

DO FRUGIVOROUS MICE CHOOSE WHERE OR WHAT TO FEED ON?

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Exhaustive analyses of plant–frugivore systems have revealed that few, if any, of these plant–animal interactions are tightly coevolved. Such lack of coevolutionary evidence could be related to frugivores selecting plants based on environmental cues, rather than on plant phenotypic traits. To evaluate this hypothesis, I examined whether the pattern and extent of fruit predation by long-tailed field mice (*Apodemus sylvaticus*) on the perennial herb *Helleborus foetidus* was directly related to mouse abundance, to environmental cues, to plant phenotypic traits, or to a combination of these. Thus, I estimated mouse relative abundance (through livetrapping) and percentages of fruit predation by mice, and quantified plant environmental and phenotypic traits in 9 populations of *H. foetidus* in southeastern Spain during 2 years (overall, 254 plants). I found substantial variation among populations in mouse trapping success (ranging from 0.0 to 21.8 individuals/100 trap nights), size of fruit crops (8.6–28.9 fruits per plant), and percentages of fruit predation by mice (0.0–93.3%). However, no simple relationship was found between mouse abundance (as estimated by trapping success) and strength of fruit predation. None of the 4 measured plant phenotypic traits (e.g., number of fruits or plant size) had a significant effect on mouse foraging. Conversely, 2 of the 6 environmental traits considered (substrate and distance to nearest tree) influenced fruit predation by mice. Plants located on rocky substrates and nearby trees experienced higher percentages of predation and this result was rather consistent across the 2 years and the 2 levels considered (inter- and intrapopulation). Even though mice could have selected other plant phenotypic traits not accounted for (e.g., chemical traits), such hypothetical phenotypic selection appears to be inconsequential as a source of individual variation in *H. foetidus* maternal fitness because its effects could have been “diluted” by the overwhelming influence of environmental factors. Thus, the results support the initial hypothesis that the net outcomes of the interaction between *H. foetidus* and mice in southeastern Spain may not have strong coevolutionary consequences.

Key words: animal–plant interactions, *Apodemus sylvaticus*, coevolutionary constraints, foraging behavior, frugivory, *Helleborus foetidus*, rocks, seed predation, Spain

Frugivores may act as either seed predators or seed dispersal agents and, therefore, play a central role on the demography and evolution of plant populations (Janzen 1980; Herrera 2002a; Wang and Smith 2002). Strength of frugivory often shows remarkable spatial and temporal variations (Herrera 1998), which rarely are a mere function of frugivore abundance (Herrera 1998). Indeed, frugivores are known to employ intricate mechanisms of selection to discriminate precisely among fruit patches of varying profitability (Sallabanks 1993). Because such a fruit selection process can be based on a myriad of plant phenotypic traits, evolutionary biologists have traditionally supported the view that frugivores have the potential to exert phenotypic selection on plant populations.

Nevertheless, comprehensive analyses of these plant–animal interactions reveals that few, if any, plant–frugivore systems are tightly coevolved (Alcántara and Rey 2003; Herrera 1985, 1998, 2002a; Jordano 2000; Lord et al. 2002; Traveset et al. 2004). This suggests that constraining factors may be impinging on the selective process between plants and frugivores. One of the most commonly advanced explanations to such lack of coevolutionary evidence is that the reciprocal selection process among plants and their counterpart frugivore animals does not take place at a species-to-species basis, but most often appears to be the sum of numerous, diffuse interactions involving dozens of species (Freeland 1991; Herrera 1998, 2002a).

Another interpretation of such lack of coevolutionary evidence is that coevolution is constrained because the selection exerted by frugivores is based on environmental variables in which plants are embedded, rather than based on plant phenotypic traits (Herrera 1998). For example, macro- and microhabitat features have been found to be important determinants for foragers, including frugivores (Herrera 1993;

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Izhaki 2002; Karban 1997; Manasse and Howe 1983). Indeed, to maximize fitness, foraging decisions made by frugivores are known to minimize predation risk and therefore they often select plants or patches on the basis of (environmental) surrogates of predation risk (Howe 1979). Both frugivorous birds and seed-eating rodents have been reported to minimize the danger of predation by selecting patches or plants with high cover in surrounding vegetation, where escaping from visual predators is easier (Díaz and Alonso 2003; Howe 1979; Morris and Davidson 2000). In addition, other environmental variables not related to predation risk, such as distance to conspecifics and availability of alternative foods, can exert a critical influence on frugivore activity (Manasse and Howe 1983; Ostfeld and Keesing 2000; Sargent 1990). Thus, if frugivores select plants based on environmental cues (e.g., habitat, distance to shelter, food, and others) not related to plant phenotype (e.g., crop size or fruit traits), the potential for phenotypic selection by frugivores on plant populations could be seriously constrained. Finally, temporal or spatial inconsistencies on selection pressures associated with animal–plant interactions also may operate against mutual adaptations of interacting species (Herrera 1998; Horvitz and Schemske 1990). Although the role of such potential constraints on plant–frugivore systems has been explicitly recognized (Herrera 2002a), most of the available studies concern seed-dispersing birds (Manasse and Howe 1983; Sallabanks 1993; Sargent 1990) but not mammals. Even more limited are those attempts at evaluating the relative importance of environmental versus plant phenotypic traits in assessing selection pressures by mammalian fruit and seed predators (García et al. 2001).

Recent studies on the perennial herb *Helleborus foetidus* L. (Ranunculaceae) have suggested the occurrence of intriguing mechanisms of phenotypic selection by its mutualistic (pollinators and seed dispersers) and antagonistic (flower and fruit predators) animal counterparts in the Iberian Peninsula (Fedriani et al. 2004; Garrido et al. 2002; Herrera et al. 2002). For instance, correlated evolution of mutualism- and antagonism-linked traits has been proposed to be a likely pathway engaged by *H. foetidus* to solve the evolutionary dilemma between enhancing its interaction with mutualisms while at the same time escaping from antagonists (Herrera et al. 2002). The feasibility of this and other hypotheses concerning the evolutionary trajectory of *H. foetidus* in the Iberian Peninsula (Fedriani et al. 2004; Garrido et al. 2002; Herrera et al. 2002) would be importantly constrained if, as stated above, environmental variables played a chief role in determining plant fitness. Surprisingly, even though this plant species is known to grow in a wide variety of macro- and microenvironmental conditions (Werner and Ebel 1994), no published study has yet paid attention to the potential role of the environment on the fitness of *H. foetidus*.

The focus of this study is the interaction between *H. foetidus* and its main fruit predator in the Iberian Peninsula, the long-tailed field mouse (*Apodemus sylvaticus*; Muridae). I evaluate the hypothesis that mice should select individual *H. foetidus* based on environmental cues rather than plant phenotypic traits, which could constrain the mutual adaptation of both interacting

species. In doing so, I seek to answer the following 3 questions: Are population, temporal, and habitat-related variations in strength of fruit predation by mice related to mouse abundance? If strength of fruit predation by mice depends on factors other than mouse abundance, what is the relative importance of environmental versus plant phenotypic traits in determining fruit predation by mice? Are the roles of environmental and plant phenotypic traits on predation of fruit by mice consistent in time and space?

