823, are very similar both morphologically and ecologically and are closely related (Pavlinov et al. 1990). Both species are desert dwellers: *P. obesus* in North Africa and the Middle East and *R. opimus* in central Asia. They both prefer damp soils (sandy or loess) with typical desert vegetation of shrubs, saltbushes and annuals (Pavlinov et al. 1990; Harrison & Bates 1991; Shenbrot et al. 1999) and construct complex deep burrows with numerous entrances. Both are diurnal and folivorous, although *P. obesus* specializes on chenopods (Daly & Daly 1973), while *R. opimus* is more opportunistic (Pavlinov et al. 1990). Nevertheless, in some areas chenopods are its major food resource (Kucheruk et al. 1972). Both species

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0003–3472/01/110965+08 $35.00/0

feed both above and below ground and store leaves in their burrows to be eaten later (Daly & Daly 1975; Pavlinov et al. 1990). Potential predators include raptors, desert cats, mustelids, monitor lizards and snakes. We have observed snakes at the burrows of both species, grey monitors, *Varanus griseus*, at the burrows of *R. opimus* and successful attacks by caracal, *Felis caracal*, on *P. obesus* and by polecat, *Vormela peregusna*, on *R. opimus*. When scanning or when alerted, both species show similar vigilant postures such as quadrupedal and bipedal semiupright or upright alert postures (Goltsman et al. 1977; Tchabovsky et al. 1995).

Psammomys obesus is strictly solitary (Daly & Daly 1975), while *R. opimus* is mainly social (Kucheruk et al. 1972; Naumov et al. 1972; Goltsman et al. 1977). The latter live in family groups of one male, one–three females and their numerous offspring of several litters inhabiting the same burrow. However, under low population density, some females of *R. opimus* live solitarily, while adult males visit several solitary females regularly within and outside the mating season (Pavlinov et al. 1990). In contrast, males and females of *P. obesus* occupy separate burrows and associate only for mating (Daly & Daly 1975; A. V. Tchabovsky, unpublished data). Females do not tolerate males and oust them from the burrows immediately after mating (A. V. Tchabovsky, unpublished data). Young animals disperse soon after or prior to maturation. Finally, *R. opimus* utters various alarm calls (Goltsman et al. 1977), while *P. obesus* rarely emits short primitive whistles (A. V. Tchabovsky, unpublished data).

Ecology has a strong effect on the time budget of *P. obesus* (Tchabovsky et al., in press). Under the high perceived predation risk in open, poorly protected habitats, solitary females of *P. obesus* are more vigilant, spend more time underground, move more, hoard more and feed above ground less (i.e. tend to delay consumption) than in highly protected habitats with dense shrub cover. In this study, we focused on the effect of the social environment on the time budgets of the two gerbil species, in particular intra- and interspecific variation in vigilance and foraging under similar ecological environments in the presence and absence of the social partner.

We compared time budgets of (1) solitary females of *P. obesus*, (2) solitary females of *R. opimus* and (3) females of *R. opimus* that lived in pairs with males (paired) in similar habitat types. Based on the group vigilance hypothesis, we predicted that females of *R. opimus* would be more vigilant and would tend to delay food consumption in the absence of the partner, that is, under the higher perceived predation risk, than when the partner was present and, thus, risk of predation was lower. In particular, we expected that solitary *R. opimus* females would spend more time underground and would allocate more of their above-ground activity time to hoarding, moving and vigilance, and less time to feeding than females in pairs with males. In addition, we predicted that feeding series would be shorter in solitary animals because the duration of foraging bouts is expected to vary inversely with group size (Burger & Gochfeld 1992; Reboreda & Fernandez 1997; Vasquez 1997). Finally, on the grounds of ecological, morphological and taxonomic similarities, we expected that the activity patterns of solitary *R. opimus* females would be similar to that of *P. obesus* females rather than to activity patterns of conspecific paired females. In other words, we suggest that under similar environmental conditions, time budgets of conspecific females of different social status (solitary or paired) would differ more than those of heterospecific females of the same social status in these closely related and ecologically similar gerbil species.

