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Foraging under predation risk in the wild guinea pig: the effect of vegetation height on habitat utilization

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Wild guinea pigs are neotropical, diurnal, herbivorous rodents which frequently inhabit field borders. They use borders as protection from predators and forage in adjacent fields. We studied the relationship between the height of field vegetation and cavy density along the border. Animal distribution was determined by an indirect method based on counting the number of faeces in circular sample units. We sampled 60 units on a 1800-m line transect placed on field borders five times between July and December 1991, at intervals of 32 to 43 days. Cavy density was highest where vegetation height in the foraging areas was lowest. This relationship was most strong in July (winter) and was progressively lost with plant growth. We interpretated these results as the population expression of individual strategies for solving the trade-off between foraging and predation risk: individual guinea pigs (1) should select a home range with shelter for daily inactive periods given by the field border, and with an adjacent rich area of very short grass to forage; and (2) should reduce danger in open areas by behavioural adaptations.

1. Introduction

Most prey are more conspicuous to predators while foraging than when they remain motionless, therefore a conflict between foraging and safety from predators is expected (Lima & Dill 1990). This behavioural trade-off has been extensively analysed by decision-making theory applied to foraging behaviour (Krebs & Kacelnik 1991). Numerous studies have shown that predation danger affects many foraging decisions, including how much time to spend foraging, which foraging strategy to use, where to eat, which types of prey to consume, and when to leave a patch. Lima & Dill (1990) recently reviewed this literature and showed that there are many experimental demonstrations, especially in fish, of predation risk negatively affecting the use of patches and habitats rich in food. They also described how, in natural conditions, some environmental features, such as rocky outcrops, provide good protection from predators, and animals

often prefer to use habitats with these antipredation resources, even if this increases the cost of foraging. In the case of many terrestrial vertebrates, dense, high vegetation is commonly used as shelter from predators.

Rodents are one of the animal groups in which the effect of vegetation cover in habitat utilization is best documented and many species have shown preferences for habitats with more cover (e.g., Eadie 1953, Dickman 1992, Drickamer 1990, Kaufman et al. 1983, Kotler et al. 1991, LoBoue & Darnell 1959). However, for herbivorous rodents, the optimal solution to the trade-off between foraging and antipredation defence is not necessarily achieved by living permanently in grassland with high and dense vegetation. This is because vegetation often decreases in nutritional quality as the age of plant tissue and the amount of dead senesced tissue increases (Crawley 1983, Croswell & Kamstra 1976, Heitschmidt et al. 1987).

Wild guinea pigs (cavies: *Cavia aperea*) are neotropical, diurnal, herbivorous rodents, which frequently inhabit field borders. They spend the majority of their time in the border which provides good refuge and use adjacent, more open areas for foraging (Rood 1972, Cassini 1991). While the vegetation of the border remains high and dense all year, that in the adjacent foraging areas varies in time. Two main dimensional axes in a cavy's home range can be defined: (1) a minor axis of several meters along which guinea pigs move daily from shelter to foraging grounds, and (2) a major axis of tenths to hundreds of meters, parallel to the field border. Movements on the major axis are related to habitat selection decisions, which will be influenced by characteristics of the vegetation in adjacent foraging fields, since the vegetation on the border is relatively homogeneous in time and space.

As part of a major project on the foraging ecology of *C. aperea*, we studied the relationship between the height of vegetation in foraging grounds and cavy density along a field border. Two main constraints on the habitat selection rules of cavies living in field borders are assumed:

1) predation risk increases with decreasing vegetation height and with distance from border, and

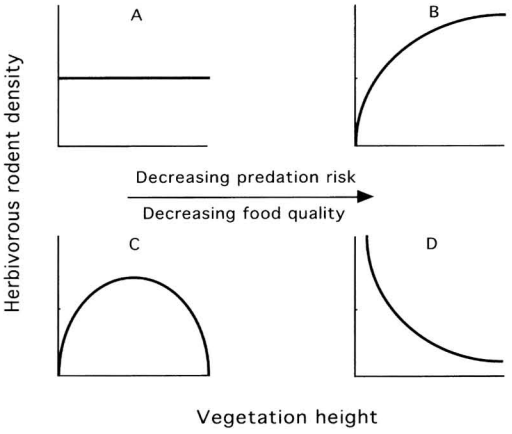

Fig. 1. Hypothetical distribution of herbivorous rodent densities in relation to vegetation height in foraging areas based on four different individual decision rules on the trade-off between foraging and predation. — A) Random behaviour. — B) Spatial preferences affected by predation risk alone. — C) A balance between predation avoidance and foraging is found by preferring vegetation of intermediate height, which provides certain protection against predators without loosing too much nutritional quality. — D) The solution to the trade-off implies using the areas of highest nutritional quality, and using antipredation adaptations to cope with the increased risk.