MATERIALS AND METHODS

Study area and system.—The study was carried out in the Cazorla Mountains of southeastern Spain (37°56'N, 2°52'W), during June–July of 2001 and 2003. Because patterns of fruit predation by rodents show remarkable interpopulation variation, I randomly selected 9 widely spaced populations of *H. foetidus* (hereafter referred to as P1–P9) in which to assess variation. All 9 selected populations occur within 1 of the following 2 macrohabitats: mixed forests of pine (*Pinus nigra*) and oak (*Quercus rotundifolia*), with scattered understory of *Juniperus oxycedrus* and *Daphne laureola*; and edges (within 30 m) of streams, with canopy of pines (*P. nigra*) and oaks (*Q. rotundifolia*) and understory of *J. oxycedrus*, *Rubus ulmifolius*, *Daphne laureola*, and *Juncus*. Preliminary observations suggest that mice are more abundant near streams than in the mixed forest, probably because the denser understory along streams provides mice with shelter to avoid predators while foraging. Substrates in all populations are comprised of a mosaic of bare ground and highly fissured rock outcrops. The elevation of all populations ranged from 1,100 to 1,350 m. Separation among populations of *H. foetidus* ranged from 0.4 to 5.2 km, with most populations separated by more than 2 km. Field mice typically show low mobility (Corp et al. 1997; Díaz et al. 1999; Díaz and Alonso 2003), particularly in woodland populations (Corp et al. 1997) such as those selected for this study. Furthermore, preliminary capture–recapture information gathered in the Cazorla Mountains during 2000–2004 supports the notion of low mice mobility, patchy distribution, and that mice from one population did not range into others.

Helleborus foetidus is a perennial herb (Werner and Ebel 1994) that is abundant in clearings, understory of mixed forest, and in scrublands in the Cazorla Mountains (Herrera et al. 2002). Plants consist of 1–5 reproductive ramets, that in winter (January–March) usually produce 25–100 flowers each in their terminal inflorescences (Herrera et al. 2002). Flowers are apocarpous, with up to 5 carpels (usually 2 or 3). Fruit maturation and seed shedding take place in June–July, when each ripe follicle releases 8–15 elaiosome-bearing seeds. The species does not show any noticeable physical defense of its fruit against predation by mice, probably because of its reliance on chemical defense (Werner and Ebel 1994). Mice can prey very heavily on fruits of *H. foetidus*, with up to 52% of fruits removed in some sites and years, mostly immediately before seed shedding (Fedriani et al. 2004). Shortly after seed shedding, mice and a diverse guild of disperser ants compete for seeds of *H. foetidus* (Fedriani et al. 2004; Garrido et al. 2002); thus, mice are also postdispersal seed predators and seeds that are not quickly dispersed by ants are often depredated by mice.

Long-tailed field mice are small rodents (14–28 g) widely distributed in the Iberian Peninsula (Mitchell-Jones et al. 1999). In the Cazorla Mountains, long-tailed field mice are relatively common in mixed forests, scrublands, and near streams (Fedriani et al. 2004; Hulme 1997), thus, overlapping widely with the local distribution of *H. foetidus*. In general, long-tailed field mice are known to forage more intensively in microhabitats well provided with shelter against

predators (vegetation, rock crevices, and so on—Díaz and Alonso 2003; Fedriani et al. 2004). Evidence of flower removal by mice in the Cazorla Mountains is anecdotal; it appears that predation on *H. foetidus* by mice is rather limited to the time span in which its fruits and seeds are available (May–July). Long-tailed field mice act exclusively as seed predators (not dispersers) and are virtually the only terrestrial rodents present in the 9 study populations. Further, there is no evidence that any other rodent species removes fruits of *H. foetidus* in the Cazorla Mountains (Fedriani et al. 2004).

Small-mammal trapping.—To estimate their local abundance, long-tailed field mice were live-trapped with Sherman traps (H. B. Sherman Traps, Inc., Tallahassee, Florida) baited with peanut butter (LoGiudice and Ostfeld 2002) during the summer (June–July) of each study year. In summer 2001, trapping was carried out in 5 populations (P3, P4, P7, P8, and P9), whereas during the summer of 2003, trapping was restricted to 3 populations (P4, P5, and P9) because of logistic reasons. Overall, I carried out 1 or 2 trapping surveys per population and per year, each lasting for up to 4 consecutive nights. Low mouse abundance in the Cazorla Mountains prevented the use of systematic small-mammal trapping grids to estimate absolute number of individuals per space unit (Schmidt and Ostfeld 2003). Consequently, to maximize number of captures and thus to attain most accurate estimates of mouse abundance, traps ($n = 40\text{--}50$ per population) were set in places with signs of mouse activity (e.g., presence of food remains) or in presumed favorable microsites (rock crevices, beneath bushes, and so on). Traps were checked daily within 2 h after sunrise and captured mice were individually marked with indelible ink on the tail and released at their respective capture sites. The ink lasted ≥ 7 days and, thus, allowed the identification of recaptured individuals during each trapping survey, which lasted up to 4 days. Simple indexes of mouse relative abundance were calculated for each population and year as: (number of different individuals captured [i.e., excluding recaptures]/trapping effort [i.e., trap nights]) $\times 100$. Macrohabitat-specific indexes of mouse abundance were calculated by averaging indexes from populations within each macrohabitat. Trapping procedures (trap locations, trapping efforts, number of traps, and so on) were fairly consistent during 2001 and 2003, allowing an accurate evaluation of interannual change in mouse abundance for particular populations. Mouse capture and handling procedures followed the guidelines of the American Society of Mammalogists (<http://www.mammalogy.org/committees/index.asp>).

Fruit predation and plant characterization.—Fruit losses caused by mice were evaluated in all 9 populations of *H. foetidus* selected during both years. Within each population and year, I randomly chose 7–30 plants (overall, $n = 254$) at the start of the ripening season (late June) and monitored them (2 or 3 times per plant) until all fruits were either removed by mice or had successfully released their seeds. Losses due to mice were precisely identified because mice prey on fruits of *H. foetidus* by chewing the pedicels and removing the whole structure from the parent plant (Fedriani et al. 2004; Herrera et al. 2002). Plant characterization took place in 8 out of the 9 populations initially selected (P9 was not characterized for logistic reasons) and, thus, sample sizes were 119 and 120 plants, for 2001 and 2003, respectively (Appendix I). Plant identities within each population differed between study years, thus avoiding the issue of pseudoreplication. To evaluate the effect of environmental and plant phenotypic traits on fruit predation by mice, I considered for each plant 6 environmental variables and 4 plant phenotypic traits that could potentially affect mouse foraging (Appendix I). Type of macrohabitat (mixed forest versus edge of streams; see “Study area and system”) in which each population is embedded was considered because it can impinge on several critical variables (mouse abundance, shelter, and so on—Díaz