METHODS

Study Area and Habitats

We observed *P. obesus* inhabiting the northern rim of the Ramon erosion cirque, Negev Highlands, Israel (30°35′N, 34°45′E) in March–April of 1999 and 2000. The study site (800 × 100 m) was established along the valley of Wadi Nizzana, and included both the bottom of the dry riverbed densely covered with tall shrubs of *Atriplex halimus* and the first fluvial terrace with scattered and low shrubs of *Anabasis articulata*. To avoid any confounding effect of the vegetation cover on the time budgets of sand rats, we considered only observations of animals within a single type of microhabitat, namely open terrace with sparse vegetation (average shrub cover=3.6%).

We observed *R. opimus* in March–April 1991 and 1994 in southeastern Karakum Desert (Turkmenistan). The study site (1500 × 500 m) was established along the South Valley of the Repetek Biosphere Reserve (38°30′N, 63°10′E). Habitat type was similar to that of *P. obesus*. Great gerbils inhabited the open sandy bottom of the valley covered with scattered shrubs of *Haloxylon* spp. and *Calligonum* spp. with average shrub cover of 2.5%.

Animals

To trap the gerbils we used wired cage traps (45 × 14 × 14.5 cm) baited with fresh leaves of *A. halimus* (*P. obesus*) and sunflower seeds (*R. opimus*). Traps were placed near the entrances of active burrows and were checked frequently during the day, so that each trapped individual stayed in a trap for no more than 15 min. Neither *R. opimus* nor *P. obesus* needs free water, so the bait satisfied their water requirements. Trapped animals were sexed, aged, weighed and marked individually by fur cutting in a symmetric pattern. Handling time took ca. 7 min/individual if it was captured for the first time. Marked females were handled for 2 min to check for signs of pregnancy or lactation, whereas marked males were released immediately.

The population density of *P. obesus* during the study period was estimated to be 5.0 and 3.8 individuals/ha in 1999 and 2000, respectively (A. V. Tchabovsky & B. R. Krasnov, unpublished data), while that of *R. opimus* during the study period was estimated to be 0.5 and 0.8 individuals/ha in 1991 and 1994, respectively (S. V. Popov & A. V. Tchabovsky, unpublished data). Multiannual spring numbers for the local population of

Table 1. Categories of activity and types of behaviour of *P. obesus* and *R. opimus*

Category of activity	Type of behaviour	Description
Motionless	Lying down	Self-explanatory
	Sitting	Quadrupedal position
	Standing semiupright	Bipedal position, back curved
	Standing upright	Bipedal position, back erected and mostly perpendicular to the ground
Moving	Walking	Self-explanatory
	Running	Self-explanatory
Foraging (feeding)	Feeding above ground	Cutting and consuming leaves or stems above ground
Foraging (hoarding)	Cutting	Cutting leaves or stems and packing them in the mouth
	Transporting	Carrying leaves or stems in the mouth
	Dropping	Dropping leaves or stems near the burrow entrance
	Storing	Disappearing in the burrow with leaves or stems in the mouth
	Packing	Gathering and packing into the mouth leaves or stems previously dropped on the ground

P. obesus were estimated as 14.5 individuals/ha (G. I. Shenbrot & B. R. Krasnov, unpublished data), while the average population density of *R. opimus* has been estimated to be 10 individuals/ha (Pavlinov et al. 1990). Thus, the population densities of *P. obesus* and *R. opimus* during the periods of observation were assumed to be low.

Age, sex and reproductive status can affect vigilance and foraging behaviour (Fragaszy 1990; Macwhirter 1991). Consequently, to avoid possible confounding effects, we used only the observations of adult females prior to emergence of weanlings from the burrow. Seven solitary *P. obesus* females, six solitary and seven paired *R. opimus* females met these requirements and were included in the analysis. For paired females, we used only observations when a male and female were active above ground together. Males did not directly interfere in the behaviour of females. Only three brief sniffing and two short allogrooming series were recorded during observations. Thus, the effect of the partner was almost entirely associated with its presence in the burrow.

Behavioural Observations

We chose a focal animal for observations on the random inspection routes walked one to three times a day. All observations were made between 0800 and 1700 hours. We did not observe the same animal more than once in the morning (0800–1300 hours) or in the afternoon (1300–1700 hours) on any one day. Thus, the interval between observations of the same individual in the same period of the day ranged from 1 to 5 days.

We observed animals from behind a natural shelter at a distance of 30–40 m through 12 × 45 binoculars. We started observations only if an animal showed no response to our occupation of the observation post by interrupting its activity or by adopting an alert posture. We observed focal individuals for 10-min periods and recorded their activity on to a constantly running tape recorder. Table 1 gives the general categories of activity and types of above-ground behaviours recorded.

