

Patch use in a diurnal rodent: handling and searching under thermoregulatory costs

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Summary

1. The role of physiological complexity in animal foraging ecology was investigated through experiments to determine how animals manage time and energy during patch use under thermoregulatory costs. The Degu *Octodon degus* (Molina 1782), a diurnal rodent inhabiting the semiarid environments of central Chile, was studied.

2. Previous studies reported that Degus are constrained to specific foraging areas mainly by limits to thermal tolerance and food quality. Predation risk may also be important. Because new evidence shows that physiological processes are important in shaping foraging ecology, it was hypothesized that Degu foraging behaviour is influenced by the risk of hyperthermia as well as by the advantages of gathering food efficiently.

3. Feeding trials were conducted in an experimental arena with food offered in an experimental patch containing sand and placed under a heater. Using video cameras, the overall time budget was measured, including frequency and duration of patch visits, and events of food gathering. Besides ambient temperature (high or low), handling time was manipulated by using husked and unhusked sunflower seeds, and searching time by using two seed distributions.

4. Ambient temperature and husk state as well as ambient temperature and seed distribution interacted in their influence on both handling time and searching efficiency. These results imply that a thermally risky patch affects both parameters associated with patch use and diet selection and that this effect disappears when animals are not risking hyperthermia.

5. Degus decreased the frequency of patch visits under thermoregulatory costs. This behaviour resulted exclusively from the effect of ambient temperature. Data on time use suggest that direct exposure to higher environmental temperatures is avoided through changes in the duration of patch visits. Degus harvested food items in shorter foraging bouts when food was under a stressful thermal patch.

6. In conclusion, a time-minimizing foraging behaviour, in face of Degus' thermoregulatory physiology and related risks, was observed.

Key-words: Chilean matorral, foraging and thermal ecology, *Octodon degus*, time and energy use

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Introduction

The study of thermal and foraging ecology has the potential to provide a mechanistic bridge between the study of physiology and its relationships with the environment and resulting life histories (Tracy & Christian 1986; Adolph & Porter 1993). The interplay between thermoregulation and foraging strategies has been seldom studied (but see Ayres & Shine 1997). Because environmental temperature varies in time and space at different time-scales, organisms are continually challenged to maintain homeostasis (Johnston &

Bennett 1996). Thus, thermal physiology may be a significant factor underlying the foraging success of animals (Caraco *et al.* 1990). This is particularly true for diurnal endotherms that inhabit arid hot environments, because when foraging, these animals must simultaneously select dietary items, avoid predators and dissipate excess heat load through behavioural and physiological mechanisms (Chapell & Bartholomew 1981).

Traditionally, foraging theory has considered search rate and handling time as fixed constraints, i.e.

factors that limit and/or define the relationships between currencies (e.g. long-term rate of energy gain) and decision variables (e.g. patch residence time) (Stephens & Krebs 1986). However, empirical studies have shown that constraints vary owing to diverse ecological factors, including predation risk (Newman *et al.* 1988; Brown 1999) and social environment (R. A. Vásquez & A. Kacelnik, unpublished data). To the best of our knowledge, no previous research has studied the effect of the thermal environment on some of these foraging parameters.

Time and space use, as well as food handling and searching, may be constrained by thermal factors if the consumer must use a thermally stressful patch to obtain its food, as is the case with the Degu, *Octodon degus* (Rodentia, Octodontidae). The Degu is a diurnal rodent inhabiting the semiarid and Mediterranean environments of northern and central Chile. In central Chile, where summers are hot and dry, some species of rodents appear to be limited in their spatial and temporal use of certain microhabitats by high ambient temperature (Bozinovic *et al.* 1995), as well as by predation risk (Jaksic 1986; Vásquez 1996). Degus have a high water conservation efficiency (Cortés, Rosenmann & Báez 1990) but a low capability for evaporative thermolysis (Rosenmann 1977), and their intolerance of environmental temperatures higher than 32 °C has been proposed as a factor explaining microhabitat use. In fact, Lagos, Bozinovic & Contreras (1995a) found that during both hot and cold seasons in central Chile, mean and maximum ambient temperature were significantly higher in open patches than underneath shrubs (covered microhabitat), and that Degus were more active in covered microhabitats than in the open during summer. These authors concluded that during the hot season Degus avoid open areas and use microhabitats under shrubs much more intensively, even in the absence of predators.