and Alonso 2003; Hulme and Benkman 2002). Substrate in which plants were located also was considered because it is known to influence foraging by seed-eating rodents (Brown et al. 1992; Kotler et al. 2001). Thus, by considering circular plots 80 cm in diameter centered on each particular plant, I visually identified 4 types of substrates: rocky (plants located in plots where $>75\%$ of their area was occupied by rocks or stones), mostly rocky (50–75% of a particular plot occupied by rocks or stones), mostly bare ground (50–75% occupied by bare ground, often with some scattered annual grasses), and bare ground ($>75\%$ occupied by bare ground). Also, an index of cover was obtained for each plant because mice could select plants underneath cover in order to elude predators (Díaz and Alonso 2003). For each monitored plant, 2 measurements of cover were estimated as the length of two 80-cm segments (centered on the plants) intersected by vegetation (or dead branches, rocks, and so on) at heights of 20 and 50 cm, respectively (Fedriani et al. 2002). These 2 measurements were assumed to correctly represent the “average shelter” of each plant along its entire height. Then, to simplify the analysis, these 2 measurements were added, and a single figure was obtained (potentially ranging from 0 to 160 cm) for each monitored plant. Distance to nearest fruiting conspecific was also measured because the number of fruits of *H. foetidus* in the vicinity of a target plant can either enhance or inhibit frugivore activity (Sallabanks 1993; Sargent 1990). Finally, other factors related to accessibility of shelter for mice, such as distances to nearest bush and tree, were included in the models (Díaz and Alonso 2003; Morris and Davidson 2000). Virtually no other plant species was fruiting simultaneously to monitored *H. foetidus*; thus, I did not consider surrogates of availability of alternative foods, although food storage by mice in caches (acorns, pine seeds, and others) was observed in some populations and food storage could affect mouse foraging. Further, for each plant, I identified 4 phenotypic traits presumably related to their profitability and size (Appendix I). The number of fruits available to mice was retrospectively estimated for each plant at the end of the fruiting period as the number of fruits releasing seeds plus the number of fruits removed by mice. Finally, because from a distance plant size and silhouette may play a role in plant selection by mice (Hulme and Benkman 2002), the numbers of reproductive and vegetative ramets and the length of the largest ramet also were included in the analyses.

The number of fruits of *H. foetidus* removed by mice is only one component of the fruit-predation process (hereafter referred to as “fruit exploitation”); whether or not mice even find a plant is another (hereafter referred to as “fruit encounter”—Hulme and Hunt 1999; Murray 1987). Because the roles of environmental and plant phenotypic traits may vary accordingly to different phases of the fruit predation process (Murray 1987; Sallabanks 1993), I first examined the relative importance of such factors as determinants of plant visitation by mice, that is, fruit encounter, defined as those plants having at least 1 fruit removed by mice. In a 2nd analysis, to further identify the relative importance of factors affecting fruit predation of *H. foetidus* by mice, I limited my analysis of percentages of fruit removal of mice-visited plants, that is, fruit exploitation. Evidence for fruit encounter necessarily required that mice removed at least 1 fruit and thus did not distinguish between plants located but ignored by mice from those plants that were never located (Hulme and Hunt 1999). However, from a plant’s fitness perspective, it is the same to be located by mice but not depredated than never to be located.

Statistical analyses.—To evaluate whether frugivorous mice responded to population rather than individual plant characteristics, I first analyzed the relationship between average values of environmental and plant phenotypic traits of each population and year (see Appendix I) and average percentages of fruit encounter and exploitation by mice

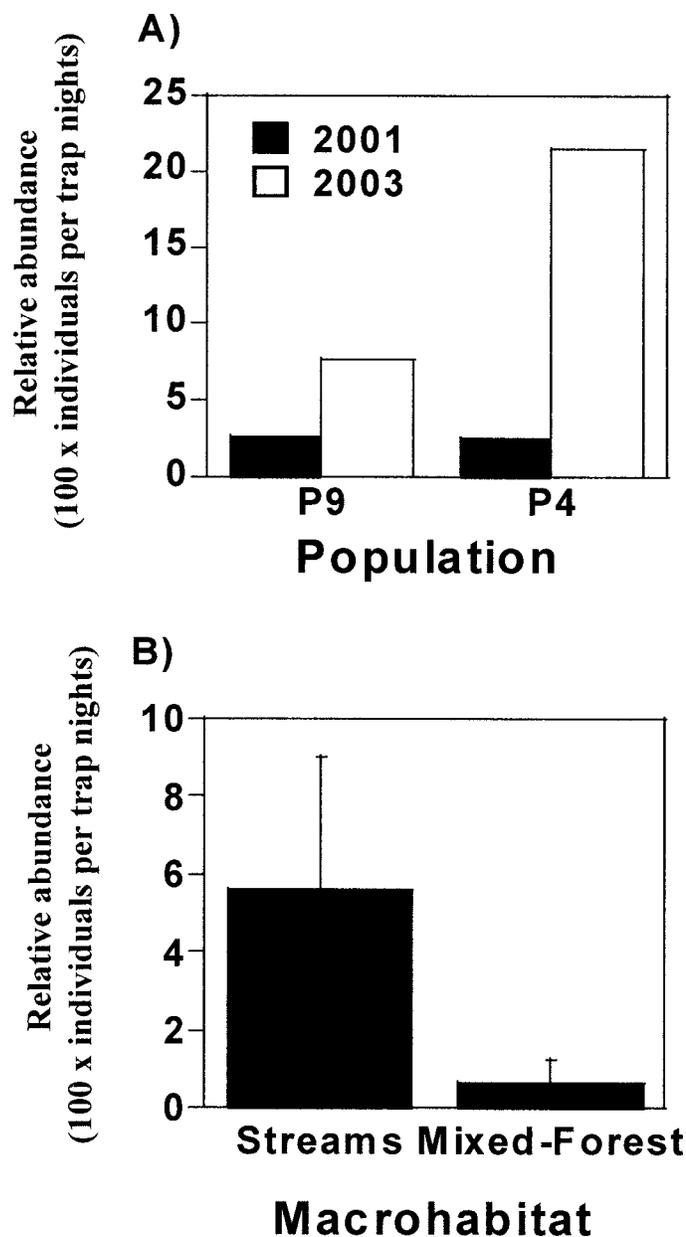


FIG. 1.—Relative abundance of *Apodemus sylvaticus* in the Cazorla Mountains, Spain. A) Abundance in 2001 and 2003 in 2 populations, populations 9 and 4 (P9 and P4), of *Helleborus foetidus*. Trapping efforts (trap nights) were 160 and 154 (P4) and 116 and 220 (P9) for 2001 and 2003, respectively. Bars represent means. B) Abundance in 2 contrasting macrohabitats (stream edges and mixed forest), shown as mean + 1 SE (estimated by averaging indexes from 4 and 5 populations in stream edges and mixed forest, respectively).

