Time Budget in Two Desert Gerbils: is the Diet Important?

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SUMMARY

We studied time budgets and dietary intake in two desert gerbillids, *Psammomys obesus*, a diurnal herbivore, and *Meriones crassus*, a nocturnal granivore feeding three different types of diet (millet seeds together with leaves of Atriplex halimus for *M. crassus*, fresh leaves of *A. halimus* or fresh stems of *Anabasis syriaca* for *P. obesus*). M. crassus spent the lowest proportion of its time budget for feeding compared to *P. obesus*. Number of feeding sessions in *M. crassus* was approximately the same but each separate feeding session was almost three times shorter than those in *P. obesus*. No difference in temporal pattern of feeding was found between *P. obesus* fed different plants, in spite of sharp differences in chemical composition of food. *P. obesus* fed *A. halimus* was active significantly less time than *M. crassus*, whereas *P. obesus* fed *A. syriaca* stayed active the same time as *M. crassus*. Dry matter intake of *P. obesus* fed *A. halimus* was much higher than that of *M. crassus* and dry matter intake of *P. obesus* fed *A. syriaca* was lower than even that in *M. crassus*.

KEY WORDS

time budget, diet, digestibility, intake, *Meriones crassus*, *Psammomys obesus*

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INTRODUCTION

Differences in time budget of animals with diets of different quality are determined by a trade-off between energetic value of food consumed and time and energetic costs for food acquisition and processing (Kam et al, 1997; Degen, 1998; Degen et al, 2000). It is clear that an animal must allocate some portion of its overall activity time for feeding in order to satisfy its nutritional and energetic requirements. Time allocated for feeding has been shown to comprise large part of the overall time budget of an individual (Degen et al, 2000), although this proportion of feeding time differs among species and is affected by different intrinsic and extrinsic factors (e. g., digestive efficiency, diet composition, density and dispersion of food resources, environment constraints; see review in Jackson & Johnson, 2002). For example, ruminants, which are able to digest cellulose, spend, usually, approximately 5 hours feeding, which comprises only 59 % of feeding time in non-ruminants. It has been suggested that the main cause of this difference is that animals consuming low quality food (that of low energy and/or high-fiber vegetation) have to compensate their poor diet by increasing dietary intake (Castle and Wunder 1995; Hammond and Wunder 1991; Loeb *et al.* 1991), and/or by decreasing basal metabolic rate (Veloso and Bozinovic 1993; Veloso and Bozinovic 2000). Consequently, we hypothesized that time allocated for feeding will be affected by diet quality in both intra- and interspecific comparisons. To test this hypothesis we studied temporal parameters of different behaviours in two species of common desert gerbillids, *Meriones crassus* Sundevall, 1842 and *Psammomys obesus* Cretzschmar, 1828 maintained on different diets. *M. crassus* and *P. obesus* cohabitate in desert habitats throughout the Middle East. Furthermore, diet of *P. obesus* consists mainly of chenopods (Daly and Daly 1973), which are relatively low in nutrient and energy content and high in ash, electrolyte and water contents (Degen 1993; Kam and Degen 1988).The ability to consume such low quality food has been shown to be facilitated by their behavioural and physiological adaptations (Degen 1988). We predicted that animals consuming food of a lower quality (1) would spend more time feeding, (2) would spend less time active in order to save energy, and (3) would increase their food intake in comparison with animals consuming food of a higher quality.

MATERIALS AND METHODS

Animals and diets

We used non-reproducing adult *M. crassus* (4 males) and *P. obesus* (6 males and 2 females). *M. crassus* received millet seeds and fresh leaves of *Atriplex halimus* as water supply (considered as high quality diet), *P. obesus* were fed either fresh leaves of *A. halimus* (considered as medium quality diet) or fresh stems of *Anabasis syriaca* (considered as low quality diet). Consideration of diet quality was based on energy-, electrolyte- and fiber-content of respective food. Food quality was considered to increase with increase in energy content and/or decrease of electrolyte and fiber content. Data on chemical composition of millet seeds and green parts of *A. halimus* and *A. syriaca* were taken from Khokhlova *et al.* (1995) and Kam *et al.* (1997).The study was carried out at a room temperature of 30ºC and a photoperiod of 12:12 L:D. The rodents were housed individually in metabolic cages (20 by 10 by 10 cm) which were equipped with a wire-meshed floor that allowed feces and food remains to pass through.