Torres-Contreras & Bozinovic (1997) reported a series of diet selection experiments conducted in an experimental arena under variable food quality and thermal regimes. They found that Degus preferred items of high quality (low fibre) but that selection was influenced by seasonal and spatial changes in food quality and environmental temperatures, coupled with feeding time, digestive processing and thermoregulatory risk. Therefore, in the field as well as in experimental arenas, foraging Degus can be temporally and spatially constrained mainly by their limited thermal tolerance, and by environmental food quality and predation risk (Meserve, Martin & Rodriguez 1984; Jaksic 1986; Bozinovic 1995; Lagos *et al.* 1995b; Bozinovic, Novoa & Sabat 1997; Torres-Contreras & Bozinovic 1997; Vásquez 1997). In addition, Degus may shift from a bimodal foraging regime in summer to a unimodal one midwinter (G. J. Kenagy *et al.*, unpublished data). These thermal opportunities for activity that shift seasonally, together with the quality and availability of food (Meserve *et al.* 1984), should

be considered when fine-tuning models of foraging behaviour. Understanding the shift in activity requires an analysis of the role of physiological responses in foraging behaviour. These considerations have not traditionally been taken into account in foraging research, because early theory considered physiological (and morphological) features as fixed constraints (Stephens & Krebs 1986).

In this study we examined the influence of thermoregulation on the foraging behaviour (harvest rates and time allocation) of Degus by using an experimental approach and some theoretical tools from the classical models of patch use and diet selection (e.g. Stephens & Krebs 1986; Brown, Kotler & Valone 1994) under different heat loads. It is hypothesized that the Degu's foraging behaviour is influenced by thermoregulatory costs as well as by the advantages of gathering food efficiently. Specifically, it was tested whether, in response to an increased cost of hyperthermia, Degus reduced or shifted foraging activity by changing the frequency and duration of foraging bouts in a thermoregulatory stressful patch. Further, it was tested whether thermally costly patches affect foraging components such as prey handling, searching efficiency and harvest rates (gain functions). Because an attempt was made to understand the role of physiological complexity in foraging ecology (Karasov 1986; Weiner 1992; Bozinovic & Martínez del Río 1996), our experiments were designed to determine how animals manage time and energy during patch use under physiological cost.

Material and methods

ANIMALS

Animals were non-reproductive and captured in Quebrada de la Plata, central Chile (70°50'W, 33°31'S). The habitat of Degus generally has an irregular topography, and the dominant evergreen vegetation commonly exhibits a mosaic of patches that vary on a broad spatial scale (Fuentes *et al.* 1984, 1986). Twelve females with a mean body mass of 227.9 ± 5.5 g (± 1 standard error) were used. Between trials rodents were individually maintained in plastic cages (300 × 300 × 150 mm³) with a photoperiod of light : dark of 12 : 12 and ambient temperature of 20 °C, with water and food (rabbit pellets) provided *ad libitum*.

PATCH USE AND TIME MANAGEMENT

Patch use trials were conducted to determine if heat stress affected foraging behaviour and time allocation. Trials were conducted in an experimental arena measuring 1900 × 2000 × 1000 mm³, with water *ad libitum*. The floor was covered with fine sand to a depth of ≈ 80 mm. Sunflower seeds were offered in an experimental patch, consisting of a metal tray (500 × 400 mm²) containing a standard volume of 6-l

fine sand and placed under a 220-V, 1000-W commercial heater located 900 mm above the experimental patch.

A video tape camera (Sony CCD-TR330, Sony Corporation, Japan) placed in front of the experimental arena allowed the animals to be recorded unobtrusively. Frequency and duration of patch visits and events of food collection were measured by inspection of the video record. The experimental ambient temperatures (T_a) were similar to those reported by Lagos *et al.* (1995a) in natural habitats of *O. degus*. In addition, the thermal patch was calibrated through measurements of surface soil and air temperature (1 cm above ground surface) inside and outside the patch. The operative temperature was also measured inside and outside the patch by use of hollow mounted skins or 'thermal mannequins' (*sensu* Bennett *et al.* 1984) that contained an internal thermocouple. Temperatures were recorded with a Digi-Sense instrument and Cu-constantan thermocouples (air and mannequin core temperatures), and an infrared Infratrace 801 thermometer (Kane May Limited, UK) (surface soil and surface mannequin temperature). Results of the patch thermal calibration are shown in Fig. 1.