(see Herrera et al. [1994] and García et al. [2001] for similar procedures). Because of departures from normality and the presence of outliers, leverage points, or both, I used robust regression (Rousseeuw and Leroy 1987) rather than least-squares regression. Robust fits are minimally influenced by outliers in the independent variable space, in the response space, or in both. Analyses were performed by using robust MM-regression procedure available in S-Plus 6 (Insightful Corporation 2001), and the significance of each variable was assessed by using robust *F*-tests. Sequential Bonferroni confidence intervals

(Rice 1989) were used in multiple comparisons to control the experimentwise error.

To evaluate whether frugivorous mice responded to individual plant characteristics, I used generalized linear mixed models with binomial error and logit link function by using SAS macro GLIMMIX (Littell et al. 1996) to assess the role of environmental and phenotypic traits of each plant on both fruit encounter (binary variable of the type “found” or “not found”) and fruit exploitation (proportion of fruits depredated with respect to total fruits available at plants). In these analyses, plants were subjects whereas population (nested within macrohabitat) was considered the random between-subject factor (Bennington and Thayne 1994) and thus the potential effects of population were controlled for. Consequently, the interaction between population (nested within macrohabitat) and year also was considered as a random effect. All 10 explanatory variables listed in Appendix I were initially considered in the models as fixed factors. Further, to identify potential interannual variations in the role of both environmental and plant phenotypic traits, I also included in the models the factor “year” and all 2-way interactions between year (2001 or 2003) and explanatory variables. Year was considered a fixed factor because 2001 and 2003 were not 2 years chosen randomly, but were chosen because they corresponded to years of low and high mouse abundances (see below). The significance of each fixed factor and their interactions with year was evaluated by stepwise backward elimination from the full model. Model-adjusted means and standard errors in the scale determined by the logit function were computed. Standard errors of such means were back-transformed by using the appropriate Taylor’s series approach (Littell et al. 1996).

RESULTS

Mouse abundance.—During the summer of 2001, a sampling effort of 772 trap nights at P3, P4, P7, P8, and P9 yielded only 7 different individuals and an overall index of abundance of 0.9 individuals/100 trap nights. During the summer of 2003, trapping (626 trap nights) was restricted to P4, P5, and P9 and yielded 63 different individuals and an overall index of 10.1 individuals/100 trap nights. Relative abundance of mice was therefore about 1 order of magnitude higher in 2003 than in 2001. To compare year-specific estimates of mouse abundance, I recalculated mouse abundance indexes only for the 2 populations where trapping was conducted in both years (P4 and P9). In P9, mouse abundance was 3-fold higher in 2003 than in 2001, whereas in P4 abundance was 1 order of magnitude larger in 2003 than in 2001 (Fig. 1A). On the other hand, considering trapping efforts made during both years, relative abundance in stream edges (populations 3, 4, 8, and 9) was 5.4-fold higher than in mixed forest (populations 5 and 7; Fig. 1B).

Fruit availability and fruit predation.—Fruit availability (overall, $n = 5,309$) was highly variable among populations, within populations, and also between years (Fig. 2A). Further, such annual variation in fruit availability was not necessarily consistent among populations. For instance, although P2, P3, and P6 showed higher availability of fruits during 2001, in P9, P5, and P4 higher fruit availability occurred during 2003 (Fig. 2A). Overall, mice preyed on 18.3% of available fruit. When the 2 components of the fruit predation process were analyzed separately, both percentages of fruit encounter and fruit exploitation showed strong spatial and temporal variation (Figs.

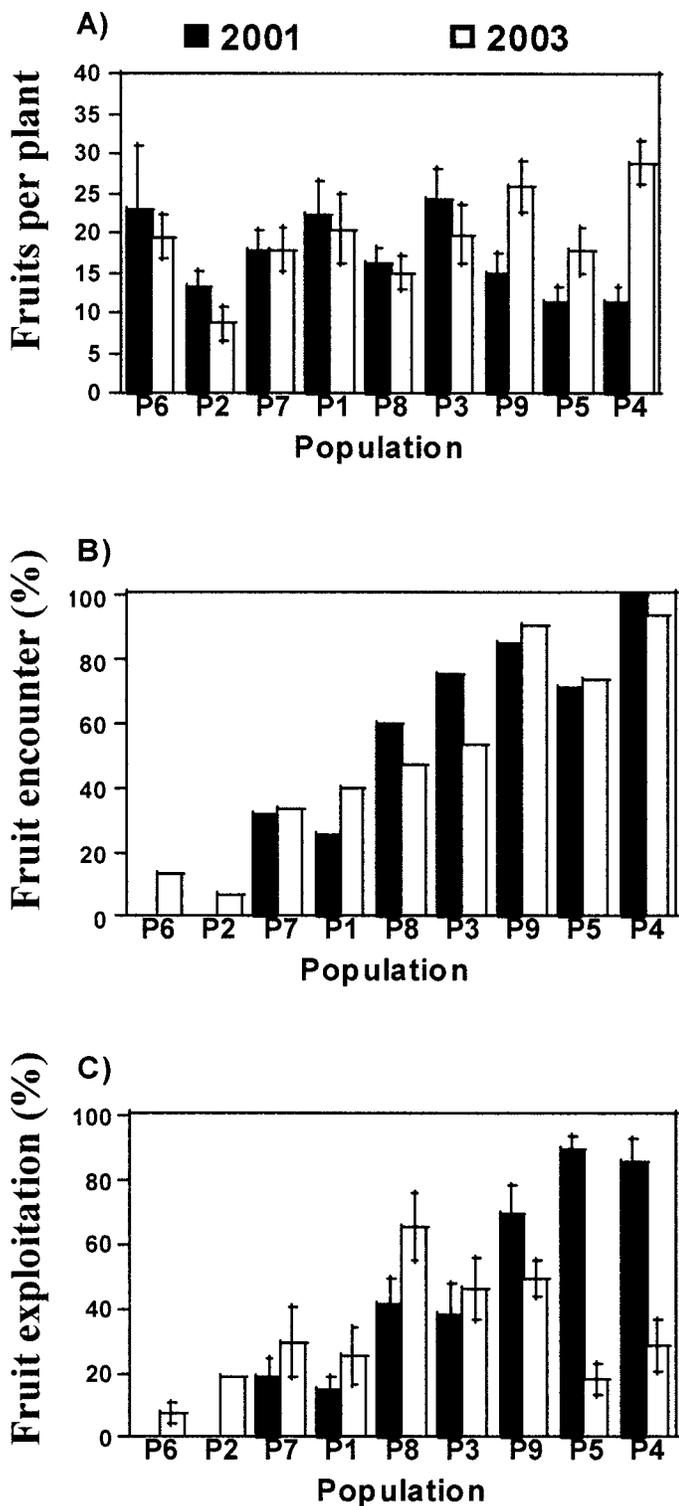


FIG. 2.—Use of fruit of *Helleborus foetidus* by long-tailed field mice (*Apodemus sylvaticus*), in Cazorla Mountains, Spain, for 9 populations and 2 years. A) Number of fruits available at plants. B) Percentage of “fruit encounter” by mice. C) Percentage of “fruit exploitation” by mice. Bars indicate means \pm 1 SE.