Digestibility trial

Experimental trial lasted 3 consecutive days. *M. crassus* were offered 55 g of millet seeds for all three days only once, while fresh leaves of *A. halimus* were added every hour as required. *P. obesus* were offered approximately 5 g of either fresh leaves of *A. halimus* or fresh stems of *A. syriaca* continuously as required. Animals were weighed on the first and the last days of the trial. To determine dry matter content (DMC) of seeds and plants, samples of each food type were weighed and oven-dried at 100ºC (Ecocell drying oven) to constant mass. Food remains and feces were separated manually every hour, oven-dried at 100ºC and weighed.

Dry matter intake (DMI) was calculated as difference between fresh matter offered (FMO) multiplied by DMC and dry matter of food remains (DML). Dry matter digestibility was calculated as proportional difference between total dry matter intake (TDMI) and dry matter of feces (FO). We calculated gross energy intake (GEI) as DMI of each food type multiplied by its gross energy. Values of gross energy for millet seeds, leaves of *A. halimus* and stems of *A. syriaca* were obtained from our previous studies (Degen et al. 2000; Kam et al. 1997; Khokhlova et al. 1997).

Behavioural parameters

We distinguished three types of behaviour. Non-feeding activity (animal moved in the cage or autogroomed). Feeding behaviour is self-explanatory. Sleeping and motionless postures were considered as energy-saving behaviour.

Data analysis

Physiological and behavioural variables conformed to assumptions of normality (Shapiro-Wilk's tests, ns). Physiological variables were analysed by 1-way ANOVAs.To characterise time budgets, we calculated the proportion of time spent being active but not

Table 1. Mean body mass (m_b), changes in body mass, dry matter content (DMC), dry matter intake (DMI), fecal output (FO), dry matter digestibility (DMD), total gross energy intake (GEI) and time required to consume 1 g of food (FT) in 2 rodent species

Rodent species	M. crassus	P. obesus	
Diet	Millet seeds + A.halimus	A. halimus	A. syriaca
Initial m_b (g)	119.7±6.1	155.6±9.5	135.6±15.8
m_b change (% day^{-1})	0.33±0.05	1.30±0.50	-0.61±0.08
DMI (g day^{-1})	6.26±0.19 for seeds; 0.79±0.24 for leaves	9.67±0.46	6.20±0.28
Total DMI (g day^{-1})	7.04±0.07	9.67±0.46	6.20±0.28
Total DMI (g g$^{-0.54}$ day^{-1})	0.53±0.02	0.63±0.06	0.44±0.02
Fecal output (g day^{-1})	0.52±0.02	2.30±0.11	1.56±0.13
DMD (% DMI)	92.6±0.3	76.2±0.4	75.0±1.6
Total GEI	132.2±1.4	141.2±10.1	102.3±6.9
FT of 1 g of food (min)	16.39±2.71 for seeds; 24.55±3.64 for leaves	9.28±0.94	25.49±2.57
FT x DMI of plants (min day^{-1})	92.47±17.0 for seeds; 14.62±2.6 for leaves	87.74±6.7	160.6±22.1
Total required FT (min day^{-1})	119.7±17.5	87.74±6.7	160.6±22.1
Total FT spent (min day^{-1})	152.4 ±6.3	453.7 ± 25.3	388.8±36.03

feeding (non-feeding activity), feeding and being non-active (energy-saving behaviour) out of the total time available. We measured duration of every behavioural event and number of events of different behaviours per diel phase (dark or light).

The influence of treatment and diel phase on total duration of behaviours within a diel phase, number of events of different behavioral types per diel phase and duration of every behavioural event was analyzed using 2-way ANOVAs. We applied an arcsine transformation on the proportion of time spent in non-feeding activity, feeding and in energy-saving behaviour out of the total time available for an individual during a day. Then, we used this dependent variable in 1-way ANOVA. Tukey's Honest Significant Difference (HSD) tests were applied for all multiple comparisons. All calculations were performed with the statistical package STATISTICA for Windows (StatSoft, Inc. 1999).

