

# Pre- and postdispersal seed predation by rodents: balance of food and safety

Jose M. Fedriani and Antonio J. Manzaneda

Estación Biológica de Doñana (CSIC), Avenida de Maria Luisa s/n, Sevilla 41013, Spain

Seed presentation and availability for seed predators change during every plant reproductive cycle. We know very little about how those changes impinge on both the ability of seed predators to impact plant populations and the foraging costs associated with seed consumption. Therefore, we conducted several field experiments to evaluate whether wood mice *Apodemus sylvaticus* balance food and safety while foraging on *Helleborus foetidus* seeds during both the pre- and early postdispersal phases of the plant reproductive cycle. Both food and safety were key determinants of mouse foraging on *H. foetidus* seeds, though their roles were not consistent along the plant reproductive cycle. Thus, augmenting ambient food reduced fruit removal by mice during the predispersal phase. During the postdispersal phase, seeds in sheltered microsites experienced higher removal rates than those located in nonsheltered microsites; however, no effect of food augmentation was detected. This apparent reversed role of food and safety on decision making by mice seemed closely linked to both the dramatic changes in accessibility and presentation of *H. foetidus* seeds and the coupled changing foraging costs faced by mice at different phases of the plant reproductive cycle. For instance, because the cost of foraging for predispersal seeds was higher than for postdispersal seeds, the effect of food augmentation on foraging by wood mice was greater during the predispersal phase. Thus, our study illustrates the need of considering differences between pre- and postdispersal seed predation in the study of granivore rodents and their impact on plant populations. *Key words*: behavioural trade-offs, foraging, granivory, *Helleborus foetidus*, mice, pre- and postdispersal seed predation, predation risk. [*Behav Ecol* 16:1018–1024 (2005)]

Seed predation is a central demographic process of plant populations that can occur repeatedly during every plant reproductive cycle (Crawley, 2000; Janzen, 1971; Vander Wall and Longland, 2004; Vander Wall et al., 2005a; Wang and Smith, 2002). Predispsal seed predation takes place when seeds are removed from the parent plant before dispersal, and it has been most often reported in frugivorous birds (Herrera, 2002; Hulme and Benkman, 2002; Jordano, 2000; Willson and Traveset, 2000), though it is also common in granivorous rodents and invertebrates that clip fruits directly from trees and herbaceous plants (Forget et al., 1999; Herrera et al., 2002; Mezquida and Benkman, 2005; Price and Joyner, 1997; Reichman and Price, 1993). Postdispersal seed predation arises once seeds have been released from the parent plant. Birds, rodents, and ants are known to be among the most pervasive postdispersal seed predators (Brown and Davidson, 1976; Brown and Heske, 1990; Gómez, 2004; Hulme and Benkman, 2002; Price and Joyner, 1997). Furthermore, postdispersal seed predation can take place at two contrasting stages: predation on the “seed rain” and predation on the “seed bank” (Price and Joyner, 1997). Whereas predation on the seed rain occurs when animals prey on released seeds usually flush with the ground surface (Hulme, 1997; Price and Joyner, 1997; Rey et al., 2002), predation on the seed bank takes place after seeds have been incorporated deeply into the soil (Price and Joyner, 1997). Consequently, seed presentation and availability change dramatically during a plant’s reproductive cycle; however, we know very little about how those changes impinge on both the ability of seed predators to impact plant populations and the foraging costs associated with seed consumption.

Rodents are among the most pervasive seed predators, and thus, they have been used frequently as model organisms to

identify the effects of seed predation on the dynamics and distribution of plant populations, as well as on the evolution of plant reproductive strategies (see Hulme, 2002; Hulme and Benkman, 2002, for reviews). For instance, ecologists have assessed whether foraging decisions by seed-eating rodents reflect an adaptive balance between food intake maximization and predation risk minimization (Brown et al., 1992; Kotler, 1997; Mohr et al., 2003; Ylönen et al., 2002). To study such foraging decisions, ecologists have routinely measured the depletion of seeds within a matrix of sand or pebbles (Brown, 1988; Brown et al., 1992; Kotler, 1997; Ylönen et al., 2002) that resembles the soil seed bank. Despite some limitations of this method (Brown, 1988; Kelt et al., 2004), the amount of seeds remaining in a patch when a forager leaves (the “giving up density” or GUD) provides valuable information on fitness cost and benefits of foraging and on the ability of rodents to assess the quality of such seed patches. Nonetheless, seed predation by rodents often occurs before seeds have been released from the parent plant (i.e., during the predispersal phase), and in many systems, postdispersal seed predation by rodents takes place primarily on the seed rain rather than on seeds incorporated into the soil seed bank (M’Closkey, 1983; Price and Joyner, 1997). Given the presentation of seeds in natural “food patches” (e.g., fruiting plants), natural GUDs may be difficult to obtain; however, even in these cases, the GUD conceptual framework (see Brown and Kotler, 2004, for review) can help us to estimate rodents’ cost and benefits of foraging during both the pre- and postdispersal phases. Surprisingly, however, no study has yet assessed foraging decisions by seed-eating rodents during the predispersal phase, and those focusing on the postdispersal phase emulate the seed bank but not the seed rain (but see Price and Correll, 2001). Consequently, our knowledge of factors governing foraging by seed-eating rodents and how those factors impinge on the role of rodents on plant populations could be incomplete at best.