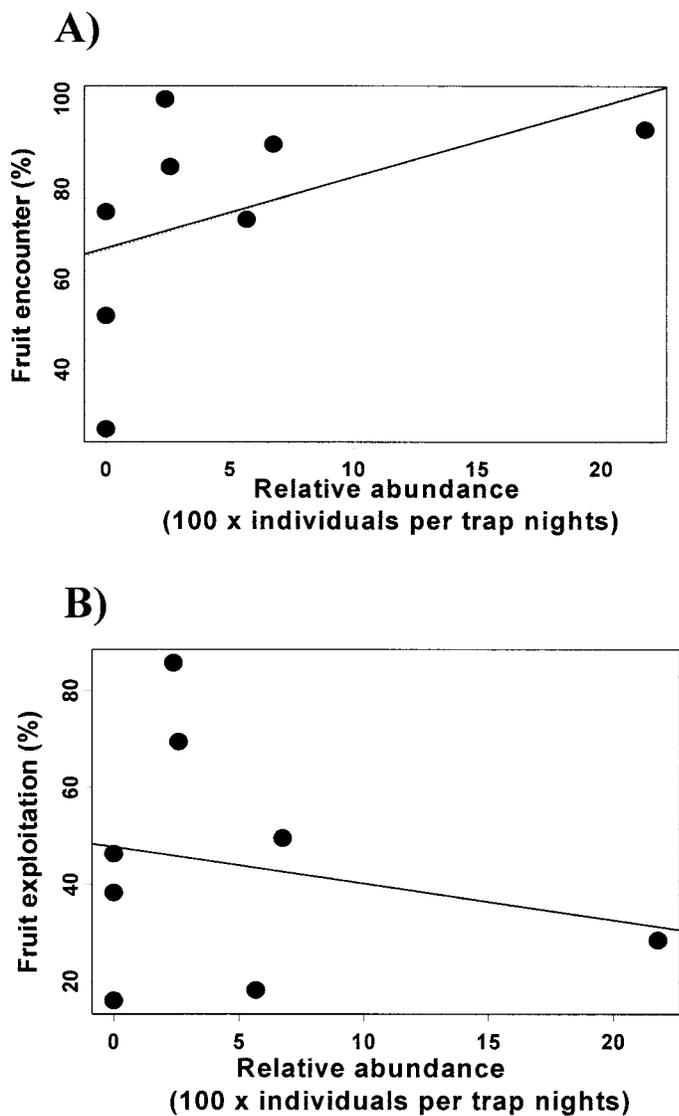


FIG. 3.—Nonsignificant relationship between relative abundance and A) encounter with fruit of *Helleborus foetidus* ($F = 1.34$, $d.f. = 1$, $P < 0.236$) and B) exploitation of fruit ($F = 0.230$, $d.f. = 1$, $P = 0.624$) for *Apodemus sylvaticus* in populations 3, 4, 5, 7, 8, and 9 (with populations 4 and 9 sampled in both 2001 and 2003). (Robust regression gives essentially the same results as least-squares regression.)

2B and 2C). For example, fruit encounter and exploitation by mice were very low during both years in P6 and P2, intermediate in P7 and P1, and much higher in the remaining populations (Figs. 2B and 2C). Nonetheless, such marked interpopulation variation in the strength of the 2 components of fruit predation was not necessarily consistent between years, particularly regarding percentages of fruit exploitation (Fig. 2C).

Role of environmental and plant phenotypic traits on mouse fruit predation.—At the interpopulation level, frugivory percentages and indexes of mouse abundance were not clearly related (Fig. 3). Even though there was an apparent positive relationship between fruit encounter and mouse abundance (Fig. 3A), the trend was not significant (Table 1), likely because data

TABLE 1.—Results of robust regressions among average population percentages of fruit encounter and exploitation of fruit of *Helleborus foetidus* by *Apodemus sylvaticus* and environmental and plant phenotypic traits in the Cazorla Mountains, Spain. Robust *F*-tests were used to evaluate the significance of each variable. Significant results after sequential Bonferroni adjustment are shown in boldface.

	Fruit encounter			Fruit exploitation		
	<i>F</i>	<i>d.f.</i>	<i>P</i>	<i>F</i>	<i>d.f.</i>	<i>P</i>
Environmental traits						
Distance to tree	0.953	1	0.317	0.292	1	0.580
Distance to bush	1.203	1	0.261	0.132	1	0.709
Distance to conspecific	0.308	1	0.570	0.295	1	0.578
Cover	0.707	1	0.389	0.095	1	0.752
% of plants on rocky substrate	8.560	1	0.003	7.804	1	0.004
Mouse abundance	1.340	1	0.236	0.230	1	0.624
Phenotypic traits						
Number of reproductive ramets	0.377	1	0.529	0.881	1	0.336
Number of nonreproductive ramets	4.198	1	0.036	2.005	1	0.147
Length of largest ramet	0.160	1	0.682	0.323	1	0.560
No. available fruits	0.158	1	0.684	1.887	1	0.159

show an asymptotic behavior (saturation curve), with percentages of fruit encounter increasing rapidly with an increase in mouse abundance and becoming stable around an abundance of 10 individuals (Fig. 3A). Percentages of fruit exploitation by mice also were not related to population-specific abundances of mice ($P > 0.624$; Fig. 3B). Conversely, I found a significant positive relationship between percentages of plants located on rocky or mostly rocky substrates and both percentages of fruit encounter ($P < 0.003$) and fruit exploitation by mice ($P < 0.002$; Fig. 4). Indeed, percentages of plants located on rocky substrates explained significant fractions (29.7% and 36.3%, respectively) of the variance in fruit encounter and fruit exploitation data. At this 1st level of analysis, no other environmental or plant phenotypic trait was found to affect percentages of fruit encounter or exploitation by mice (Table 1).

At the intrapopulation level, no fixed factor or interactions with year were found to impinge on fruit encounter by mice (in all cases, $P > 0.060$). Conversely, fruit exploitation by mice was strongly affected by the substrate on which the plants were located ($F = 9.06$, $d.f. = 3, 89$, $P < 0.0001$; Fig. 5), which was consistent with results reported above. Plants growing on rocky and mostly rocky substrates experienced significantly higher fruit predation by mice than those on bare and mostly bare grounds (Table 2). Furthermore, no significant interaction was found between substrate and year ($F = 1.36$, $d.f. = 3, 71$, $P > 0.263$), indicating that higher percentages of fruit exploitation by mice took place on plants located on rocky substrates during both years. In addition, fruit exploitation by mice was affected by distance to the nearest tree ($F = 5.19$, $d.f. = 1, 89$, $P < 0.026$). Specifically, the negative sign of the parameter estimate for distance to tree (-0.002 ± 0.001 ; mean $\pm SE$) indicated that plants away from trees experienced less fruit exploitation by mice than those near trees. Substrate and distance to nearest tree altogether explained a considerable (25.3%) fraction of the overall deviance in the fruit exploitation data. No other factor