The tape-recorded observations were analysed on a real time scale with the help of EthoLog software (version 1.0, developed by E.B. Ottoni, Department of Experimental Psychology, Institute of Psychology, University of São Paulo, Brazil and distributed as freeware, http://www.geocities.com/ebottoni/ethohome.html). We analysed observations of individuals that were active above ground for at least 5 min during a 10-min focal sample and foraged for at least 10% of their above-ground activity. In total, there were 53 such observations and among them 16 observations of seven solitary *P. obesus* females (from two to three 10-min observations/individual), 20 observations of six solitary *R. opimus* females (from two to four/individual), and 17 observations of seven paired *R. opimus* females (from two to three/individual). Every animal was observed both in the morning and in the afternoon. The percentage of morning observations was similar among the three categories of females (44, 55 and 59%, respectively; χ^2_2=0.81, *P*=0.662). Thus, time of observations, which is known to affect vigilance (Quenette 1990), was assumed not to bias the data.

Animals were considered vigilant when they stood still in the fully erect upright posture with or without hindfeet extended and with their backs straight and mostly perpendicular to the ground (Wistrand 1974; Goltsman et al. 1977; Mateo 1996; Arenz & Leger 1999). Such postures were considered to correspond to the highest level of alertness among above-ground stationary postures in ground squirrels, *Spermophilus beldingi* (Mateo 1996), and *Spermophilus tridecemlineatus* (Arenz & Leger 1999), and *R. opimus* (Goltsman et al. 1977) and may be classified as a high-cost, high-quality overt vigilant posture (after Lima & Bednekoff 1999). Vigilance in many animals is also associated with other less expressive and motivated alert postures: horizontal quadrupedal (sitting or lying) or bipedal semiupright postures (Mateo 1996; Jones 1998; McAdam & Kramer 1998; Arenz & Leger 1999). However, both *P. obesus* and *R. opimus* spend much time in such stationary postures not only being vigilant but also resting or sunbathing (Daly & Daly 1975;

S. V. Popov & A. V. Tchabovsky, unpublished data). Usually, head-elevated position and scanning behaviour are used as criteria to differentiate vigilance from non-vigilance in a motionless (lying down, sitting or semi-upright) animal (Rose & Fedigan 1995; Blumstein 1996; Hare 1998; Jones 1998). However, apparently vigilant animals do not always show scanning movements of the head (McAdam & Kramer 1998; A. V. Tchabovsky, unpublished data) and a resting individual can survey its surroundings unless its eyes are closed or the view is obstructed; many animals including gerbils do this while handling or chewing food (Wistrand 1974; Lipetz & Bekoff 1982; Illius & FitzGibbon 1994; Smirin & Smirin 1999; Arenz & Leger 2000). Thus, the level of alertness of motionless individuals in bimodal (resting or low-cost vigilant) postures of similar configuration may be misinterpreted.

In this study, we used posture duration as an indirect criterion to assess a state of alertness of the motionless individual. Duration of stationary postures (full upright excluded) ranged from 1 to 379 s (N=485). The distribution of posture lengths tended to be bimodal with peaks at ca. 20 and 120 s and a low at ca. 45 s. Low-cost vigilant postures are usually shorter than resting postures of the same configuration (S. V. Popov & A. V. Tchabovsky, unpublished data). Thus, we calculated the portion of time allocated to short (<45 s) stationary postures (full upright excluded), expecting that vigilant postures, in contrast to resting postures, would be more likely to occur within this duration interval. We used this indirect measure of low-cost vigilance level in motionless individuals in addition to the portion of time allocated to high-cost full upright postures, which we treated separately.

Data Analysis

To characterize time budgets, we calculated the proportion of time spent underground out of the total observation time and then the proportion of above-ground activity time allocated to feeding, hoarding, moving, short (low-cost vigilant) motionless postures (lying, sitting and semiupright pooled) and full-upright postures. We also measured duration of feeding series.