RESULTS

Physiological parameters

Dry matter content of millet seeds, leaves of *A. halimus* and stems of *A.syriaca* averaged 90.4 ±0.82 %, 26.9±0.26 % and 29.5±0.28 %, respectively. Mean initial body mass of animals did not differ among treatments (F=2.28, ns). Animals of different treatments demonstrated significant difference in body mass change during the trial (F=8.35, p<0.01) as follows. *M. crassus* maintained body mass, whereas *P.obesus* fed *A. halimus* gained and *P.obesus* fed *A. syriaca* lost their body mass. Total DMI, mass-specific total DMI, fecal output and total GEI differed significantly among treatments (Table1; F=14.72, F=5.54, F=37.65 and F=8.19, respectively, p<0.05 for all), being highest in *P. obesus* fed *A. halimus* and lowest in *P. obesus* fed *A. syriaca*. Dry matter digestibility differed significantly between *M. crassus*

and *P. obesus* (F=45.89, p< 0.001), but no difference was found among *P. obesus* offered different diets (Tukey's HSD test, ns).

Daily time budget

Rodents from different treatments allocated their time differently (Fig. 1). In *M. crassus*, the least amount of time was allocated for feeding, whereas the largest fraction of time was allocated for energy-saving behaviour. Feeding activity of *P. obesus* took similar fraction of daily time budget independently on diet and was significantly higher that that of *M. crassus*.
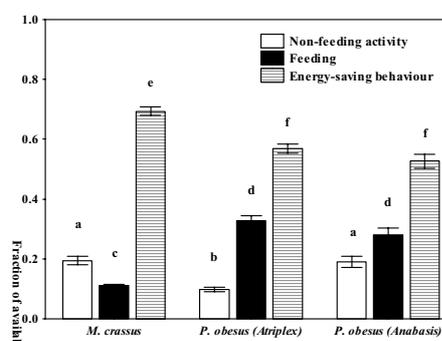

Figure 1. Fraction of available time (per day) spent in three types of behaviour in two rodent species offered different diets. Different letters denote statistically significant differences between treatments for the same behaviour (Tukey's HSD tests, p<0.05).

Effect of diet and diel phase on time spent in different types of behaviour

During dark phase, shortest duration of non-feeding activity was observed in *P. obesus* fed *A. halimus*, whereas longest duration was observed in *M. crassus*. In contrast, during light phase, *M. crassus* and *P. obesus* fed *A. halimus* spent similar time for non-feeding activity, whereas duration of non-feeding
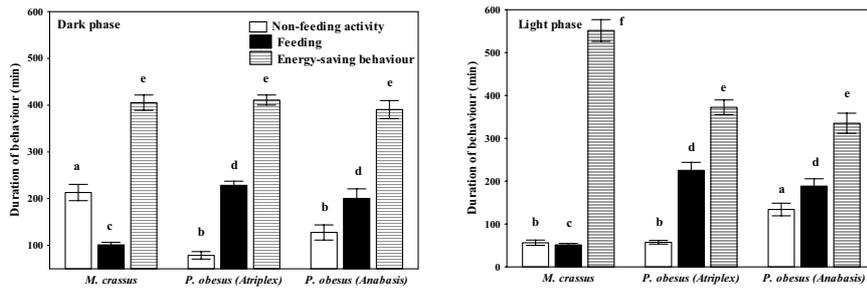
Figure 2.
Duration (per phase) of three types of behaviour in two rodent species offered different diets. Different letters denote statistically significant differences between treatments for the same behaviour (Tukey's HSD tests, p<0.05).
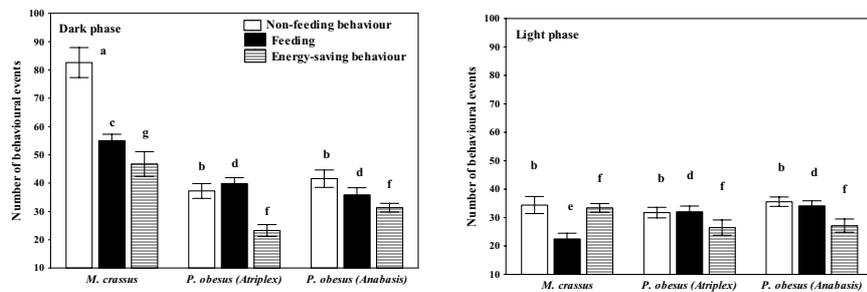