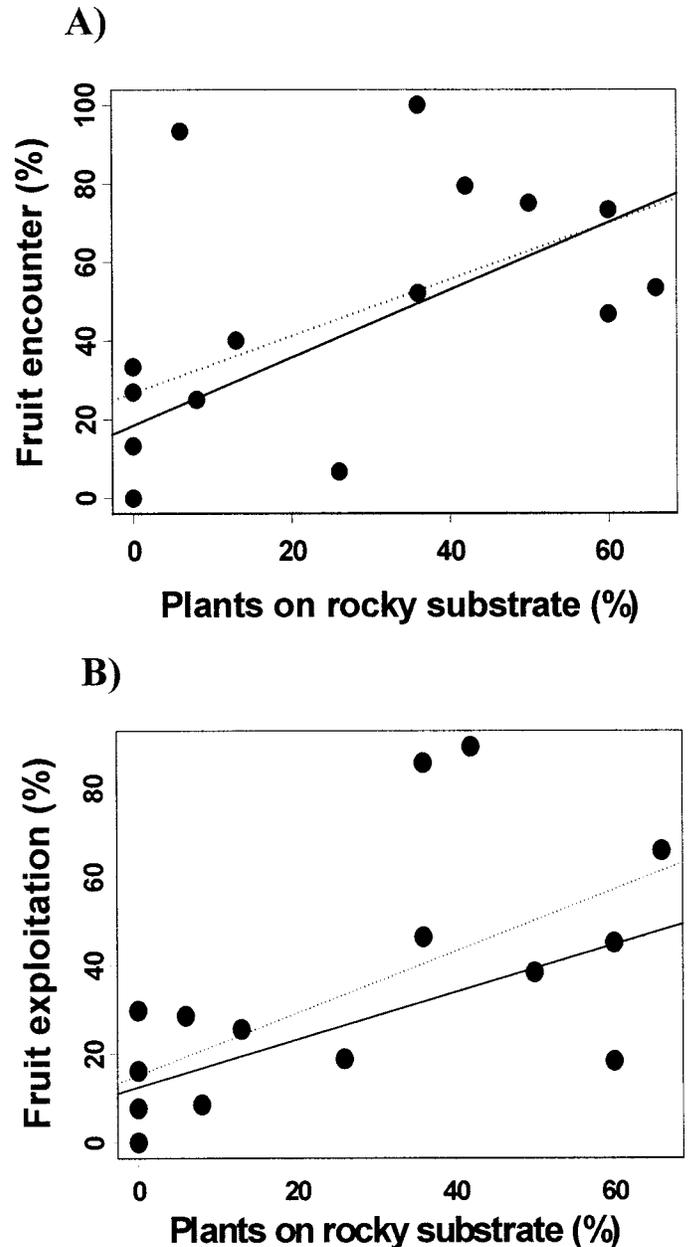


FIG. 4.—Positive relationship between percentages of *Helleborus foetidus* located in rocky or mostly rocky substrates and A) encounter with fruit ($F = 8.56$, $d.f. = 1$, $P < 0.003$) and B) exploitation of fruit ($F = 7.80$, $d.f. = 1$, $P < 0.004$) by *Apodemus sylvaticus*. Note that robust regression (continuous line) differs somewhat from least-squares regression (dotted line).

(or its interaction with year) was found to affect fruit exploitation by mice.

DISCUSSION

This study has shown strong variation among populations in mouse abundance (as estimated by trap catches), size of fruit crops, and strength of fruit predation by mice, which is consistent with reports for other plant–frugivore systems (Herrera 1998, 2002a; Jordano 2000; Levey 1988; Willson

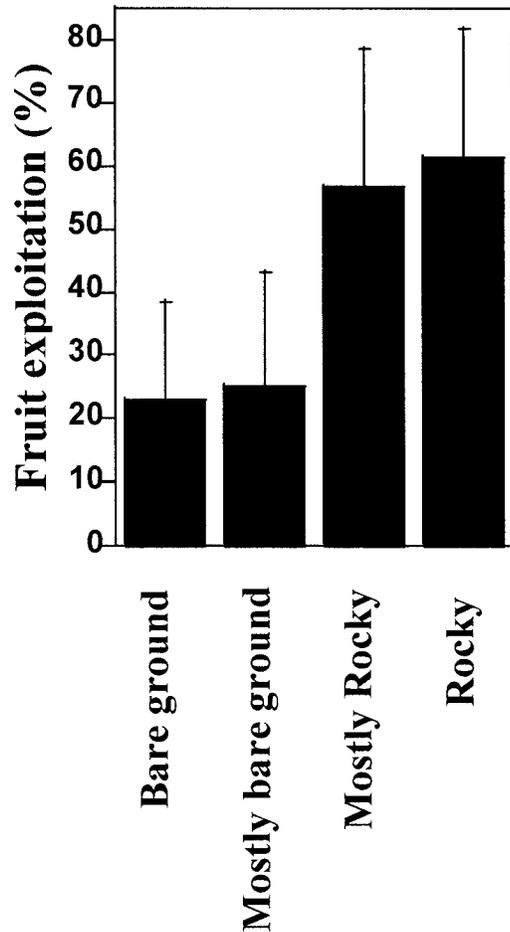


FIG. 5.—Model-corrected mean square percentages (bars) of fruit exploitation by *Apodemus sylvaticus* (+ 1 SE) on *Helleborus foetidus* ($n = 239$) on 4 substrate types (bare ground, mostly bare ground, mostly rocky, and rocky) in the Cazorla Mountains, Spain.

and Traveset 2000). Despite noticeable variation between years and between macrohabitats in mouse abundance, rates of fruit predation by mice did not differ between years or between macrohabitats. Thus, no simple relationship existed between mouse abundance and strength of fruit predation, which is also a common feature of plant–frugivore systems (Herrera 1998, 2002a; Jordano 2000; Levey 1988), including those involving seed-eating rodents (Rey et al. 2002). These results suggest that the field mouse–*H. foetidus* system is likely to be impinged by environmental traits, plant phenotypic traits, or both.

Environmental variables (substrate and distance to tree) influenced fruit predation by mice, whereas the measured plant phenotypic traits did not have any appreciable effect on mouse foraging. The role of the environment was consistent across the 2 years and the 2 levels considered (inter- and intrapopulation), supporting the view of environmental variables as determinants of mouse foraging. Nonetheless, the possibility that predation pressure exerted by mice might have acted over phenotypic traits of *H. foetidus* not measured in this study cannot be ruled out. Such traits could be related to both nutritional variables and presence of plant secondary compounds (Izhaki 2002). In fact,

TABLE 2.—Differences among least-square means of percentages of fruit exploitation by *Apodemus sylvaticus* on *Helleborus foetidus* located on 4 substrate types in the Cazorla Mountains, Spain. Significant results are shown in boldface.

