Frequency-dependent seed size selection on *Cryptocarya alba* (Mol.) Looser (Lauraceae): testing the effect of background

JUAN L. CELIS-DIEZ* and RAMIRO O. BUSTAMANTE

Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, casilla 653, Santiago, Chile

Seed size affects the probability of seed predation. Large seeds should be preferred over small seeds but the selective responses of seed predators may also be frequency-dependent. Seed predators may prefer the most common seed sizes (apostatic selection), the rarest ones (antiapostatic selection) or even be unresponsive to the size of seeds. Moreover, seed density may further modify the selective responses of seed predators. We expect that at a low seed density seed consumption should be concentrated on common seed sizes, and at high seed density it should be concentrated on rare seed sizes, as common ones act as a background that makes rare phenotypes more conspicuous (the effect of background). We tested this prediction in a field experiment with seeds of *Cryptocarya alba* (Lauraceae) at La Campana National Park, central Chile. We presented large and small seeds in two contrasting seed densities (ten and 100 seeds per m^2) and at five frequencies of large seeds: 0.1, 0.25, 0.5, 0.75 and 0.9. After 28 days we measured the proportions of the two size classes in the remaining seeds. Large seeds were always preferred to small seeds, even when they were at low frequency. Contrary to the predictions, at low seed density consumption was antiapostatic whereas at high seed density selection was independent of frequency. We discuss the causes and consequences of such selective responses expressed by seed predators.   © 2005 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2005, **84**, 137–142.

ADDITIONAL KEYWORDS: apostatic selection – frequency-independent selection – La Campana National Park, Chile – Mediterranean shrubland – seed density – seed predation.

INTRODUCTION

Frequency-dependent prey selection refers to the selective foraging responses of predators exposed to alternative prey that differ in their relative abundance (Greenwood, Blow & Thomas, 1984,Greenwood, Johnston & Thomas 1984; Greenwood, 1984; Allen, 1988). 'Apostatic selection' occurs when the commonest item is disproportionately consumed by predators, while 'antiapostatic selection' refers to a preference for rare prey. Sometimes selection may also be frequency-independent (Horsley *et al*., 1979; Willis *et al*., 1980; Allen & Anderson, 1984; Sherratt & Harvey, 1993).

Optimal foraging theory predicts that selection by predators will be apostatic if concentrating on the common form leads to the maximization of energy

(Hubbard *et al*., 1982; Greenwood, 1984; Allen, 1988). If the prey are varieties of the same species, the selective behaviour has the potential to modify the phenotypic distribution of the surviving prey, thus constituting a potentially powerful selective force leading to maintenance of variation (Clarke, 1962 in Allen, 1988; Endler, 1988; Rodríguez-Gironés & Vásquez, 2002).

Prey density may even change the magnitude and direction of frequency-dependent prey selection (Greenwood, 1969; Horsley *et al*., 1979; Willis *et al*., 1980; Allen, Raison & Weale, 1998; Weale *et al*., 2000). At low density, predators tend to prefer common prey as expected by the optimal foraging theory (Hubbard *et al*., 1982). However, at high prey densities, the conspicuousness of rare prey may be enhanced by the background of common prey, thereby making it more likely to be eaten (Horsley *et al*., 1979; Allen & Anderson, 1984). Thus, a change from apostatic to antiapo-

*Corresponding author. E-mail: jlcelis@uchile.cl

static prey selection is predicted as prey density increases. Most experiments that have tested the relationship between density and frequency-dependent selection have used wild birds as predators and artificial prey differing in colour (Cook & Miller, 1977; Horsley *et al*., 1979; Allen, 1988; Allen *et al*., 1998). As far as we are aware, there have been no studies using natural prey under field conditions.

In plants, seed predation is an ideal biotic interaction for examining frequency-dependent prey selection (Greenwood, 1985). Indeed, phenotypic attributes of seeds such as colours and odours have often been examined to determine the quantity and quality of seed predation (for experimental data, see Moegenburg, 1996; Hulme & Borelli, 1999). While seed size is regarded as an important cue for predators (Price & Reichman, 1987), this attribute has been overlooked in the context of frequency-dependence, yet it is well known that seeds are often selected by size, with larger ones being preferred (e.g. Hulme, 1993; Vander Wall, 1995; Moegenburg, 1996). In this study, we examined frequency-dependent seed size selection on seeds of *Cryptocarya alba* (Mol.) Looser (Lauraceae), a common endemic tree of central Chile. We conducted a field experiment at two contrasting seed densities. We predicted that frequency-dependent seed size selection would be apostatic at low density and antiapostatic at high density.