Figure 3.
Number of behavioural events (per phase) in two rodent species offered different diets. Different letters denote statistically significant differences between treatments for the same behaviour (Tukey's HSD tests, p<0.05).
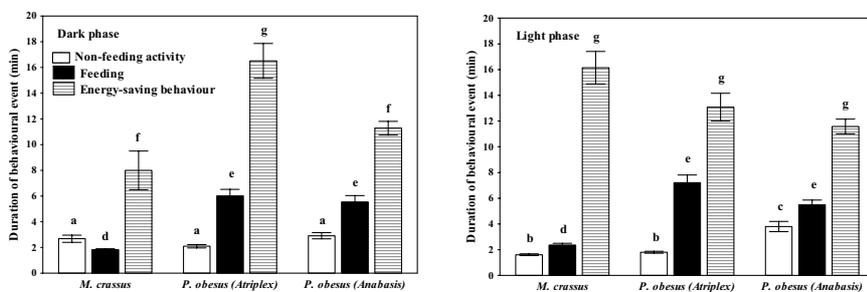

Figure 4.
Mean duration of a single behavioral event in two rodent species offered different diets. Different letters denote statistically significant differences between treatments for the same behaviour (Tukey's HSD tests, p<0.05).

activity in *P. obesus* fed *A. syriaca* was twice more. (Fig. 2).

Number and duration of different behavioural events

The number of events of non-feeding active and energy-saving behavioural events was affected by both treatment and diel phase factors. The number of events of non-feeding active behaviour was significantly higher in *M. crassus* during dark phase than in all *P. obesus* and *M. crassus* during light phase. The same was true for energy-saving behaviour (Fig. 3).

The number of feeding events was affected by diet but not by diel phase. This number was similar in both treatments of *P. obesus* and was significantly higher in *M. crassus* during light phase and significantly lower during dark phase (Fig. 3).

The duration of a non-feeding activity event was strongly affected by treatment but not by diel phase, although interaction between these two factors was significant. This suggest different among-treatments patterns in dark and light phase. During light phase, average duration of a non-feeding activity event was the lowest in *M. crassus* and the highest in *P. obesus* fed *A. syriaca*, wherteas during dark phase no difference in this parameter was found among treatments. In addition, in *M. crassus*, a non-feeding activity event during dark phase took significantly more time than that during light phase (Fig. 4).

The durations of feeding and energy-saving behaviours events were affected by treatment only. Average feeding session in *M. crassus* was significantly shorter than that in P. obesus fed both diets (Fig. 4). In addition, interaction between factor of treatment and factor of diel phase for energy-saving behaviour was significant. During dark phase, *M. crassus* had the lowest and *P. obesus* fed *A. halimus* had the highest average duration of an energy-saving event (Fig. 4), whereas no difference in this parameter was found during light phase.

Average time between consecutive feeding sessions differ significantly between diel phases n *M. crassus* but not in *P. obesus* (F=26.2, p<0.001 for interaction term Treatment x Diel phase in ANOVA). During dark phase, average time between feedings in *M. crassus* was significantly shorter than in *P. obesus*, whereas the opposite was true for light phase (Fig. 5). In *P. obesus*, diet had no effect on time between consecutive feedings.

Frequency of coprophagy differed significantly among treatments (F=21.2, p<0.001) and was independent on diel phase within-treatement (F=0.02, ns). Coprophagy was significantly less frequent in *M.*
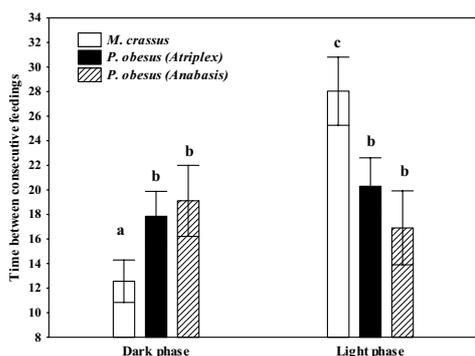
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Figure 5.