Substrates	<i>df.</i>	<i>t</i>	<i>P</i>
Bare versus mostly bare	89	−0.35	0.765
Bare versus mostly rocky	89	−3.79	0.0003
Bare versus rocky	89	−4.60	<0.0001
Mostly bare versus rocky	89	−4.01	0.0001
Mostly bare versus mostly rocky	89	−3.16	0.0022
Rocky versus mostly rocky	89	0.49	0.624

H. foetidus relies on chemical, rather than physical, defenses to protect its fruits (Werner and Ebel 1994). Thus, concentration of secondary compounds could be of critical importance to this species in order to avoid seed predation by mice (e.g., Cipollini and Levey 1997a, 1997b). *H. foetidus* contains several poisonous glycosides, which can be lethal for mammals when even small quantities of its aerial parts are ingested (Cooper 1998; Holliman and Milton 1990). Consequently, I hypothesize that the strong inter- and intrapopulation variation in percentages of mouse fruit predation found in this and earlier studies (Fedriani et al. 2004; Herrera et al. 2002), could partly be due to differing concentration of glycosides in the fruits of individual plants or populations (Danell and Bergström 2002; Freeland 1991). However, even if variation in chemical traits accounted for contrasting percentages of mouse predation, the proportion of within-population variation in plant reproductive success explained by chemical attributes might still vary widely, depending on the relative importance of environmental factors extrinsic to plants (Benkman et al. 2001; Herrera 1993, 1995, 1998). Thus, it is possible that even if phenotypic selection by mice on *H. foetidus* occurred on traits not considered here (e.g., chemical traits), this selection might be inconsequential as a source of individual variation in maternal fitness because its effects could be diluted by the overwhelming influence of environmental factors (see Herrera [1993] for a comparable conclusion for *Viola cazorlensis*). On the other hand, variation in food choice by mice may not only reflect changes in food availability or profitability but, rather, changes in mouse physiology (Belovsky and Schmitz 1994; Bozinovic and Martínez del Río 1996; Mangione et al. 2000). For instance, Mangione et al. (2000) have shown striking interpopulation differences in the tolerance of desert woodrats (*Neotoma lepida*) to secondary compounds present in one of their staple plant foods, the creosote bush (*Larrea tridentate*). Thus, conceivably, the reported interpopulation differences in percentages of fruit predation by mice could be partly related to differing tolerance to glycosides present in *H. foetidus*. Current research is being directed to evaluate these possibilities.

In an assessment of geographic variation in the interaction between seeds of *H. foetidus* and its ant dispersers in the Iberian Peninsula, Garrido et al. (2002) found a mosaic of well-matching and mismatching situations (sensu Thompson 1994, 1999) between seed traits and the structural and functional characteristics of local ant communities. One possible mecha-

nism explaining such matching–mismatching patterning has recently been attributed to the spatially variable incidence of mice as fruit predators (Fedriani et al. 2004), which could interfere in the ant–seed mutualism both by limiting the number of seeds available to ants and also by counterselecting on phenotypic traits of *H. foetidus*. Results from this study corroborate the idea that mice significantly decrease the total number of seeds released by plants and thus may limit plant recruitment (Fedriani et al. 2004; Herrera et al. 2002). By reducing the fitness of plants and limiting the number of seeds that subsequently would be dispersed by ants, mice likely reduced the chance for selection by this mutualistic agent (Fedriani et al. 2004) and, in this manner, could constrain the ant–seed mutualism. However, this study provides little support to the 2nd component of the hypothesis stated by Fedriani et al. (2004) regarding the potential ability of field mice to constrain ant–seed mutualism by counterselecting plant phenotypic traits (e.g., seed mass). It appears that, at least in the Cazorla Mountains, the potential phenotypic selection exerted by mice should be diluted by the influence of environmental variables. Likewise, the predominant role exerted by the environment on the fitness of *H. foetidus* (Figs. 4 and 5) probably adds a restriction to some evolutionary mechanisms proposed for this plant, such as correlated evolution of mutualism- and antagonism-linked traits in response to correlational selection (Herrera et al. 2002).

Why field mice preferred plants located on rocky substrates remains to be elucidated. Two nonexclusive possibilities exist. First, substrates can differ in their nutrient composition as well as in water accessibility (Forkner and Hunter 2000; Hawkes and Sullivan 2001; Herrera 2002b). Plants located on rocky substrates may be more limited of nutrients (or water) and thus less able to allocate resources to the synthesis of chemical defenses (Meyer 2000; Meyer and Root 1993). This is consistent with preliminary observations that plants located on rocky substrate experienced higher percentages of flower predation by lepidopteran larvae (mostly *Trigonophora flammica*; Noctuidae). Local availability of resources also could explain the lower percentages of fruit predation on plants located away from trees because these plants likely received more solar radiation and thus could be better able to produce chemical defenses. However, a simpler explanation is that field mice select substrates most favorable to escaping from predators (Brown et al. 1992; Kotler et al. 2001; Schmidt and Ostfeld 2003). In the Cazorla Mountains, rocky substrates offer abundant crevices where mice can easily hide. Indeed, seed-offering experiments suggest that field mice in Cazorla gave up at much higher seed densities in depots located on bare grounds than in those located on rocky substrates, suggesting enhanced escape opportunities on rocky substrates (Brown et al. 1992; Kotler et al. 2001; Schmidt and Ostfeld 2003). Finally, plants on bare ground near rocks also seem to experience higher fruit predation by mice (C. M. Herrera, pers. comm.).

Frugivorous mice seemed to select plants based on where they were located rather than on their appearance. Thus, examination of results suggests that the net outcomes of the interaction between *H. foetidus* and mice in Cazorla may not

have strong coevolutionary consequences because their effects could be potentially constrained by factors external to the interaction itself. The strength of this plant–frugivore interaction was dependent on mouse microhabitat usage rather than abundance, which supports the idea that “unequal use of space by a population of predators can lead to improper characterizations of interactions based solely on their density” (Schmidt and Ostfeld 2003:3276). In addition, this study exemplifies a case in which an explicit consideration of the spatial distribution of plants is crucial to assess the impact of herbivores on plant populations (Thomson et al. 2002). Rock outcrops act as refuges or enemy-free space for several plant species experiencing extensive belowground herbivory (Cantor and Whitham 1989; Thomson et al. 2002). It would appear that for plants experiencing severe aboveground herbivory, rock outcrops might represent either source (*V. cazorlensis*—Herrera 1993) or sink (*H. foetidus*—this study) habitats (sensu Pulliam and Danielson 1991).