To reveal the importance of both phases of plant reproductive cycles on the study of rodent foraging and their impact on plant populations, we chose the perennial herb *Helleborus foetidus* L. (Ranunculaceae) and its main seed predator, the

Address correspondence to J.M. Fedriani. E-mail: fedriani@ebd.csic.es.

Received 5 January 2005; revised 14 June 2005; accepted 27 July 2005.

wood mouse *Apodemus sylvaticus* L. (Muridae). Fedriani et al. (2004) report marked variations in both pre- and postdispersal seed predation by mice within several *H. foetidus* populations of the Iberian Peninsula. These authors suggested that ambient food was a chief determinant responsible for such variation. Besides, Fedriani (2005) provided observational data supporting that predation risk played a role in mice foraging on *H. foetidus* fruits (predispersal phase). The present study describes several field experiments where ambient food was manipulated and microsite cover was accounted for in order to evaluate the hypothesis that wood mice respond to food and safety while foraging on *H. foetidus* seeds during both the predispersal and early postdispersal phases (i.e., seed rain). Because we aimed to simulate as much as possible the actual presentation of *H. foetidus* seeds and the scale of environmental heterogeneity (in terms of both food and safety) occurring during both the pre- and postdispersal phases, we did not use standardized artificial food patches (Brown, 1988) in our field experiments. Consequently, seed presentation and mouse foraging behaviors were clearly different between the pre- and postdispersal phases, which made results from experiments carried out during both phases not directly comparable. However, we suggest that our procedure likely resembled more accurately the complexity behind the interaction between seed-eating rodents and their plant resources.

Under the assumption that foraging wood mice trade off food and safety, optimal foraging theory yields three predictions (Brown, 1988; Brown and Kotler, 2004; Brown et al., 1992; Holt and Kotler, 1987). (1) Seed predation by mice should be higher in safe (sheltered) than in risky (open) microsites. (2) Augmenting background food should reduce predation on *H. foetidus* seeds due to foraging mice experiencing a lower marginal value of energy and higher missed opportunity costs. (3) The effect of food augmentation on foraging by wood mice should be contingent on seed foraging costs; thus, if the cost of foraging for predispersal seeds is higher than for postdispersal seeds, then the effect of food augmentation on foraging by wood mice should be greater during the predispersal phase.

## METHODS

### Study sites and system

The study was carried out in the Cazorla Mountains of southern Spain (37° 56' N, 2° 52' W), during the summer (May–July) of 2002. In Cazorla, summer corresponds to a period of low food availability for small mammals, thus being an appropriate season to evaluate the effects of food addition (LoGiudice and Ostfeld, 2002). To encompass a representative range of ecological conditions in which both *H. foetidus* and mice co-occur, we selected three study sites within Cazorla at an elevation of 1250–1300 m. These three sites (Roblehondo, Aguaderillos, and Guadahornillos, hereafter referred to as “RH,” “AD,” and “GH,” respectively) occur within pine (*Pinus nigra*) and oak (*Quercus rotundifolia*) mixed forests with variable understory of *Juniperus oxycedrus*, *Rubus ulmifolius*, and *Daphne laureola*. Livetrapping with Sherman traps was carried out during May–June 2002 (overall trapping effort = 437 trap-nights) over an area of ~0.5 ha in each study site. Overall, trapping yielded only three, five, and four individuals captured within the RH, AD, and GH populations, respectively. However, based on capture-recapture data gathered in the three populations between 2000 and 2005, we estimate that, during years of low mice abundance (such as 2002), at least from six to eight individuals occur within each population (Fedriani, 2005; Fedriani JM, unpublished data). Distances among target *H. foetidus* populations ranged from 700 to

2100 m, ensuring that mice from one population did not range into others (Fedriani, 2005). Climate is of a Mediterranean type, and average annual rainfall in the Cazorla Mountains ranges 550–1660 mm. For more information about the study area see Fedriani (2005).