Average time between consecutive feeding sessions in two rodent species offered different diets

crassus (0.5±0.2 events per day, in average) than in *P. obesus* fed both food types (Tukey's HSD tests, p<0.001), whereas it was similarly common in *P. obesus* independently on diet (6.2±1.0 and 3.8±0.8 events per day, respectively; Tukey's HSD tests, ns, respectively).

DISCUSSION

Our predictions appeared only partly true. The results of the study supported predictions about relatively long overall feeding time and relatively low food intake under high quality diet, and contradicted to prediction about low proportion of active behaviour under low quality diet. Indeed, *M. crassus* fed the highest quality food spent the lowest proportion of its time budget for feeding compared to *P. obesus*. Nevertheless, number of feeding sessions in *M. crassus* was approximately the same but each separate feeding session was almost three times shorter than those in *P. obesus*. No difference in temporal pattern of feeding was found between *P. obesus* fed different plants, in spite of sharp differences in chemical composition of food. *A. syriaca* has higher fiber content but lower electrolytes than *A. halimus*. Nevertheless, *P. obesus* lesser their electrolyte intake by scraping the salt from the hypersaline cuticular layers of leaves before consuming them (Degen, 1988; Kam & Degen, 1988). Such leaf-scraping behaviour has previously been reported for chisel-toothed kangaroo rat, *Dipodomys microps* which feeds on the saltbush *A. confertifolia* (Kenagy, 1972; Kenagy, 1973).The absence of differences between two treatments in *P. obesus*, in spite of differences in their diet quality, can be partially explained by their manipulating with the food. They presumably scraped the hypersaline cuticular layer of leaves of *A. halimus* and avoid consuming fibers from the stems of *A. syriaca*, improving, thus, the quality of the consumed food parts. The occurrence of this cost is supported by the difference between calculated and realized time required by *P. obesus* for feeding. This difference was observed in both treatments of

P. obesus (see Table 1). *P. obesus* fed *A. halimus* was active significantly less time than *M. crassus*. Dry matter intake of *P. obesus* fed *A. halimus* was much higher than that of *M. crassus*. while dry matter intake of *P. obesus* fed *A. syriaca* was lower than even that in *M. crassus*.Unexpectedly, behavioural patterns in *P. obesus* did not differ between dile phases, although this species is considered as strictly diurnally active (Ilan and Yom-Tov, 1990).

We are aware of the fact that the number of animals used in presented experiment is not adequate to make a general conclusion. Due to the small size of the sample the difference between species is not clearly seen. The presented study provides only preliminary results. However, on the basis of these results it can be concluded that the examination of dietary intake and time budget in two desert rodents should be studied in detail on a larger sample in order to see the adjustment of animals regardless the type of diet they get.

REFERENCES

Castle, K. T. and Wunder, B. A. (1995). Limits to food-intake and fiber utilization in the prairie vole, *Microtus-ochrogaster* - effects of food quality and energy need. *Journal of Comparative Physiology, B*, 164: 609-617.

Daly, M. and Daly, S. (1973). On the feeding ecology of *Psammomys obesus* (Rodentia, Gerbilidae) in the Wad Saoura, Algeria. *Mammalia*, 37: 547-561

Degen, A A. (1993). Energy requirement of the fat sand rat (*Psammomys obesus*) when consuming the saltbrush, *Atriplex halimus*, a review. *Journal of Basic and Clinical Physiology and Pharmacology*, 4: 13-27.

Degen, A A. (1998). Energy expenditure and efficiency of energy use in rodents: desert and non-desert species. Journal of Basic and Clinical Physiology and Pharmacology, 9: 29-49.

Degen, A A., Kam, M., Khokhlova, I. S., Krasnov B.R. and Barraclough, T.G. (1998). Average daily metabolic rate of rodents: habitat and dietary comparisons. Functional Ecology, 12: 63-73.