2) food quality decreases as vegetation height increases.

At least four possible trends were expected depending on the solution individual cavies found to the conflict between foraging and predation (Fig. 1):

1) if guinea pigs select habitats exclusively in terms of reducing predation risk, a positive relationship is expected (Fig. 1b).
2) if food is the exclusive factor, they will use fields with the shortest vegetation, irrespective of the shelter these provide. This hypothesis was disregarded because Rood (1972) observed that cavies consistently foraged within a few metres of shelter, and this observation has been quantitatively confirmed (Cassini 1991).

If cavies balance the costs and benefits of both activities, at least two solutions are possible:

3) To remain in the shelter during periods of inactivity and to forage in vegetation of a height which provides some protection against predators while retaining good nutritional value; according to this hypothesis, maximum cavy density is expected at some intermediate vegetation height (Fig. 1c).
4) To use areas of highest food quality near a shelter; a positive relationship between vegetation height and cavy abundance would therefore be predicted (Fig. 1d). As will be addressed in more detail in the discussion, this strategy should be complemented with behavioural adaptations to cope with increased danger in open areas.

2. Methods

2.1. Study area

The study was conducted between July and December 1991 on the Lujan University campus, in the northwestern part of the Buenos Aires Province (Argentina). This area is part of the grassland steppe of the Pampean planes (34°40′S and 59°10′W), at present extensively exploited by agricultural systems. In the study area, cavies were found to live in continuous zones of high vegetation along railways, and to forage in the adjacent University fields. We sampled a 1800-m line transect placed on the boundary between these two zones, crossing six fields with different crops.

Potential predators on the study area included four species of hawks (*Cyrus ayaneus*, *Milvago chimango*, *Polyborus plancus*, *Rupornis magnirostris*), the marsupial *Lutreolina crassicaudata* and feral dogs and cats.

2.2. Procedure

Animal distribution was determined by an indirect method based on counting the number of faeces in circular sample units (NFSU) of 0.5 m diameter (Putman 1984). This method was used instead of direct census because it is not affected by vegetation height. Sixty sample units (SU) were marked at 30 m intervals along the transect. At these points, the vegetation height in the fields was recorded at 3, 5, and 8 m along a line perpendicular to the transect into the fields. Faeces found in these units were removed on five occasions on July 7, August 18, September 30, November 30, and December 12, giving intervals between sampling of 32 to 43 days. Absolute animal densities were estimated on each occasion using the following equation:

$$\text{density} = \frac{\text{NFSU} \times \text{short axis} \times \text{long axis}}{\text{time} \times \text{DDR} \times \text{SU area}} \quad (1)$$

The length of short axis was arbitrarily established as 20 m, taking into account the width of the shelter and the foraging area with highest expected use. Daily defaecation rate (DDR) was estimated as 145 faeces per animal, from cavies maintained in captivity.

Samples of vegetation composition and biomass were taken in July and October as part of another study on the foraging ecology of cavies (Galante & Cassini in preparation).

3. Results

We estimated the total density of cavies per month in the study area using equation (1), with the long axis length equal to 1800 m. Fig. 2a shows how total density decreased with time. This phenomenon was also observed in the previous year, and is discussed elsewhere in the context of an analysis of cavy population fluctuations (Cassini & Galante in press, Cassini & Galante, in preparation). We subjected the vegetation height to a two way-analysis of variance. We took distances (independent measures) and samples (repeated measures) as the treatments. Highly significant differences were found between samples ($F_{4,536} = 90.23$, $P < 0.0001$, Fig. 2b), while no significant differences existed between distances ($F_{2,134} = 0.70$, $P = 0.45$).