*H. foetidus* is an abundant perennial herb in understories of mixed forest and scrublands of Cazorla. Plants consist of several (one to five) reproductive ramets that in winter (January–March) usually produce 25–75 flowers in their terminal inflorescences (Herrera et al., 2002). Flowers are apocarpous, with up to five carpels (usually two to three). Fruit maturation and seed release take place in June–July, when each carpel releases 8–15 seeds that, after seed release, lay spread next to parental plants and flush with the ground surface. Wood mice (*A. sylvaticus*) are small rodents (14–28 g) common in mixed forest and scrublands at our study area, where virtually no other terrestrial rodent species is present. Mice can prey very heavily on both *H. foetidus* fruits and, shortly after seed release, seeds spread out in the surroundings of parent plants (Fedriani et al., 2004). Though is not possible to know the fate of all seeds removed by mice (Hulme and Kollmann, 2005; Vander Wall et al., 2005b), several lines of evidence strongly support that wood mice act exclusively as predators (not dispersers) of *H. foetidus* seeds (Fedriani et al., 2004). Wood mice rely on acorns (*Q. rotundifolia*) and pine seeds (*P. nigra*) in the three target populations (Fedriani JM, unpublished data). These seeds are patchily distributed at a fine-grained spatial scale due to the caching behavior of mice (Fedriani JM, unpublished data) and other consumers. Thus, as found in several other systems (e.g., Price and Reichman, 1987), availability of alternative foods for mice often shows noticeable changes at the scale of few meters and even centimeters. Local natural predators of mice include the red fox, *Vulpes vulpes*, Eurasian badger, *Meles meles*, Stone marten, *Martes foina*, and Tawny Owl, *Strix aluco* (Herrera, 1989; Fedriani JM, unpublished data).

### Mice predispersal fruit removal

To evaluate how ambient food affects predispersal mouse predation on *H. foetidus* seeds, we compared fruit losses of plants located in sites with natural levels of food availability with those of plants supplemented with sunflower seeds (LoGiudice and Ostfeld, 2002). Because captive wood mice showed a clear preference for sunflower over *H. foetidus* seeds (Fedriani JM, unpublished data), we would expect similar mouse foraging responses to those reported in this study when other alternative preferred foods are available (e.g., under natural masting events; LoGiudice and Ostfeld, 2002). Because spacing between adjacent reproductive *H. foetidus* plants is variable (typically from 0.5 to 5 m; Fedriani, 2005), we could not use a randomized block design for the predispersal experiment. As an alternative, we proceeded by choosing randomly from 22 to 30 plants prior to fruit ripening over an area of ~0.5 ha within each population. Then, half of the chosen plants were supplemented with 50 g of sunflower seeds by dispersing them within a radius of 40 cm centered in each plant (“food-supplemented plants”) while the other half was used as “control.” Adjacent monitored plants were separated by  $\geq 2$  m. The scale of the food augmentation makes probable that mice foraging at both types of plants (supplemented and nonsupplemented) have similar marginal value of energy and missed opportunities (Brown, 1988), which could constrain the predicted effects of food augmentation. However, because in our system, and in other similar ones (e.g., Price and Reichman, 1987), abundance of alternative foods on ground (acorns and pine seeds in catches) varies greatly over the space of a few meters (Fedriani JM, personal observation), we suggest that the spatial scale of our food augmentation resembles the

patchy distribution of alternative foods occurring under field conditions. Sunflower seeds were renewed when depleted (usually every 2–3 days). For each plant, we recorded the final fruit production and losses by mice. Fruit removal rates refer to the proportion of fruits removed by mice with respect to those available on plants at the start of the experiment (on 11 June). Numbers of available fruits on plants were retrospectively estimated as the number of fruits releasing seeds at the end of the fruiting period plus the number of fruits removed by mice. In addition, for each plant, two measurements of shelter were estimated as the amount of two 80-cm segments (centered in the plants) intersected by vegetation (or dead branches, rocks, etc.) at the heights of 20 and 50 cm, respectively (Fedriani et al., 2002). These two measurements represented the “average shelter” of each plant along its entire height. Then, to simplify a posteriori analysis, both measurements were added, and a single figure was obtained (potentially ranging 0–160 cm) for each monitored plant. We assumed that low and high indices of shelter corresponded to high and low risk of predation for mice from visually searching predators (Fedriani, 2005; Morris and Davidson, 2000).