Two-hour trials were conducted using animals that had been starved for 24 h. In addition to providing two thermal regimes (high = T_{a+} ; low = T_{a-}), handling time was manipulated by using husked ($H-$) and entire (i.e. unhusked, $H+$) sunflower seeds (see Kaufman & Collier 1981); previous experiments demonstrated that Degus do not consume sunflower seed husks (R. A. Vásquez, unpublished data). Search time was also manipulated by placing seeds in one of

two configurations: grouped seeds ($G+$) occupied an area of $\approx 100 \times 100 \text{ mm}^2$ on the surface in the middle of the patch, whereas ungrouped seeds ($G-$) were randomly distributed in the patch with half of the seeds on the surface and the other half mixed with the sand. A total of 30 seeds were offered in each trial. Thus, the factorial experimental design included all combinations of T_{a+}/T_{a-} , $G+/G-$ and $H+/H-$. Treatments were presented in random order to each subject.

Following Kotler & Brown (1990), and Brown *et al.* (1994) the data were fitted to Holling's (1965) disc equation to estimate the two parameters of the model: search efficiency or attack rate (a) and handling time (h), under our experimental treatments. We used the following equation:

$$t(s) = \frac{1}{a} \left[\ln \left(\frac{N_0}{N} \right) \right] + h(N_0 - N), \quad \text{eqn 1}$$

where t = time spent foraging in the patch, $N_0 = 30$ sunflower seeds as the initial amount of food in the patch, and N = giving-up density, i.e. the number of seeds remaining within the patch after the Degu has spent time harvesting seeds (Brown 1988). Searching efficiency represents encounter probability of a Degu with seeds, and handling time represents the time interval required to extract an encountered seed from the substrate, husk it (if necessary), and place it in its mouth for consumption (Kotler & Brown 1990).

TOTAL DIGESTIBLE ENERGY INTAKE AND HARVEST RATE

To determine total digestible energy intake of sunflower seeds during the different treatments, digestibility (D) was first measured on five subjects housed individually in metabolic cages with metal trays underneath to collect faeces. Water was provided *ad libitum*, photoperiod was L : D = 12 : 12, and ambient temperature was set at approximately 20 °C. Nutritional trials were conducted for 7 days offering seeds *ad libitum*. Each day, the collected faeces and the remaining uneaten food were weighed, after drying at 60 °C to constant mass. Apparent digestibility of seeds was calculated as: (daily amount of food intake – daily amount of faeces production)/daily amount of food intake. Digestibility is called apparent because this method underestimates digestive efficiency by the contribution of metabolic wastes and non-reabsorbed secretions of the digestive system (Karasov 1990; Veloso & Bozinovic 1993). Energy content (Q) of sunflower seeds without husks was determined in a Parr 1261 computerized calorimeter (Parr Instruments, Moline, IL, USA). Two replicates were determined to be ash free and reliable when the difference between two measurements was less than 1%.

Total digestible energy intake (DEI) under our experimental conditions was calculated according to:

$$\text{DEI} = D \times Q \times N_i, \quad \text{eqn 2}$$

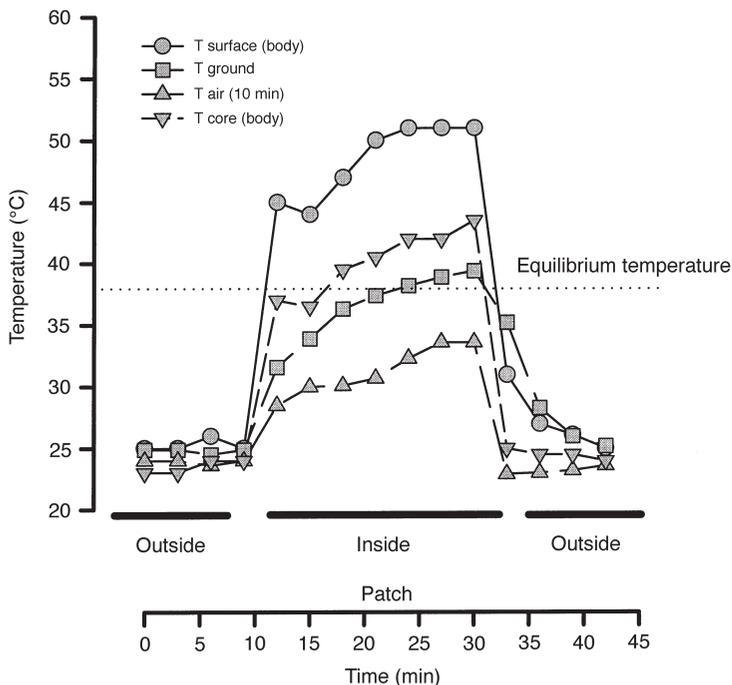


Fig. 1. Patch thermal calibration. Environmental (T_{ground} and T_{air}) and operative (T_{surface} and T_{body} of thermal mannequins) temperatures as a function of time inside and outside the experimental patch.