Since behavioural variables did not conform to the assumptions of normality, we applied a square-root transformation to normalize data. Kolmogorov–Smirnov $D_{\max}$ ranged for six normalized variables (time spent underground, time allocated to feeding, hoarding, moving, low-cost vigilance and full-upright postures) from 0.076 to 0.141 (NS in all cases). To assess effect of partner and species affiliation on time budget characteristics we performed ANOVA to contrast (1) solitary *R. opimus* versus paired *R. opimus*, and (2) solitary *R. opimus* versus *P. obesus*. Since the data set included some repeated observations of the same individuals we used a nested design of ANOVA with individuals nested within each category of animal to control for possible nonindependence of data from the same animal. To assess multivariate behavioural similarities between categories of gerbils we applied principal components analysis (PCA) to all six normalized variables. The first two components extracted were then analysed separately by ANOVA with the same nested design applied as described above. The nested ANOVA did not reveal a significant effect of individual in either analysis ($F_{11,24}$ and $F_{11,23}$ for the two contrasts ranged from 0.66 to 2.07, NS for all dependent variables analysed).

One variable, namely duration of feeding series, could not be normalized. For this, we used nonparametric Kruskal–Wallis ANOVA to contrast categories of gerbils. To avoid pseudoreplication we averaged all series of a single individual and used averages as dependent variables for each individual.

Since solitary *R. opimus* appeared in two contrasts we used a significance level of 0.025 adjusted using the Dunn-Sidak procedure (Sokal & Rohlf 1995). Values are presented as means ± SE. Figures show untransformed data. All statistical tests are two tailed and, in general, followed Zar (1984).

RESULTS

Paired *R. opimus* spent significantly less time underground (nested ANOVA: $F_{1,24}$=8.32, P=0.008), moved above ground less (borderline significance, $F_{1,24}$=4.47, P=0.045) and spent less time in low-cost vigilant postures ($F_{1,24}$=18.33, P=0.0002) than solitary conspecifics (Fig. 1a, b, c). However, time spent in full-upright postures was similar in the presence and in the absence of the partner ($F_{1,24}$=0.06, P=0.812). Paired females fed above ground more ($F_{1,24}$=17.56, P=0.0003) and hoarded less ($F_{1,24}$=14.76, P=0.0008) than solitary females (Fig. 1d) and had longer feeding series (Kruskal–Wallis: $H_{1,13}$=6.61, P=0.01; Fig. 1e).

No difference was found between solitary *R. opimus* and *P. obesus* in time spent underground ($F_{1,23}$=0.02, P=0.897), time spent moving above ground ($F_{1,23}$=0.24, P=0.626), time spent in low-cost vigilant postures ($F_{1,23}$=0.01, P=0.929), hoarding time ($F_{1,23}$=0.01, P=0.908; Fig. 1) and duration of feeding series (Kruskal–Wallis: $H_{1,13}$=0.51, P=0.474). However, solitary *R. opimus* allocated more time to feeding ($F_{1,23}$=27.13, P<0.0001) than *P. obesus*, while *P. obesus* stood upright more frequently than solitary *R. opimus* ($F_{1,23}$=19.40, P=0.0002).

Two principal components extracted from the model with six normalized dependent variables explained 72% of variance in the time budgets of gerbils (Table 2). The first principal component axis reflected an increase in time spent underground, hoarding, locomotion and low-cost vigilance, and a decrease in feeding, whereas the second axis was closely and almost entirely associated with full-upright postures. The first principal component distinguished mainly between solitary and paired individuals, while the second component distinguished between species (Fig. 2). The nested ANOVA revealed a strong effect of social status (for solitary and paired *R. opimus* contrasted $F_{1,24}$=18.02, P=0.0003) and no significant effect of species affiliation (for solitary *R. opimus* and *P. obesus* contrasted $F_{1,23}$=2.16, P=0.155) on the first time budget component. In contrast, species affiliation