MATERIAL AND METHODS

STUDY SITE

The study was carried out at La Campana National Park (32°57′S 71°08′W), Ocoa sector, coastal range, central Chile. The vegetation is Mediterranean shrubland dominated by the tree species *Cryptocarya alba*, *Peumus boldus* Mol., *Quillaja saponaria* Mol. and *Lithraea caustica* (Mol.) H. et A. (Villaseñor & Serey, 1980/81). *Cryptocarya alba* (Lauraceae), is a 4–30 m high, shade-tolerant, evergreen tree, inhabiting south-facing slopes and humid ravines (Armesto & Martínez, 1978). Fruits are red to pink one-seeded drupes (Hoffmann, 1998) that vary in seed size, both within and among populations (0.1–3.4 g, Celis-Diez, Bustamante & Vásquez, 2004). The main seed predators that consume seeds of *C. alba* are rodents (including *Abrothrix longipilis* (Waterhouse)*, Abrothrix olivaceus* (Waterhouse)*, Octodon degus* (Mol.), *Oligoryzomys longicaudatus* (Bennett), and *Phyllotis darwini* (Waterhouse)) and birds (such as *Diuca diuca* (Mol.), *Curaeus curaeus* (Mol.)*, Mimus tenca* (Mol.), *Patagioenas araucana* (Lesson) and *Nothoprocta perdicaria* (Kittlitz)) (Bustamante & Vásquez, 1995; Celis-Diez, 2002). Other potential seed predators are exotic rodents such as *Mus musculus* (Linnaeus) and *Rattus*

rattus (Linnaeus) and exotic birds such as *Callipepla californica* (Shaw) (Celis-Diez, 2002).

SEED SIZE DISTRIBUTION

We collected a total of 15 000 seeds at random from 50 individual trees separated from one another by at least 50 m, with 300 seeds from each individual tree. As one fruit of *C. alba* contains only one seed, a seed was operationally defined as the whole dispersal unit, i.e. the seed plus its pericarp. We fresh-weighed all seeds collected to determine the seed size distribution (Fig. 1). We defined 'small seeds' as those falling within the lower 15% of the distribution (range 0.01–0.81 g, Fig. 1), and 'large seed' as those falling above the 85% percentile of the population distribution (1.81–3.6 g, Fig. 1). In this way, we maximized the difference between the two seed-size classes.

FIELD EXPERIMENT

Between 2 and 30 July 2001, we conducted a field experiment with five frequency treatments, each with a different proportion of large seeds: 0.1, 0.25, 0.50, 0.75 and 0.9. We used two contrasting seed densities, simulating the extremes variations observed in the field: ten seeds per m^2 and 100 seeds per m^2 (Bustamante & Simonetti, 2000). For each combination of seed density and frequency of large seeds, we arranged ten replicate stations, each 1 m^2, and arranged them in a grid of about 1.14 ha with each station 10 m apart. Each replicate was disposed at random but preventing the occurrence of three contiguous stations with identical treatments. We evaluated
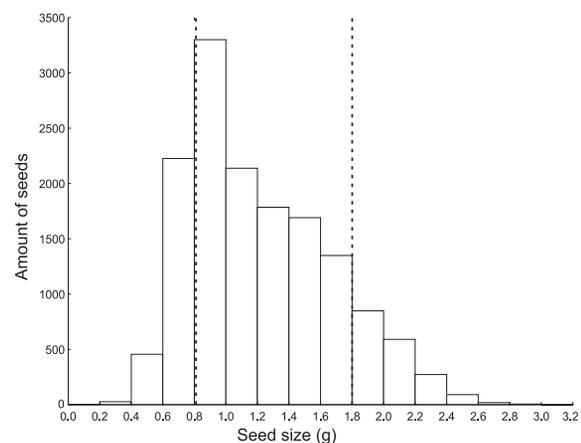

Figure 1. Seed size distribution of *Cryptocarya alba*, La Campana National Park (2001). Data was obtained from 50 parental trees (300 seeds per individual). Dotted lines represent percentiles 15 and 85%, respectively.

the number of seeds removed after 28 days. After that, no further seed removal was observed.