### Postdispersal seed removal

To evaluate how ambient food and risk of predation affected postdispersal seed removal by mice, we monitored the removal of *H. foetidus* seeds placed in artificial depots in a  $2 \times 2$  factorial design where “Food” (supplemental food/no food) and “Microsite” (sheltered/nonsheltered) were the main effects. As in the previous experiment, the level of “supplemental food” consisted of 50 g of sunflower seeds dispersed within a radius of 40 cm centered in each *H. foetidus* seed depot and renewed when depleted. The level “no food” consisted of *H. foetidus* seed depots where no food was added. The “sheltered” microsites were located at the entrances of rock or trunk crevices similar to those where remains of fruits and seeds consumed by mice are often found. The “nonsheltered” microsites were located at sites with no crevices, no understory, and little or no ground vegetation. Predation risk for mice from visually searching predators in nonsheltered microsites was assumed to be higher than in sheltered microsites (Fedriani, 2005; Morris and Davidson, 2000). Ten fresh *H. foetidus* seeds (5–19 mg ea; Garrido et al., 2002) comprised each seed depot. To prevent removal by ants while allowing the access to mice, *H. foetidus* seeds were presented glued (using a low-odor glue when dry) from one of their extreme on pieces ( $7 \times 4$  cm) of fiberglass (Herrera et al., 1994; Rey et al., 2002), fixed with a nail flush to the ground surface. Preliminary field assays indicated that mice easily removed the seeds by chewing the fiber threads, while ants (and birds) did not remove them. *H. foetidus* seeds were thus exposed to four treatment combinations (according to our  $2 \times 2$  experimental design), and each set of four treatment combinations formed a block or random replicate. In each population (RH, AD, and GH), 15 blocks were haphazardly set (overall 45 blocks) in a way that maximized the spatial overlap with the distribution of plants monitored previously. Within each population, separation among adjacent blocks was  $\geq 3$  m. Within each block, the treatments were placed  $\sim 1$  m apart of each other. During 3 consecutive days, we checked all seed depots within 2 h after dawn, recording the number of remaining seeds. The response variable used to quantify mouse foraging was the number of seeds removed after 3 days divided by the number of seeds offered in each seed depot ( $n = 10$ ). That time span (3 days) corresponds with the maximum time that, in Cazorla, seeds are usually available to mice before being removed by seed disperser ants (Fedriani et al., 2004). The

experiments were undertaken during the natural postdispersal seed period of *H. foetidus* (end of June to early July).

### Statistical analyses

For the predispersal fruit predation experiments, the effect of food addition on the proportion of fruits removed by mice was evaluated separately in each population by fitting generalized linear models (GLMs) with binomial error and logit link function using the GENMOD procedure from Statistical Analysis System (SAS) (Stokes et al., 1995). Because the number of fruits available at monitored *H. foetidus* plants was very variable and it could affect mice predation (Sallabanks, 1993), we accounted for its possible effect on fruit predation by including it in our models as covariable. Thus, our models included Food as main effect, Shelter and “Number of fruits” as covariates, and also the interaction between Food and Shelter. This interaction was included to evaluate whether foraging mice balanced those two conflicting demands. Model-adjusted means and standard errors (SE) were also computed and back transformed (Littell et al., 1996).

For the postdispersal seed predation experiments, we evaluated the potential effect of supplemental food and microsite on the cumulative number of seeds removed by mice over three consecutive nights (divided by the number of seeds offered [ $n = 10$ ]) by fitting generalized mixed linear models using the SAS macro GLIMMIX (Littell et al., 1996). This program iteratively calls SAS procedure Mixed and allows the modeling of the nonnormal response variables, such as Binomial (number of seeds removed/number of seeds offered), as well as the treatment of fixed and random effects. As the experiment followed a randomized-block design (see above), block was included in models as a random factor to control for its potential effects. Food and Microsite and their two-way interaction were considered as fixed effects in the model. Model-adjusted means and SEs were computed and back transformed.

As mentioned above, both the pre- and the postdispersal field experiments were intended to resemble the natural conditions under which wood mice typically encounter *H. foetidus* seeds. Therefore, our variable responses differed from the GUDs used by many researchers (Brown, 1988; Brown et al., 1992; Kotler, 1997). Nonetheless, because all experimental units (i.e., plants and seed depots in the pre- and postdispersal phases, respectively) were exposed for the same periods (i.e., until seed release and 3 days, respectively), they yielded comparable measurements of consumption for each experiment and allowed for rigorous comparisons of the number of fruits/seeds consumed by mice under different treatment combinations.