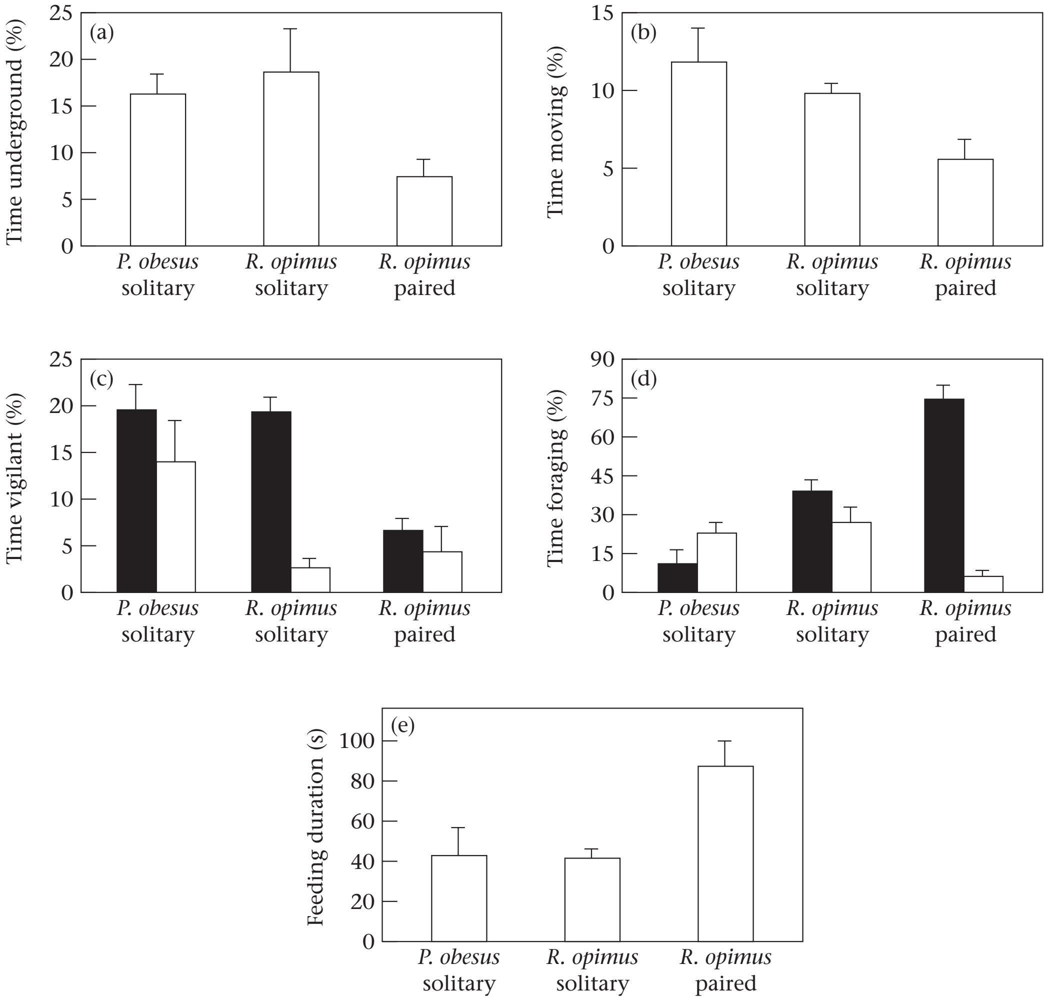

Figure 1. Time budget characteristics of three categories of females: mean+SE percentages of time allocated to various behaviours, averaged for each individual. Sample sizes: *P. obesus* solitary, *N*=7; *R. opimus* solitary, *N*=6; *R. opimus* paired, *N*=7. (a) Percentage of observation time spent by females underground; (b) percentage of above-ground time spent moving; (c) percentage of above-ground time allocated to low-cost (■) and high-cost (□) vigilance; (d) percentage of above-ground time allocated to feeding (■) and hoarding (□); (e) duration of feeding series.

strongly affected the second time budget component (for solitary *R. opimus* and *P. obesus* contrasted $F_{1,23}$=23.23, P<0.0001), whereas effect of social status was borderline significant (for solitary and paired *R. opimus* contrasted $F_{1,24}$=5.24, P=0.031).

Table 2. Summary of principal components analysis of six behavioural variables

Information	PC1	PC2
Eigenvalue	3.32	1.00
Percentage of total variance explained	55.00	17.00
Factor loading		
Time spent underground	0.77	0.26
Time spent moving above ground	0.76	0.05
Time spent in low-cost vigilant postures	0.78	0.30
Time spent in full-upright postures	0.47	−0.84
Time spent feeding	−0.78	0.32
Time spent hoarding	0.85	0.21

PC1 and PC2 are the first two principal components (both significant: P<0.001).

DISCUSSION

Our predictions that solitary *R. opimus* females would be more vigilant and would show a stronger tendency to delay food consumption than females in pairs appeared to be partly true. Solitary *R. opimus* spent more time underground, more time motionless in low-cost vigilant postures, moved more, hoarded more, fed above ground less and had shorter feeding series than paired conspecifics. These results support the suggestion that solitary females would suffer higher perceived predation risks than paired females and are consistent with the group size effect hypothesis.