STATISTICAL ANALYSIS

We first constructed seed survival curves (following Lee, Desu & Gehan, 1975), to examine whether seed predators prefer large seeds to small seeds. For this analysis, we used only the 0.5 proportion of large seeds. As seed survival analysis registers the fate of seeds belonging to only one cohort, no confidence intervals can be obtained from this method (Lee *et al.*, 1975).

We tested for frequency-dependent seed size selection following the method of Greenwood & Elton (1979):

$$\frac{e_L}{e_S} = \left(V \frac{A_L}{A_S} \right)^b$$

where A_L/A_S, is the ratio of large to small seeds present in the environment and e_L/e_S, is the ratio of large to small seeds consumed by seed predators. From this model the parameter b evaluates frequency-dependence. If $b > 1$, then the selection is proapostatic; if $b < 1$, then the selection is antiapostatic; if $b = 1$, then seed selection is independent of frequency. On the other hand, the parameter V evaluates the bias of seed predators for a particular prey type. If $V > 1$, then a preference for large seeds exists; if $V < 1$, then a preference for small seeds exists and if $V = 1$, no preferences exist. To estimate b and $b \log V$, we conducted a log–log regression analysis. The parameter b was estimated through $t = (b - 1)/\text{SE}(b)$. The parameter V was tested through $t = b \log V/\text{SE}(b \log V)$ with $n - 2$ degrees of freedom (Greenwood & Elton, 1979).

A two-way ANOVA was used to evaluate the effect of seed density and the frequency of large seeds on the consumption of large seeds at day 28, and an ANCOVA was used to compare the slopes of the frequency-dependent seed size selection curves obtained from the two contrasting seed densities.

DATA CORRECTION

As the experiment was conducted during the rainy season (July–August) we corrected for possible losses caused by running water. We installed an additional ten experimental stations (protected by a metal fence, to avoid seed predation) with a 0.5 frequency of large seeds. Thus, five stations were presented at low seed density and five stations at high seed density. After 28 days, we evaluated the number of seeds removed. Run-off effects were detected only for low seed density, with about 4% of large seeds and 12% of small seeds removed by water. With this information, the experimental data were corrected before statistical analysis for all experimental frequencies.

RESULTS

SEED SURVIVAL

Seed survival was significantly lower in large seeds for both low and high seed density (average ± 2 SE, 0.30 ± 0.23 and 0.66 ± 0.19 of large and small seed, low density; 0.51 ± 0.16 and 0.83 ± 0.13 of large and small seed, high density; Log Rank L = 8.194; $P < 0.0001$ for low density, Fig. 2A; Log Rank L = 24.788; $P < 0.0001$ for high density, Fig. 2B).

FREQUENCY-DEPENDENCE

At low seed density, seed size selection was antiapostatic ($b = 0.77$; $t = -2.91$; d.f. = 1, 25; $P = 0.008$; Fig. 3A), with $b \log V$ significantly higher than zero ($t = 5.42$; d.f. = 25; $P < 0.05$). At high seed density, selection was independent of frequency ($b = 1.03$; $t = 0.02$; d.f. = 1, 39; $P = 0.50$; Fig. 3B), with $b \log V$ significantly higher than zero ($t = 10.81$; d.f. = 39; $P < 0.05$). We also detected significant differences in seed predation at different frequencies of seed sizes (log ratio eaten vs. log ratio available) between high and low seed densities (ANCOVA $F_{1,64} = 4.24$; $P < 0.04$).

There was a significant effect of the frequency of large seeds (ANOVA, $F_{4,61} = 9.69$, $P << 0.001$; Table 1), and seed density (ANOVA, $F_{1,61} = 11.89$, $P = 0.001$; Table 1) on e_L/e_S, with a significant interaction between these two factors (ANOVA, $F_{4,61} = 3.49$, $P = 0.012$).