## RESULTS

### Mice predispersal fruit removal

Results from our predispersal fruit removal experiments are based on the fate of 82 monitored plants (30, 30, and 22 in RH, AD, and GH, respectively) that overall produced 1935 fruits available to mice (each fruit usually comprised from one to three carpels). Mean number of available fruits per plant was highly variable at all three study sites, ranging from 8 to 42, 3 to 104, and 7 to 50 in RH, AD, and GH, respectively. However, within each population, there was no difference among plants assigned to different treatments in their availability of fruits (GLMs with Poisson error;  $\chi^2 = 0.28\text{--}2.01$ ,  $df = 20\text{--}28$ ,  $p > .156$ ), suggesting no bias in our treatment assignment. On average, mice preyed on 6.9% of available fruits ( $n = 1935$ ), though this rate was variable among populations

(Figure 1a). While in RH and AD percentage of fruit losses due to mice was affected by fruit availability, in GH there was no evidence of any effect of fruit availability (Table 1a). Specifically, the negative sign of the “parameter estimates” ( $-0.094 \pm 0.039$  [mean  $\pm$  1 SE] and  $-0.037 \pm 0.018$  for RH and AD, respectively) indicated that plants with fewer available fruits experienced higher rates of fruit predation by mice. This result suggests that, during the predispersal phase, wood mice used a fixed time strategy of fruit exploitation rather than a quitting harvest rate strategy.

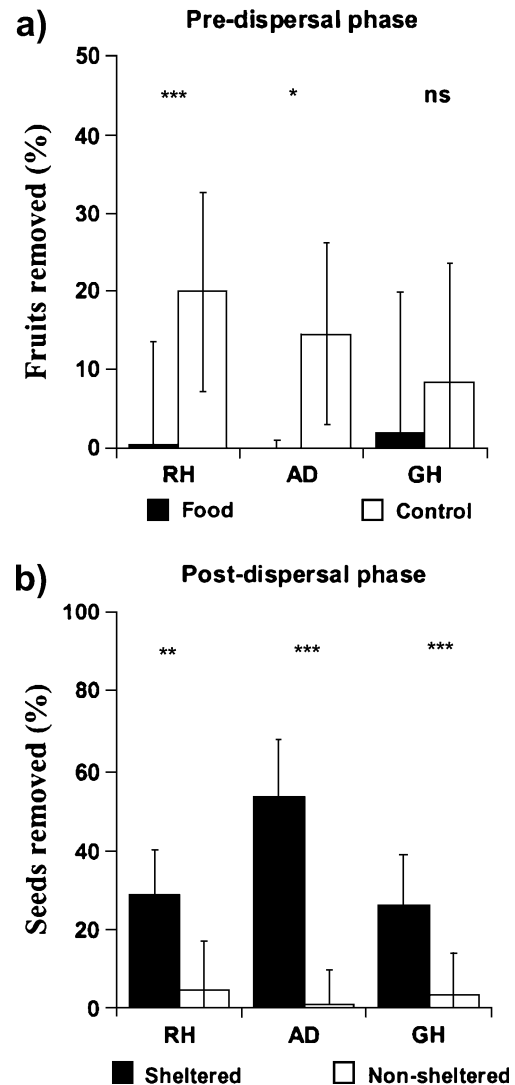
After statistically accounting for the effect of fruit availability on predation by mice, we found in all study sites that, as predicted, food-supplemented plants experienced less mouse fruit removal than control plants (Figure 1a). Differences were highly significant in RH, marginally significant in AD, and nonsignificant in GH (Table 1a). In addition, in RH, Shelter had both a significant main effect on fruit removal by mice (Table 1a) and also had a joint effect (or interaction) with the factor Food (Table 1a). To illustrate the interaction between Food and Shelter, monitored plants from RH were classified into two groups according to their measured indices of shelter. Thus, we called “low-sheltered plants” those with shelter indices  $<10\%$  ( $2.71 \pm 1.23$  [mean  $\pm$  1 SE] and  $3.29 \pm 1.15$  for treated and control plants, respectively) and “high-sheltered plants” those with indices  $\geq 10\%$  ( $25.50 \pm 6.15$  and  $36.88 \pm 7.90$  for food-supplemented and control plants, respectively). For food-supplemented plants, Shelter did not have an effect on fruit predation by mice, while for control plants the index of shelter had an important effect, with fruits on high-sheltered plants more intensively depredated than those on low-sheltered ones (Figure 2). In other words, under natural levels of food availability (control plants), mice did consume fruit ( $\sim 37\%$ ) and, as predicted, reduced their consumption in the absence of cover (higher predation risk; Figure 2). However, when mice were already not consuming *H. foetidus* fruits because the level of ambient food was augmented, they could not consume fewer fruits when under higher predation risk (Figure 2).