Table 1 summarises the results of the relationship between the estimated cavy density and the mean vegetation height (calculated from the heights at the three distances from the transect) per 30-m segment of transect. The model which best fits the observed values was the logarithmic function, suggesting that cavies are especially

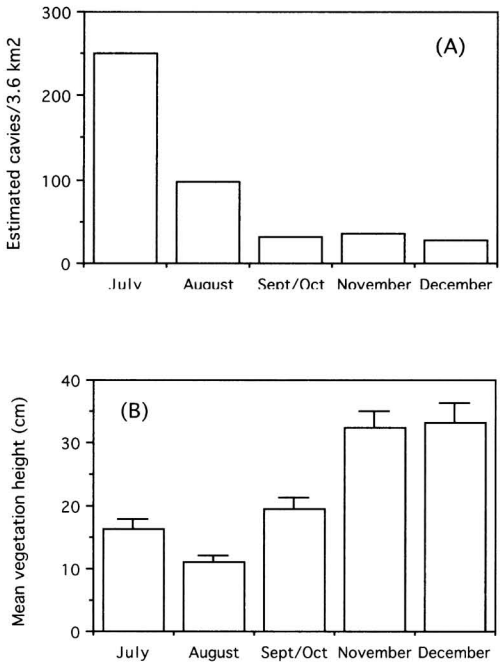

Fig. 2. Estimated guinea pig density (A) and mean vegetation height (±SE) per sample unit (B) in the study area in relation to samples.

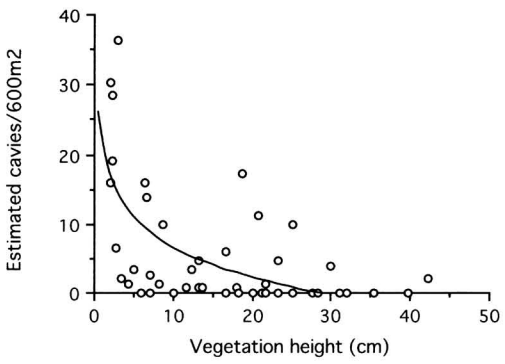

Fig. 3. Estimated guinea pig density per 30-m segment of transect in relation to vegetation height, in July 1991. Parameters and significance of the adjusted logarithmic function are described in Table 1.

abundant in very short grass and their density rapidly decreases as vegetation height increases. The best fit was obtained in July (Fig. 3), with a lower significance of the regression for August and a non-significant relationship in the following three months.

In July, vegetation height did not significantly correlate with the relative biomass of any of the 24 plant species present in the area (Pearson correlations, $t < 1.78$, $df = 11$, $P > 0.05$) meaning that the observed greater cavy density in very short grass is not related to floristic composition.

4. Discussion

The height of vegetation varied in space and time in the foraging grounds. The cavy population responded to both these spatial and temporal changes by increasing in density when vegetation height decreased. This response was maximal in July, when vegetation in some foraging areas was very short. This result supports the fourth hypothesis proposed in the Introduction (Fig. 1d), that individual animals solve the problem of trade-off between foraging and protection from predators attack by selecting a home range with shelter for inactive periods and an adjacent area of rich short grass in which to forage. Many predators are more efficient in capturing rodents in this type of habitat (e.g., Kotler et al. 1991, Longland & Price 1991), requiring behavioural responses from prey to minimize predation risk

Table 1. Statistical relationships between the estimated cavy density (y) and vegetation height (x). For details of methods see text.

Sample	Linear, $y = a + bx$				Polynomial, $y = a + b \log(x)$			
	a	b	r^2	t	a	b	r^2	t
16/7	18.17	–0.61	0.24	3.77***	32.11	–22.03	0.40	5.43***
18/8	5.59	–0.27	0.07	1.87	9.12	–6.66	0.12	2.37*
30/9	1.39	–0.01	0.01	0.27	3.72	–1.87	0.04	1.31
12/11	1.68	–0.01	0.01	0.44	5.16	–2.62	0.03	1.25
18/12	0.26	0.02	0.03	1.09	–1.70	1.75	0.05	1.55

while maximizing foraging efficiency. A previous study showed results which support the existence of such responses in wild guinea pigs (Cassini 1991): foraging in groups and increasing scanning rates with increasing distance from shelter allowed individual cavies to spend a greater amount of time in food patches, and to spend more time foraging during patch visits.