where DQ = total digestible energy intake per gram of sunflower seeds, and N_i (g) = total seed weight ingested during each trial (2 h). Based on the requirements of equation 2, number of seeds (N_s) were transformed to mass (N), through the calibration curve: N (g) = $0.01223 + 0.04148N_s$, $r = 0.983$, $F_{1,33} = 958.31$, $P < 0.00001$. Brown *et al.* (1994) was followed to calculate the quitting harvest rate (HR):

$$\text{HR (kJ/s)} = DQ \left(\frac{aN}{1 + ahN} \right), \quad \text{eqn 3}$$

with N = weight of seeds (g) remaining within the patch after each *Degu* has spent time harvesting seeds.

STATISTICS

Statistical analyses were performed using the STATIS-

TICA (StatSoft 1997) statistical package for Windows 95. Data were analysed by non-linear estimation procedures, multiway within subject ANOVA and Tukey tests for multiple comparisons. Data fulfilled the assumptions of the ANOVA. Results are reported as mean \pm 1 standard error.

Results

PATCH USE AND TIME MANAGEMENT

The number of seeds harvested as a function of time in patch were plotted (Fig. 2), and the parameters h (handling time) and a (search efficiency) under each treatment were estimated (Fig. 3).

As expected, results of a multi-way within-subject ANOVA (Table 1) revealed a significant effect of presence

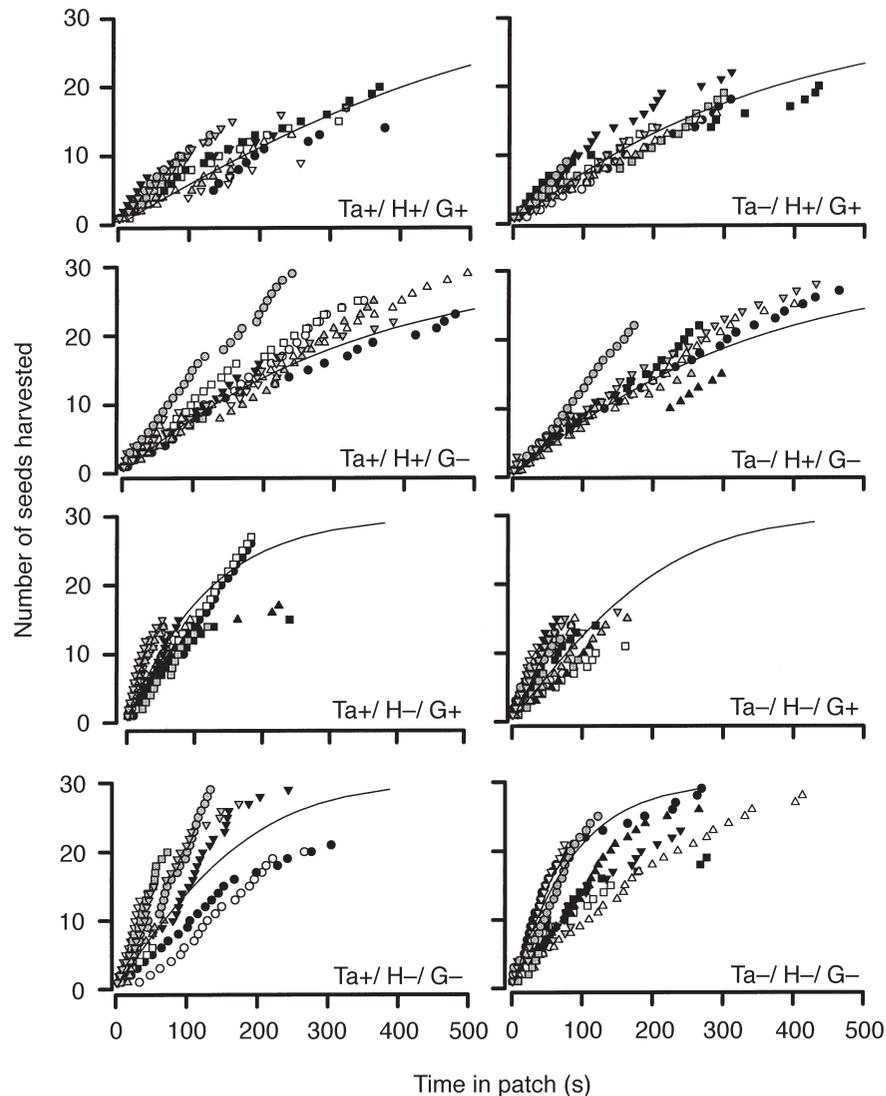


Fig. 2. Number of seeds harvested by *Octodon degus* from the seed tray as a function of time spent foraging in the patch under different experimental conditions. Individuals are identified with different symbols. Abbreviations are: high (T_{a+}) and low (T_{a-}) ambient temperature, sunflower seeds with husk ($H+$) and without husk ($H-$), grouped ($G+$) and ungrouped ($G-$) seeds. Average gain functions (thin lines) were obtained by fitting the data to equation 1 (see Methods).