### Postdispersal seed removal

By monitoring the fate of 1800 *H. foetidus* seeds during three consecutive nights, we assessed the effect of ambient food and predation risk on early postdispersal seed removal by mice. After statistically accounting for the block effect in our field experiments ( $z < 1.28$ ,  $p > .100$ ), we found that microsite had a strong significant effect on mouse seed removal in all three study sites (Table 1b). Removal rates by mice of seed depots located in sheltered microsites were always higher than those located in nonsheltered microsites (Figure 1b). Specifically, model-adjusted mean numbers of seeds removed were 6.2- (RH), 68.3- (AD), and 8.3-fold (GH) higher in sheltered than in nonsheltered microsites. However, ambient food did not affect postdispersal seed predation by mice in any study site (Table 1b). Furthermore, we did not find a significant interaction of Microsite and Food at any study site, indicating that the sign and magnitude of the effect of microsite on postdispersal seed removal by mice did not vary across the levels of ambient food.

### DISCUSSION

Plant populations frequently experience considerable predation from both pre- and postdispersal seed-eating rodents (Figueroa et al., 2002; Forget et al., 1999; Hulme and Benkman, 2002; Moles et al., 2003), while the pattern and extent of seed predation by rodents is often impinged by levels of ambient food and safety (Brown, 1988; Brown and Kotler, 2004; Kotler,



**Figure 1**  
(a) Model-adjusted means of percentage ( $\pm$  1 SE) of fruits removed by mice in food-supplemented and control plants for each study site (RH, AD, and GH) during the predispersal phase. (b) Model-adjusted mean numbers of *Helleborus foetidus* seeds removed by mice from seed depots located in sheltered and nonsheltered microsites during the postdispersal phase for each study site (\*\*\*)  $p < .0001$ , \*\*  $p < .01$ , \*marginally significant [ $p = .064$ ]).

1997; Sullivan, 1979; Sullivan and Klenner, 1993). However, this is the first study evaluating the role of those two determinants of rodent seed predation during both the pre- and postdispersal phases of a plant's reproductive cycle. Furthermore, this study assesses mice foraging on *H. foetidus* seeds in the absence of other seed removers, thus avoiding the potential simultaneous seed consumption by multiple species that may have contrasting microhabitat and dietary preferences, an issue that could make interpretation of results difficult.

The most simplistic interpretation of our results suggests that, in general, ambient food reduces fruit removal by mice during the predispersal phase, while during the postdispersal phase seed removal by mice was lowered only in microsites with high predation risk. Nevertheless, this apparently inconsistent role of our estimates of ambient food and predation risk on mouse foraging can be also expected in a scenario where both variables were important determinants of mice foraging during both the pre- and postdispersal phases. In

Table 1

Effects of availability of supplemental food (Food) and Shelter and effects of supplemental food and Microsite on *H. foetidus* predation by mice

	RH			AD			GH		
	$\chi^2/F$	df	<i>p</i>	$\chi^2/F$	df	<i>p</i>	$\chi^2/F$	df	<i>p</i>
(a) Predispersal phase									
Food	15.0	1,25	<b>.0001</b>	3.4	1,25	<b>.064</b>	1.4	1,17	.241
Shelter	5.2	1,25	<b>.023</b>	1.2	1,25	.282	0.03	1,17	.874
Food × Shelter	4.9	1,25	<b>.027</b>	0.47	1,25	.491	0.01	1,17	.913
Number of fruits	6.8	1,25	<b>.009</b>	7.1	1,25	<b>.008</b>	0.00	1,17	.959
(b) Postdispersal phase									
Food	0.70	1,42	.382	0.04	1,42	.835	0.48	1,42	.493
Microsite	11.18	1,42	<b>.002</b>	25.51	1,42	<b>.0001</b>	12.4	1,42	<b>.001</b>
Food × Microsite	0.87	1,42	.355	0.86	1,42	.360	0.01	1,42	.942

(a) Effects of availability of supplemental food (Food) and Shelter on predispersal *Helleborus foetidus* fruit predation by mice *Apodemus sylvaticus* on each of the three study sites. Because plants differed in crop size, the number of fruits available to mice was included in the models as a covariate, (b) Effects of supplemental food and Microsite on *H. foetidus* postdispersal seed predation by mice in the same study sites. For the predispersal analyses,  $\chi^2$  statistic (instead of *F* statistic) was used because the deviance of the models was scaled due to overdispersion in the data. Significant results ( $p < .5$ ) are shown in bold.