Degen, A. A. (1988). Ash and electrolyte intakes of the fat sand rat, *Psammomys obesus*, consuming saltbrush, *Atriplex halimus*, containing different water content. *Physiological Zoology* 61: 137-141.

Degen, A. A. 1993. Energy requirements of the fat sand rat (*Psammomys obesus*) when consuming the saltbush, Atriplex halimus: a review. J *Journal of Basic and Clinical Physiology and Pharmacology* 4: 13-28.

Degen, A. A., Kam, R., Khokhlova, I. S. and Zeevi, K. 2000. Fiber digestion and energy utilization of fat sand rats (*Psammomys obesus*) consuming the chenopod *Anabasis articulata. Physiological and Biochemical Zoology* 73: 574-580.

Degen, A.A., Kam, M., Khokhlova and Zeevi Yaffa (2000). Fiber digestion and energy utilization of fat sand rat (*Psammomys obesus*) consuming the chenopod *Anabasis articulata. Physiological and Biochemical Zoology*, 73: 574-580.

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Agric. conspec. sci. Vol. 68 (2003) No. 4

Hammond, K. A. and Wunder, B. A. 1991. The role of diet quality and energy need in the nutritional ecology of a small herbivore, *Microtus ochrogaster. Physiological Zoology* 64: 541-567.

Ilan, M. and Yom-Tov, Y. (1990). Diel activity patterns of a diurnal desert rodent, *Psammomys obesus. Journal of Mammalogy*, 71: 66-69

Jackson, S. M. and Johnson, Ch.N. (2002). Time allocation to foraging in the mahogany glider *Petaurus gracilis* (Marsupialia, Petauridae) and a comparison of activity times in exudivorous and folivorous possums and gliders. *Journal of Zoology*, London, 256: 271-277

Kam, M. and Degen, A A. (1988). Efficiency of use of saltbrush (*Atriplex halimus*) for growth by fat sand rat (*Psammomys obesus*). *Journal of Mammalogy*, 70: 485-493.

Kam, M. and Degen, A. A. 1988. Water, electrolyte and nitrogen balances of fat sand rats (*Psammomys obesus*) when consuming the saltbush *Atriplex halimus. Journal of Zoology, London* 215: 453-462.

Kam, M., Khokhlova, I. S. and Degen, A A. (1997). Granivory and plant selection by desert gerbils of different size body. *Ecology*, 78: 2219-2229.

Kenagy,G.J. (1972). Saltbush leaves - excision of hypersaline tissue by a kangaroo rat. *Science*, 178: 1094.

Kenagy,G.J. (1973). Adaptations for leaf eating in Great Basin kangaroo rat, Dipodomys microps. *Oecologia*, 12: 383-412.

Khokhlova, I.S., Kam, M. & Degen, A.A. (1997). A small gerbil that maximizes intake of energy from low-energy food. *Journal of Mammalogy*, 78: 158-162.

Krasnov, B. R., Shenbrot, G. I., Khokhlova, I. S., Degen, A A. and Rogovin, K.A. (1996). On the biology of Sundevall's jird (*Meriones crassus* Sundevall, 1842) (Rodentia: Gerbillidae) in the Negev Highlands, Israel. *Mammalia*, 60: 375-391.

Loeb, S. C., Schwab, R. G. and Demment, M. W. 1991. Responses of pocket gophers (*Thomomys bottae*) to changes in diet quality. *Oecologia* 86: 542-551.

Tchabovsky, A. V. and Krasnov, B. R. 2002. Spatial distribution of *Psammomys obesus* in relation to vegetation in the Negev desert of Israel. Mammalia 66: 361-368.

Veloso, C. and Bozinovic, F. 1993. Dietary and digestive constraints on basal energy-metabolism in a small herbivorous rodent. *Ecology* 74: 2003-2010.

Veloso, C. and Bozinovic, F. 2000. Interplay between acclimation time and diet quality on basal metabolic rate in females of degus *Octodon degus* (Rodentia : Octodontidae). *Journal of Zoology, London* 252: 531-533.

Yigit, N., Colak, E. and Sözen, M. (1996). Investigation on biology of Meriones crassus Sundevall, 1842 (Mammalia, Rodentia) in Turkey. Turkish Journal of Zoology, 20: 211-215.

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