However, differences in foraging tactics, that is, in feeding/hoarding ratio, between solitary and paired *R. opimus* may be explained in part by factors other than perceived predation risk. Great gerbils store food not only

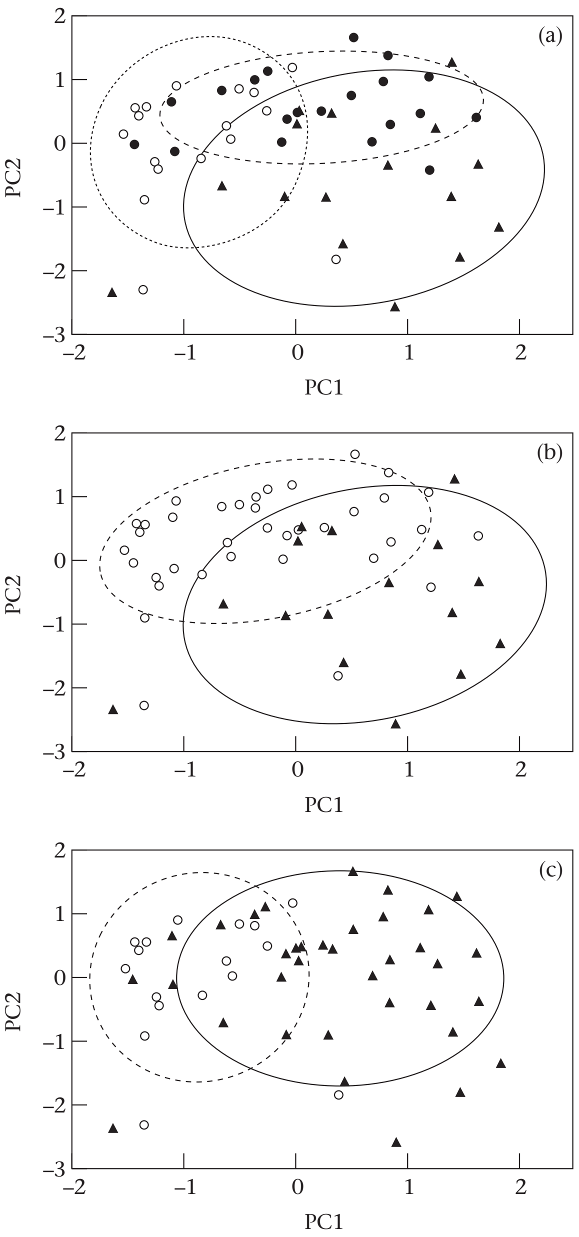

Figure 2. Distribution of observations (75% confidence intervals) in the space of two principal components (PC1 and PC2) according to female category, species and social status (solitary or paired). (a) ▲, ——: solitary *P. obesus*; ●, – – –: solitary *R. opimus*; ○, · · ·: paired *R. opimus*. (b) ▲, ——: *P. obesus*; ○, – – –: *R. opimus*. (c) ▲, ——: solitary females; ○, – – –: paired females.

to satisfy current nutritional needs, but also strategically (up to 30 kg/burrow, Traut & Gamov 1941) to be used by all members of a family group in the dry summer season or in winter (Kucheruk et al. 1972). Adult males in stable pairs contribute substantially to storing food and hoard more than females (S. V. Popov, A. V. Tchabovsky & G. Ågren, unpublished data). Thus, paired females may allow more time for feeding and less time for hoarding, while solitary females have to compensate for the lack of contribution of males to family storage.

Although it is difficult to distinguish whether the reduction in predation risk from the group size effect or the contribution of males to food storing is responsible for increased feeding time and less hoarding in paired females of *R. opimus*, they clearly benefit from staying with males by reducing the time spent vigilant and lowering energetic costs associated with increased hoarding, in particular, expenditure on increased locomotor activity.