of husk on seeds on handling time (h ; Table 1b), but not of seed distribution or ambient temperature. Nevertheless, a significant effect of the interaction between ambient temperature and husk ($T_a \times H$), and temperature and seed distribution ($T_a \times G$) was observed (Table 1b). Under high ambient temperature and the joint condition of seeds with husk and grouped ($H+/G+$), h -values were larger than when seeds were husked and ungrouped ($H-/G-$). Interestingly, under low temperature, h -values were similar among treatments involving experimental manipulation of husk and seed distribution (see Fig. 3). On the other hand, multi-way within-subject ANOVA (Table 1) on attack rates (a) revealed a significant effect of seed distribution (Table 1a), but not of husk or ambient temperature. As in the case of handling time, a significant positive effect was observed on search efficiency by the interaction between ambient temperature and husk ($T_a \times H$) and between ambient temperature and seed distribution ($T_a \times G$; Table 1a). In contrast to the increased handling time under high temperature (T_a+) and unhusked and grouped seeds ($H+/G+$), a -values were lower than for husked dispersed seeds ($H-/G-$) (Fig. 3). Also under low ambient temperature, a -values were similar among treatments (Fig. 3).

It is hypothesized that in response to an increased risk of hyperthermia *Degus* shift the duration and frequency of patch visits, decreasing the time spent in a thermoregulatory costly patch and increasing the time allocated to more favourable areas. Comparisons involving time budget and patch use as functions of ambient temperature and food quality (H and G) presumably provide information about how animals select food and use time when feeding. Inspection of the video records and multi-way within-subject ANOVA of medians of the frequency distribution of patch visit duration revealed a significant effect of ambient tem-

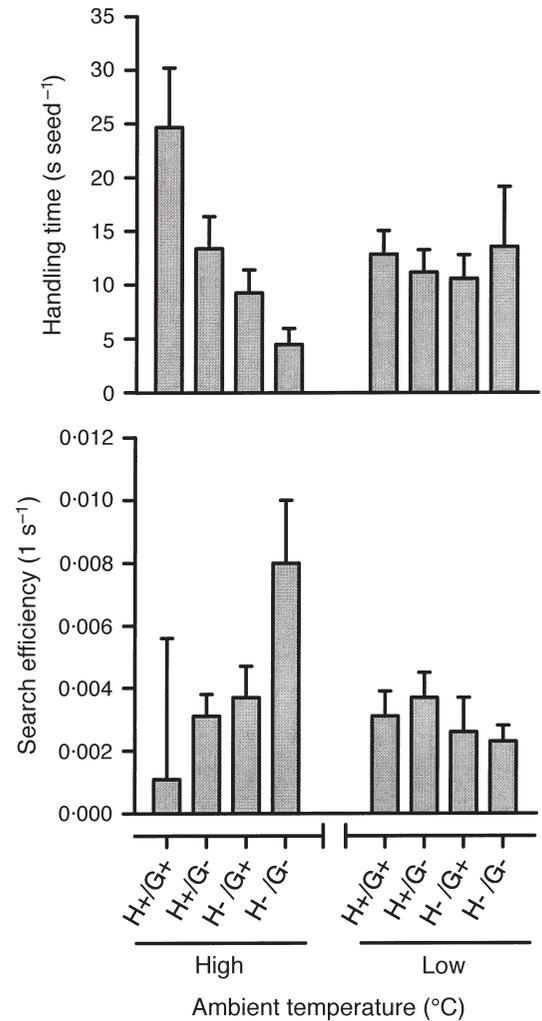


Fig. 3. Effect of ambient temperature, husk state (H) and seed distribution (G) on handling time and search efficiency of *Octodon degus*. Parameters were obtained from equation 1 (see Fig. 2). Results of statistical analyses are shown in Table 1.