RESUMEN

Análisis exhaustivos de sistemas planta–frugívoro han mostrado que casi ninguna de estas interacciones planta–animal han coevolucionado estrechamente. Esto podría deberse a que los frugívoros seleccionen las plantas en función del ambiente donde éstas se ubican y no de sus características fenotípicas. Para evaluar esta hipótesis, examiné si el patrón de depredación de frutos por el ratón de campo (*Apodemus sylvaticus*) en la hierba perenne *Helleborus foetidus* estaba directamente relacionado con la abundancia de ratones, con características ambientales, o con rasgos fenotípicos de estas plantas. Para ello, estimé la abundancia relativa de ratones y las tasa de depredación de frutos por ratón, y cuantifiqué las características ambientales y rasgos fenotípicos de plantas en nueve poblaciones de *H. foetidus* del sureste de España durante 2 años (254 plantas en total). Encontré una fuerte variación entre poblaciones en la capturabilidad de los ratones (0.0–21.8 individuos capturados/100 noches-trampa), en la cosecha de las plantas (8.6–28.9 frutos por planta) y en las tasas de predación de frutos (0.0–93.3%). No obstante, no hubo una relación directa entre la abundancia de ratones (capturabilidad) y la intensidad de predación de frutos. Ninguno de los 4 caracteres fenotípicos considerados (e.g., número de frutos o tamaño) tuvo efecto significativo sobre el forrajeo de los ratones. Por el contrario, 2 de las 6 características ambientales consideradas (tipo de sustrato y distancia a árbol) influyeron sobre la predación de frutos. Así, las plantas localizadas en sustratos rocosos y cercanas a árboles experimentaron las mayores tasas de predación. Además, el efecto del ambiente en el forrajeo de los ratones fue consistente en los 2 años y los 2 niveles espaciales (intra e interpoblacional) considerados. Aparentemente, una hipotética selección de los frutos de los ratones basada en rasgos fenotípicos no considerados en este estudio (e.g., rasgos químicos) no tendría consecuencias en el éxito reproductivo de *H. foetidus*, ya que su efecto sería “diluido” por la mayor influencia de los factores ambientales. Por tanto, este estudio apoya la hipótesis de que la interacción entre *H. foetidus*

y el ratón de campo en el sureste de España podría no tener consecuencias coevolutivas importantes.

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APPENDIX I

Average population values ($\pm 1 SE$) of environmental and plant phenotypic traits considered as potentially affecting fruit depredation by long-tailed field mice (*Apodemus sylvaticus*) in 8 populations of *Helleborus foetidus* (overall 239 plants) in the Cazorla Mountains (southeastern Spain) during 2001 and 2003. Number of plants monitored in each population and year also is presented.

	Population 1	Population 2	Population 3	Population 4	Population 5	Population 6	Population 7	Population 8
2001								
Number of monitored plants	12	12	12	11	14	7	26	25
Distance to tree (cm)	163.0 \pm 40.4	360.6 \pm 54.8	392.1 \pm 76.2	179.5 \pm 19.0	300.4 \pm 23.3	426.6 \pm 122.1	182.3 \pm 20.0	205.6 \pm 25.2
Distance to bush (cm)	48.7 \pm 13.0	42.4 \pm 15.8	122.4 \pm 32.5	30.9 \pm 6.5	33.8 \pm 7.5	145.1 \pm 45.5	74.0 \pm 15.3	142.9 \pm 31.9
Distance to <i>H. foetidus</i> (cm)	341.0 \pm 95.9	144.7 \pm 38.6	274.2 \pm 76.5	49.1 \pm 6.5	164.3 \pm 33.9	223.6 \pm 84.1	519.6 \pm 109.3	541.6 \pm 78.2
Index of cover (cm)	8.2 \pm 2.6	16.2 \pm 5.4	7.8 \pm 3.4	3.0 \pm 0.7	10.6 \pm 3.1	1.4 \pm 0.3	7.1 \pm 1.7	9.6 \pm 3.1
% of plants on rocky substrate	8.3	0	50.0	36.4	42.9	0	0	36.0
Macrohabitat type	Forest	Forest	Stream edge	Stream edge	Forest	Forest	Forest	Stream edge
Number of available fruits	22.3 \pm 4.4	13.4 \pm 1.7	24.3 \pm 3.8	11.5 \pm 1.8	11.4 \pm 2.0	23.1 \pm 8.1	17.7 \pm 2.8	16.0 \pm 2.0
Number of reproductive ramets	1.3 \pm 0.2	1.3 \pm 0.1	1.3 \pm 0.1	1.4 \pm 0.2	1.1 \pm 0.1	2.1 \pm 0.6	1.5 \pm 0.2	1.3 \pm 0.1
Number of vegetative ramets	2.8 \pm 0.7	4.3 \pm 0.6	3.1 \pm 0.4	2.0 \pm 0.5	3.4 \pm 0.5	5.6 \pm 1.4	4.9 \pm 0.9	3.3 \pm 0.5
Length of largest ramet (cm)	70.3 \pm 5.9	59.9 \pm 3.5	55.0 \pm 3.4	56.3 \pm 3.2	62.1 \pm 2.6	56.3 \pm 3.9	74.0 \pm 2.7	74.1 \pm 3.2
2003								
Number of monitored plants	15	15	15	15	15	15	15	15
Distance to tree (cm)	305.3 \pm 42.2	218.7 \pm 29.9	395.3 \pm 46.1	185.3 \pm 20.5	205.0 \pm 26.6	330.0 \pm 50.8	194.7 \pm 34.3	228.5 \pm 33.2
Distance to bush (cm)	81.0 \pm 18.9	149.7 \pm 28.0	218.0 \pm 30.9	70.5 \pm 22.4	198.0 \pm 32.7	400.0 \pm 84.1	244.7 \pm 31.4	226.7 \pm 43.7
Distance to <i>H. foetidus</i> (cm)	182.3 \pm 30.3	203.3 \pm 42.3	176.9 \pm 39.3	199.3 \pm 38.8	259.3 \pm 38.5	218.3 \pm 44.2	233.3 \pm 41.2	278.1 \pm 63.7
Index of cover (cm)	19.7 \pm 6.3	10.9 \pm 2.8	7.9 \pm 2.1	29.2 \pm 8.4	16.7 \pm 5.8	12.1 \pm 2.5	11.9 \pm 3.2	11.1 \pm 2.8
% plants on rocky substrate	13.3	26.7	60.0	6.7	60.0	0	0	66.7
Macrohabitat type	Forest	Forest	Stream edge	Stream edge	Forest	Forest	Forest	Stream edge
Number of available fruits	20.5 \pm 4.3	8.6 \pm 2.2	19.9 \pm 3.6	28.9 \pm 2.8	17.7 \pm 2.9	19.5 \pm 2.7	17.9 \pm 2.8	15.0 \pm 2.1
Number of reproductive ramets	1.6 \pm 0.2	1.2 \pm 0.1	1.4 \pm 0.2	2.5 \pm 0.2	1.7 \pm 0.3	1.2 \pm 0.2	1.3 \pm 0.2	1.1 \pm 0.1
Number of vegetative ramets	4.9 \pm 0.9	3.5 \pm 0.4	3.4 \pm 0.7	5.1 \pm 0.9	2.7 \pm 0.6	3.1 \pm 0.6	4.1 \pm 0.9	1.8 \pm 0.4
Length of largest ramet (cm)	62.1 \pm 1.8	55.3 \pm 3.7	53.9 \pm 4.0	68.0 \pm 2.3	79.1 \pm 5.8	60.2 \pm 2.2	73.5 \pm 3.7	60.5 \pm 3.1