Although many predators, specially aerial ones, are more efficient hunters in short than in long grass, some terrestrial carnivores can also be good predators when prey are foraging in long grass (e.g., Coyotes *Canis latrans*, Bekoff & Wells 1986). Grisons (*Galictis cuja*), a major predator of cavies, has a long, low, narrow body which allows it to pursue prey through the runs constructed by cavies between the dense clumps of grass of the cover (Sunquist & Sunquist 1989). Therefore, foraging in short vegetation patches should not only improve food quality, but should also increase the probability of detecting a terrestrial predator approaching from the high vegetation of the field border. Cassini (1991) found that, although cavies always foraged at less than 4 m from the cover, they stayed for longer periods of time outside the shelter when foraging further from cover. It is possible that cavies perceive borders both as protective places from aerial predators and as potential sources of attack from terrestrial predators (as some species of passerine birds seem to do, Lima et al. 1987). Therefore, maintaining an intermediate distance to cover should minimize predation risk.

We concluded that the inverse relationship between cavy density and vegetation height was the population expression of individual habitat selection rules for solving the trade off between foraging efficiency and predation risk. There are two other alternative explanations for the observed trends in the data: (1) a direct effect of the foraging activity of guinea pigs on vegetation, which would reduce its height close to the shelter, and (2) a direct predatory effect via removal of guinea pigs on long grass. These hypothesis were disregarded because (1) there were no statistical differences in the vegetation height between the three distances to the shelter, and (2) direct predation does not seem to have an important role in regulating cavy abundance (Cassini & Galante in press, Cassini & Galante in preparation). Future field experiments are needed to give a full explanation of the effect of these factors in cavy distribution.

Many studies on habitat selection have found that vegetation cover is an important determinant of rodent distribution. Most of theses interpretated — or experimentally demonstrated — that plant cover was used as an antipredation refuge (Desy et al. 1990, Drickamer 1990, Eadie 1953, Kaufman et al. 1983, Kotler et al. 1991). However, the utilization of shelter by rodents differs greatly between species. This is the case for several sympatric rodent species which showed differential microhabitat preferences associated with species-specific uses of cover. These cases are especially interesting because the species that were compared used the same macrohabitat, meaning that they were influenced by the same general environmental conditions. LoBue & Darnell (1959) found that as vegetation increased in height and cover, the meadow vole *Microtus pennsylvanicus* increased utilization of the field, while the deer mouse *Peromyscus maniculatus* showed the opposite response. In a study of the habitat preferences of two sympatric species of *Peromyscus*, Drickamer (1990) found that *P. leucopus* were found more often with significant amounts of plant cover, while this did not generally affect *P. maniculatus*. Kotler et al. (1991) also found differences in patch use related to the amount of shrub cover in two species of gerbils. Microhabitat specializations of desert rodent communities also seem to be related to differential use of cover by bipedal and quadrupedal species (Kotler 1984, Longland & Price 1991).

Species which prefer to forage in open areas, adjacent to shelter, therefore showing a negative relationship between density and the amount of cover in the foraging area (if cover is negatively related to food availability), have evolved abilities to cope with a high predation risk while foraging. For example, Kotler (1984) suggested that kangaroo rats are better able to exploit open areas than other sympatric quadrupedal heteromyd rodents because they have developed adaptations to increased predation risk, these being inflated auditory bullae and bipedal locomotion. Another example of morphological adaptation is the 'mara' or Patagonic cavy, *Dolichotis patagonicus*, a long-legged, hare-like rodent

which can run at speeds of up to approximately 45 km per hour over long distances (Macdonald 1984).

However, many adaptations seem to be of a behavioural rather than morphological nature. Behaviour relating to the high predation risk described in rodents include (1) foraging in groups (Brown & Willan 1991, Cassini 1991, Hoogland 1981), (2) transporting food to shelter (Lima et al. 1985), (3) increasing vigilance at greater distance to cover (Cassini 1991), (4) reducing activity on moonlit nights (Drickamer 1990, Daly et al. 1992), and (5) reducing movements when a predator is detected (Desy et al. 1990, Dickman 1992).

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