Table 1. Multi-way within-subject ANOVA testing for the influence of ambient temperature (T_a), husk state (H) and distribution of seeds (G) in the patch, on search efficiency (a) and handling time (h) in *Octodon degus*

Effect	df effect	MS effect	df error	MS error	F	P
(a) Search efficiency						
T_a	1	54 230.0	11	139 410.8	0.389	0.544
H	1	608 185.0	11	239 511.8	2.539	0.139
G	1	796 765.0	11	139 622.6	5.707	0.035
$T_a \times H$	1	1 639 274.0	11	200 542.9	8.174	0.016
$T_a \times G$	1	824 446.0	11	106 252.0	7.759	0.017
$H \times G$	1	383 797.0	11	131 608.5	2.916	0.116
$T_a \times H \times G$	1	162 460.0	11	89 394.2	1.817	0.205
(b) Handling time						
T_a	1	20.209	11	151.099	0.134	0.722
H	1	876.815	11	150.709	5.818	0.034
G	1	329.108	11	88.749	3.708	0.080
$T_a \times H$	1	893.699	11	182.329	4.902	0.048
$T_a \times G$	1	449.887	11	41.398	10.867	0.007
$H \times G$	1	186.924	11	123.699	1.511	0.244
$T_a \times H \times G$	1	5.113	11	143.855	0.035	0.854

perature (Table 2). Duration of patch visits is significantly lower under high in comparison with low ambient temperature (*a posteriori* Tukey test, $P = 0.017$, 5.9 ± 0.57 s vs 7.8 ± 0.51 s under T_a+ and T_a- treatments, respectively; see Fig. 4).

TOTAL DIGESTIBLE ENERGY INTAKE AND HARVEST RATE

It was tested whether in response to an increased risk of hyperthermia *Degus* increase energy return. Consequently, total digestible energy intake and harvest rate were evaluated in the patch (equations 2 and 3, respectively). Our independent measurements of sunflower seed digestibility in *Degus*, indicated an apparent digestibility (D) of 0.972 ± 0.002 ($n = 5$). Also, energy content (Q) of husked sunflower seeds was measured as being 30.2 ± 2.2 kJ g⁻¹ ($n = 4$). Thus, total digestible energy intake (DQ) was 29.35 kJ g⁻¹. Using this value in equation 2, total DEI in kJ was calculated

under all different treatments. Multi-way within-subject ANOVA (Table 3a) revealed a significant effect of seed distribution on DEI. Against our expectations, DEI was lower with grouped seeds. Also, the interaction among ambient temperature, husk and seed distribution ($T_a \times H \times G$) was marginally significant (Table 3a). Nevertheless, multi-way within-subject ANOVA revealed that quitting harvest rate (HR in kJ s^{-1}) was not significantly different among treatments (Table 3b).

Summarizing, seed distribution and husk state significantly affected both handling time and searching efficiency, and there was a significant interaction with ambient temperature. Thus, our conclusions regarding Degu responses to experimental treatments are the following. Handling time (s seed^{-1}) was 5.5 times higher under high thermoregulatory risk for unhusked grouped seeds than compared with husked dispersed seeds ($24.6 \pm 5.5 \text{ s seed}^{-1}$ vs $4.5 \pm 1.5 \text{ s seed}^{-1}$, respectively, *a posteriori* Tukey test $P = 0.034$, Fig. 3), with intermediate values for the other treatments (Fig. 3). Interestingly, under no thermoregulatory cost, handling time was almost invariant across all treatments (range: 10.6–13.5 s seed^{-1}). The pattern for searching efficiency ($1/\text{s}$) was quite different from that for handling time. Searching efficiency ($1/\text{s}$) was eight times lower under high thermoregulatory cost, unhusked grouped seeds, compared with high thermoregulatory cost, husked and dispersed seeds ($0.0011 \pm 0.0005 \text{ 1/s}$ vs $0.009 \pm 0.002 \text{ 1/s}$, respectively, *a posteriori* Tukey test, $P = 0.036$, Fig. 3). As with handling time, searching efficiency was not affected when ambient temperature was not restrictive (Fig. 3).

The significant interactions between ambient temperature and husk, as well as between ambient temperature and seed distribution on both seed handling time and searching efficiency (Table 1), revealed that a thermally stressful patch affects both 'foraging constraints' associated with patch use and diet selection and that this effect, under our experimental treatments, disappears when animals are not under the cost of hyperthermia. The effect of heat load on *a* and *h* is biologically meaningful. Nevertheless, it is necessary to be careful with this kind of analysis because it is not very sensitive, for example, to changes in portions of the gain curves.