*H. foetidus*, as in most plant species (Crawley, 2000; Hulme and Benkman, 2002), spatial distribution of seeds, their presentation and accessibility clearly differ between the pre- and postdispersal phases (Fedriani et al., 2004; Herrera et al., 2002). Finding *H. foetidus* fruits by mice was likely facilitated by their spatial and temporal aggregation on conspicuous parent plants (Crawley, 2000). Once found, however, exploitation of *H. foetidus* fruits requires mice to climb to the extreme of the reproductive ramets and then chew the pedicels and remove the whole fruit structure (sepals and carpels). Consequently, during the predispersal phase, reaching and processing *H. foetidus* seeds was not only a highly energy- and time-consuming activity for mice, but it also probably entailed greater predation risk than foraging at ground level (postdispersal phase). When a highly preferred food is added at the ground level (emulating thus the presentation of other seeds in caches; e.g., acorns, pine seeds), it is reasonable to expect that climbing should be the first activity to be dropped from rodents' repertory, which should be interpreted, at least

partly, as a response to predation risk. Our results also suggest that, during the predispersal experiment, the marginal value of food was set by the background level of food and thus that the supplemental food at a plant acted to draw off foraging effort on *H. foetidus* fruits. Accordingly, our experimental results support one of our initial predictions because the cost of foraging for predispersal seeds was higher than for postdispersal seeds and the effect of food augmentation on foraging by wood mice was greater during the predispersal phase.

Then, why was there not a greater effect of food supplementation and microhabitat on mouse foraging during the predispersal phase? Differences among populations in vegetation, background food availability, and rodent density may have contributed to changes in the magnitude of predation risk and food addition (Mohr et al., 2003; Ylönen et al., 2002). Also, as suggested by the large SEs around the mean values of the Food treatment (Figure 1a), the possibility cannot be ruled out that predation by mice might have been impinged by environmental cues and/or plant traits not accounted for in our field experiments. For instance, *H. foetidus* plants located on rocky substrates can experience higher rates of predispersal fruit predation by mice as compared with plants located on bare grounds (Fedriani, 2005). Besides, mouse preferences likely also are contingent on the relative nutritional and chemical attributes of *H. foetidus* plants available in each population (Fedriani, 2005). On the other hand, mouse antipredator behavior might also have been affected by the long time span that fruits were available to mice (up to 14 nights since the experiment started). This notion is consistent with the predation risk allocation hypothesis (Lima and Bednekoff, 1999; Sih and McCarthy, 2002), which predicts that when a high-risk situation becomes frequent or lengthy the allocation to antipredator effort by prey should decrease due to the need to feed. Extensively replicated field experiments will be needed to evaluate these possibilities.

As predicted, during the postdispersal phase, seeds located in sheltered microsites experienced higher removal by mice as compared with seeds in nonsheltered microsites. This result corroborates those from other "postdispersal seed offerings" supporting the view that most rodents respond behaviorally by lessening foraging on microhabitats lacking cover due to higher associated risk of predation (e.g., Brown and Kotler, 2004; Mohr et al., 2003; Morris and Davison, 2000; Ylönen et al., 2002). It remains to be explained why, contrary to our expectation, food augmentation did not reduce seed removal

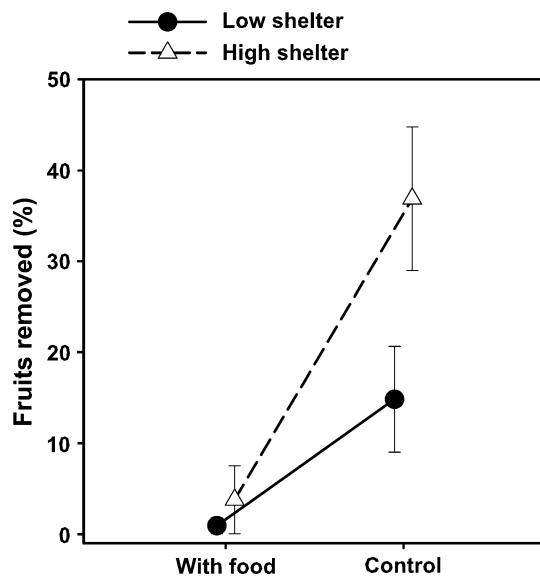


Figure 2 Graphical representation of the interaction between Food and Shelter in the RH study site.