Contrary to our expectations, time spent in high-cost, high-quality full-upright postures that manifest the highest level of alertness (overt scans, after Lima & Bednekoff 1999) was similar in *R. opimus* females when males were present or absent. This contradicts the hypothesis that vigilance, and especially its high-cost component, should decrease with increasing group size because of collective predator detection or dilution effects (Roberts 1996; Lima & Bednekoff 1999). Previously we found that the frequency of full-upright postures in *R. opimus* males was similar in the presence and in the absence of a social partner (Popov et al. 1997). Thus, we suggested that full-upright posture in great gerbils is associated with nonspecific behaviour to gain information about the environment whether it is social or ecological. This viewpoint is consistent with the multifunctional explanation of vigilance or scanning as a general process of acquisition of information, which may be aimed equally at scanning for a predator, competitor, partner or resources (Desportes et al. 1991; Slotow & Rothstein 1995; Bekoff 1996; Gould et al. 1997; Treves 2000). Therefore, full-upright postures in paired *R. opimus* can be, at least in part, attributed to within-group vigilance masking a decrease in antipredator vigilance. In that case high costs (both energetic and associated with exposure to predators) of full-upright postures can be explained if they are the best, if not the only, way to scan for partners.

As we expected, time budgets of solitary females of *P. obesus* and *R. opimus* appeared to be similar under similar ecological environments. The major differences between heterospecific females of the same social status were in feeding time (greater in *R. opimus*) and time spent in full-upright posture (greater in *P. obesus*). Similar behavioural patterns were shown by solitary females of both species with regard to other types of activity.

Differences in feeding time and time spent in full-upright postures between *P. obesus* and solitary *R. opimus* suggest differences in perceived predation risk and correspond to species-specific differences in predator detection. *Psammomys obesus* lacks a long-distance early warning system via alarm calls and, thus, can rely only on itself to detect and avoid predators, whereas *R. opimus*, even when solitary, can enjoy the benefits of earlier detection of a predator via alarm calls of neighbours (Kucheruk et al. 1972; Goltsman et al. 1977). Thus, *P. obesus* may perceive itself as more vulnerable in open habitats and, consequently, feeds above ground less than solitary *R. opimus*. Increased time spent in high-quality full-upright postures may compensate for the lack of long-distance alarm calling in *P. obesus* by extending their long-lateral view and, thus, allow long-distance detection of predators in open habitats where vision is not obstructed.

Nevertheless, on the whole, between-species differences in time budgets of individuals of the same social status were less pronounced than differences between conspecifics of different status. This suggests basic behavioural similarity in terms of time allocation in these ecologically and morphologically similar and closely related species, while the major variation in activity pattern under similar ecological conditions may be explained by varying social environment within and between species.

Previously, we have shown that the protective properties of vegetation cover affect the time budget in *P. obesus* (Tchabovsky et al., in press). In open habitats, *P. obesus* perceived itself more vulnerable and suffered increased costs associated with vigilance and delayed consumption of food, whereas in highly protected habitats it was much less vigilant, hoarded less and fed mainly above ground. We concluded that highly protective habitats with dense shrub cover better suits the demands of this solitary species. This suggests two alternatives in adaptation to avoid predation in these two species: either 'to have a safe roof overhead' (*P. obesus*) or 'to have a partner' (*R. opimus*).

It is generally accepted that evolution of group living is associated with the benefits of reduced predation risk (Alexander 1974; Krebs & Davies 1993), while costs of increased competition for food set limits on group size (MacFarland 1988; Wrangham et al. 1993; Janson 2000). One might suppose that the striking dissimilarities in the social behaviour of these two ecologically similar species are determined just by differences in their feeding habits. We suggest that food specialization of *P. obesus* sets constraints on group living and favours a sneaking predator avoidance strategy given an opportunity to live in highly protective habitats. Low tolerance to conspecifics, high perceived vulnerability in open habitats and preference for burrowing under bushes (Daly & Daly 1975; Harrison & Bates 1991; Tchabovsky et al., in press) supports this hypothesis. *Rhombomys opimus* is more opportunistic in its food habits, and may encounter less food competition and, thus, can tolerate conspecifics and enjoy the benefits of a socially based strategy of predation avoidance and other advantages of group living.

Acknowledgments

We are grateful to Irina Khokhlova and Georgy Shenbrot for assistance in collecting field data. Allan Degen, Daniel Blumstein and two anonymous referees provided valuable comments on the manuscropt. This work was partly funded by the Blaustein Center for Scientific Cooperation at the Jacob Blaustein Institute for Desert Research, Ben-Gurion University of the Negev, Israel (for A.V.T.), Israel Ministry of Science and Local Council of Mizpe Ramon (for B.R.K.). This is publication no. 118 of the Ramon Science Center.

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