Table 2. Multi-way within-subject ANOVA testing the influence of ambient temperature (T_a), husk state (H) and distribution of seeds (G) in the patch, on the medians of the frequency distribution of patch visit time by *Octodon degus*

Effect	df effect	MS effect	df error	MS error	F	P
T_a	1	81.218	11	10.394	7.814	0.017
H	1	0.017	11	23.569	0.001	0.979
G	1	28.492	11	15.682	1.817	0.205
$T_a \times H$	1	0.467	11	7.873	0.059	0.812
$T_a \times G$	1	32.318	11	21.435	1.508	0.245
$H \times G$	1	44.418	11	15.423	2.879	0.118
$T_a \times H \times G$	1	67.838	11	28.226	2.403	0.149

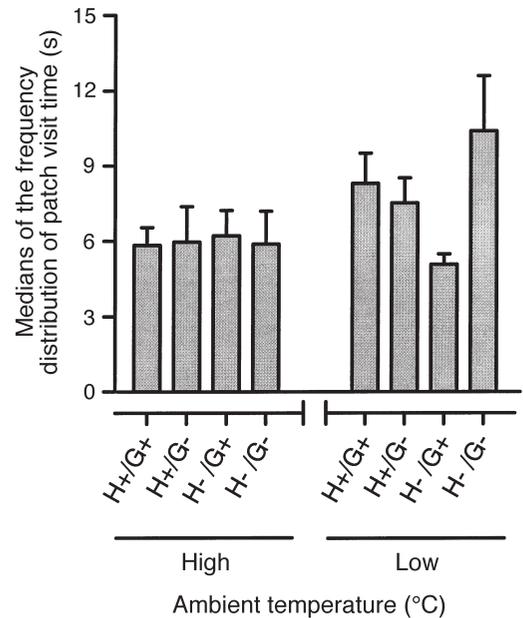


Fig. 4. Effect of ambient temperature, husk state (H) and seed distribution (G) in the experimental patch on the medians of the frequency of patch visit time by *Octodon degus*. Results of statistical analyses are shown in Table 1.

Regarding the responses of Degus in terms of time allocation during patch exploitation it was found that the medians of the frequency of patch visit durations (s) revealed a decrease in frequency under thermoregulatory cost. This behaviour arises from the effect of ambient temperature and not from the main effect of husk and seed distribution, nor from the interaction among these factors (Table 2, Fig. 4). Direct exposure to higher environmental temperatures is avoided through changes in the frequency of patch visits. When food was under a stressful thermal patch, Degus preferred to consume it during shorter bouts of foraging. Therefore, in the field, heat stress may change patch visit patterns, thus explaining previous field observations of thermal constraints for foraging activity.

Discussion

Patch exploitation and food selection, like any behaviour, are hierarchical processes. Animals select habitats where they differentially allocate efforts among distinct food patches, and within these they choose some dietary items. Consequently, factors that determine patch utilization and diet depend not only on food quality and availability, but also on multiple factors, including physiological trade-offs and constraints. Because our approach spans a much more general problem, which is how animals manage time and energy during diet selection and patch use, Degus were experimentally tested for patch exploitation under physiological–thermoregulatory cost. A time-minimizing thermoregulatory costly

foraging behaviour, in the face of Degus's physiological constraints, such as its low evaporative thermolysis (Rosenmann 1977; Cortés, Zuleta & Rosenmann 1988), was observed. In the field, Degus may have greater flexibility in the sense that they could use high-temperature patches briefly such as was observed in our experimental patch, by accessing high-temperature microhabitats, spend brief bouts of seed consumption and/or pick up food quickly and then return to a cooler location to ingest it. On the other hand, although total digestible energy intake was affected by seed distribution, harvest rate was not significantly different among treatments. Our observations revealed that when Degus are exploiting a clump of seeds (grouped seed distribution treatment), they can easily find those seeds located on the surface. However, they end up sitting on top of the clump while they forage on a given seed, thereby burying many other seeds, hence making them more difficult to find. This may explain why the harvest rate is almost constant when seeds are clumped, and exploitation ceases quite suddenly after a given amount of seeds has been collected. When seeds are more evenly distributed, Degus successfully collect most of the available seeds.