by mice during this phase. Three nonexclusive possibilities can be drawn. First, a decrease in the rates of *H. foetidus* seed removal could result from predator satiation or hoarding of extra food available (LoGiudice and Ostfeld, 2002; Vander Wall, 1990). Conversely, if mixed-seed depots, containing highly preferred sunflower seeds, had attracted wood mice more often or if mice spent more time foraging at those depots than in monospecific depots of *H. foetidus* seeds, harvest rates by mice should increase (e.g., Veech, 2001), leading to “apparent competition” (sensu Holt and Kotler, 1987). The lack of any positive or negative effects of food augmentation on *H. foetidus* seeds during the postdispersal phase could be due to food augmentation having these two opposing influences on mice harvesting *H. foetidus* seeds. A second possibility is that *H. foetidus* and sunflower seeds are complementary resources (sensu Tilman, 1982). Mice might have actively selected a mixed diet of *H. foetidus* and sunflower seeds, obtaining thus a most balanced mix of nutrients or reducing the intake of any one plant toxic compound (Dearing and Schall, 1992; Schmidt et al., 1998). Finally, the small scale of our food augmentation (which resembles variation in the availability of alternative foods observed in the field) probably resulted in mice foraging at both type of seed depots (supplemented and not supplemented) having similar marginal values of energy and missed opportunities, leading to similar rates of seed predation in both seed depot types. This would suggest that, under field conditions, changes in the availability of alternative food resources taking place at a fine-grained spatial scale might have little effect on postdispersal seed predation by rodents.

Results from this experimental study may be of relevance from a plant dynamics perspective. For instance, during the predispersal phase, food-supplemented plants suffered less seed predation by mice as compared with control plants. This reduction in seed losses of plants with high local ambient food availability implies that, as reported elsewhere (Ostfeld and Keesing, 2000), any negative effect of mice on *H. foetidus* fitness during the predispersal phase (e.g., Herrera et al., 2002) may be contingent on the spatial and temporal availability of seeds of other plant species. For example, during the summer of 1999, there was a particularly low incidence of mouse predation on plants such as *H. foetidus* and *D. laureola* in Cazorla, coinciding with a high availability of acorns and pinecones during the preceding winter (Herrera CM, personal communication; Pulido F, personal communication). Furthermore, low rates of predispersal seed predation by mice on *H. foetidus* have also been observed in northwestern Spain after masting events of *Fagus sylvatica* (Guitián J, personal communication). Also, during the postdispersal phase, in all study sites, seeds located in sheltered microsites (e.g., rock outcrops; Fedriani, 2005) experienced higher removal by mice as compared with seeds in nonsheltered microsites. Any negative effect of mice on *H. foetidus* fitness during the postdispersal phase may also be a function of microhabitat features (e.g., vegetation cover, presence of refuge). Thus, seed shadows of *H. foetidus* located in sheltered microsites may suffer a more intensive “filtering” by mice as compared with plants located in nonsheltered microsites (Hulme and Benkman, 2002). If this process is relatively consistent and continuous, it might confer wood mouse some sort of “habitat-shaping” role (sensu Herrera, 1988), promoting *H. foetidus* populations to occur away from some microsites such as rock outcrops (Fedriani, 2005).

Spatial and temporal heterogeneity in the presentation and availability of resources molds ecological processes at many levels, from the behavior of individuals to the dynamics of populations, coexistence of species, and functioning of ecosystems (Price and Joyner, 1997). Our study is novel in exemplifying a case in which changes in seed presentation and

availability during a particular plant reproductive cycle might have a strong impact on foraging decisions by its main seed predator, which could be consequential for the plant population dynamic and spatial distribution. Therefore, it seems safe to predict that a knowledge of plant-granivore interactions that accounts for changes in seed presentation is necessary to comprehensively understand the joint dynamics of plants and their predators.

We are grateful to Hala Abdallah for field assistance. We are indebted to Burt Kotler, Douglas Morris, Stephen Dobson, Johannes Kollman, Göran Arnqvist, Mónica Medrano, Javier Guitián, Pedro Rey, and an anonymous reviewer for numerous and helpful comments on earlier drafts. The Consejería de Medio Ambiente (Junta de Andalucía) provided working facilities. This study was supported by Ministerio de Educación y Ciencia grants CGL2004-00094/BOS and BOS2000-1122-C03 (02 subproject). During the writing of this manuscript, J.M.F. was supported by a “Ramón y Cajal” postdoctoral contract (Ministerio de Educación y Ciencia, Spain).

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