Handling time and searching efficiency have commonly been treated as fixed parameters of an animal's behavioural repertoire (Stephens & Krebs 1986). Although the gain function (harvest rate curve) is also commonly regarded as constrained for a given patch (Stephens & Krebs 1986), there are a number of patch features, besides resource density, that may alter it. Newman *et al.* (1988) found that handling time and hence gain functions of grey squirrels, *Sciurus carolinensis*, feeding on seed patches were affected by predation risk (manipulated as distance to protective cover). More recently, R. A. Vásquez & A. Kacelnik

(unpublished data) found that starlings, *Sturnus vulgaris*, show slower gain functions in social than in solitary situations. A number of studies have reported the effect of environmental temperature on foraging decisions (e.g. Grubb & Greenwald 1982; Caraco *et al.* 1990; Bowers, Jefferson & Kuebler 1993); however, our study seems to be the first to show the effect of thermal cost on foraging parameters as they are defined in standard foraging theory (see Stephens & Krebs 1986).

The disc equation assumes that handling and searching are mutually exclusive behaviours, and that both can explain the asymptotic plateau observed in studies of the functional response (Holling 1965; Hassell 1978; Krebs, Stephens & Sutherland 1983). As prey density increases, the predator allocates an increasing proportion of time to prey handling until an asymptotic feeding rate is reached (see also Brown *et al.* 1994). The values obtained for handling time of sunflower seeds with and without husk for *O. degus* are similar to those reported by Kaufman & Collier (1981) using rats *Rattus norvegicus* a species with a similar body size to Degus and offering food as clumps with no depletion (no mixture with substrate). Because these authors assessed seed handling directly, the curve fitting approach seems to be, to some extent, validated.

Patch use as well as diet selection depend on the ecological context in which foraging takes place, and the maximization of the net rate of energetic gain provides the basis of the models of patch utilization and diet choice (Stephens & Krebs 1986). Nevertheless, the physiological features of the animals, in combination with the availability, structural and chemical properties of food can also have an important, albeit relatively unstudied effect on foraging choice (see Caraco *et al.* 1990). On the other hand, ecological approaches to foraging often attempt to test whether economic principles are followed by organisms in time and space. Foraging ecology in exhaustible food patches should reveal the animal's foraging economics and its perception of biotic and abiotic environmental quality (Brown 1988; Houston 1995; McNamara & Houston 1997). Theoretically, when an animal minimizes the time spent to meet its nutritional requirements or maximizes the energy obtained, it is considered to be maximizing its fitness (Schoener 1971; Pyke, Pulliam & Charnov 1977). Based on these arguments and our results, it is predicted that under physiological stress the optimal foraging strategy is to maximize the instantaneous harvest rate and to minimize feeding time. These physiological determinants may explain why animals are not capable of foraging during all of the available time and why in many circumstances they choose options with lower rates of net energy gain (Bozinovic & Martínez del Río 1996). In spite of the well-known role of predation costs associated with patch use and diet selection (Brown 1988; Lima 1988; Vásquez 1996; see Lima 1998 for a recent

Table 3. Multi-way within-subject ANOVA testing the influence of ambient temperature (T_a), husk state (H) and distribution of seeds (G) in the patch, on (a) digestible total energy intake and (b) quitting harvest rate by *Octodon degus*

Effect	df effect	MS effect	df error	MS error	F	P
(a) Digestible energy intake						
T_a	1	80.037	11	79.429	1.008	0.337
H	1	0.247	11	18.505	0.013	0.910
G	1	830.993	11	94.297	8.813	0.013
$T_a \times H$	1	10.437	11	33.477	0.311	0.588
$T_a \times G$	1	10.437	11	48.434	0.215	0.652
$H \times G$	1	1.544	11	63.525	0.024	0.878
$T_a \times H \times G$	1	154.390	11	34.404	4.488	0.058
(b) Harvest rate						
T_a	1	966.5	11	40 126.16	0.024	0.879
H	1	781.1	11	38 011.58	0.021	0.888
G	1	4972.5	11	23 692.51	0.209	0.656
$T_a \times H$	1	103 724.2	11	37 750.58	2.747	0.126
$T_a \times G$	1	33 366.0	11	26 814.87	1.244	0.288
$T_a \times H \times G$	1	50 556.7	11	26 729.93	1.891	0.196
$T_a \times H \times G$	1	634.3	11	23 753.36	0.026	0.873

review), the wide temporal and spatial range of available thermal conditions and the thermoregulatory homeostasis of animals under both hot and cold conditions may play a major role in foraging ecology and in the potential to minimize energy costs. That is, given that activity in a given time period is dependent on cumulative thermal budgets, time of day and previous activity, the dynamic state-dependent physiology should be extremely important in deciding when and how a food patch should be used.

Certainly, the generality of our findings needs to be tested in the field and in other species of diurnal animals to determine whether our conclusions apply to other systems. For instance, the thermal properties of different microhabitats should be measured in conjunction with food manipulation experiments.

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