DISCUSSION

The seed predators preferred large seeds of *Cryptocarya alba* at both low and high seed density. These results agree with theoretical expectations, which on optimal foraging grounds predict a preference for large seeds because of their higher energetic content relative to smaller seeds (Janzen, 1969; Vander Wall, 1995; Moegenburg, 1996; Geritz, 1998; Brewer, 2001). On the other hand, it has been widely documented that seed density can modify the rate of seed consumption (Notman, Gorchov & Cornejo, 1996; Hulme & Borelli, 1999). In this study, we found that seed density resulted both in increased consumption of large seeds and a change from antiapostatic to frequency-independent seed size selection. These results do not agree with theoretical models of frequency-dependence. Firstly, we expected apostatic selection at low seed density (Allen, 1968; Hubbard *et al.*, 1982) and we observed antiapostatic selection. Secondly, we expected that an increase of seed density would result in antiapostatic selection (Horsley *et al.*, 1979; Willis *et al.*, 1980; Church, Jowers & Allen, 1997; Allen *et al.*, 1998; Weale *et al.*, 2000; Fernandez-Juricic *et al.*,
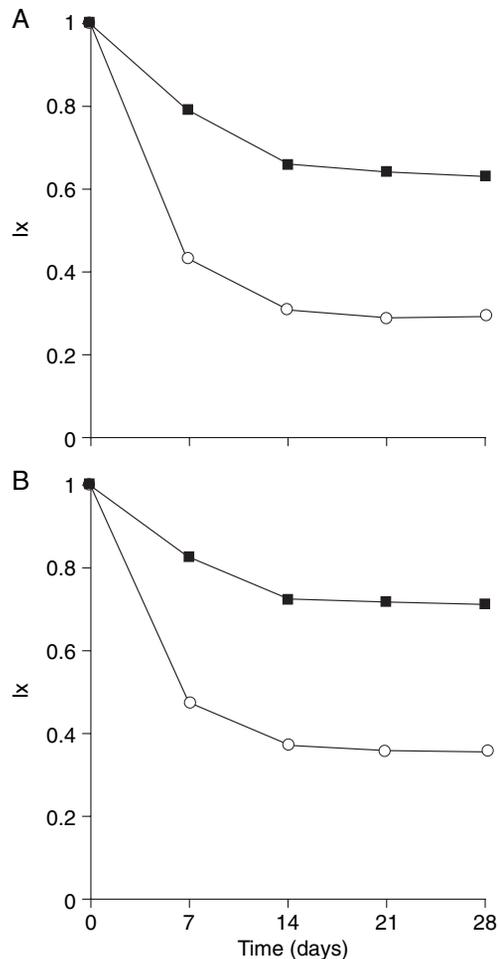
Figure 2. Seed survival (lx) of large and small seeds at equal relative abundance in *Cryptocarya alba,* La Campana National Park (2001). A, low density (ten seeds per m²); B, high density (100 seeds per m²). ●, small seeds; ○, large seeds.

Figure 3. Seed consumption of large seeds of *Cryptocarya alba* as a function of the frequency of large seeds available in the field, La Campana National Park. A, low seed density (ten seeds per m²); B, high seed density (100 seeds per m²). Broken lines represent no selective response ($b = 1$).

Table 1. Means ± standard deviation of the ratio of large to small seeds consumed at different frequency of large seeds, at two contrasting seed density (ten and 100 seeds per m²), after 28 days

Seed density			
Frequency	Low	High	Total
0.1	0.57 ± 0.45	0.32 ± 0.35	0.47 ± 0.42
0.25	0.74 ± 0.29	1.10 ± 0.72	0.88 ± 0.51
0.5	5.12 ± 3.28	2.60 ± 1.76	3.93 ± 0.70
0.75	13.77 ± 7.31	2.31 ± 2.04	8.48 ± 7.99
0.9	29.34 ± 26.80	8.75 ± 0.50	21.11 ± 22.63
Total	8.07 ± 14.19	2.61 ± 2.89	

2001) and we actually observed that increased seed density modified selection from antiapostatic to frequency-independence.

Antiapostatic prey selection could be the result of variation in individual preferences within a population of predators. Populations of predators rarely consist of individuals with identical preferences for particular prey types; while some individuals prefer to eat one particular type of prey others prefer to eat alternative prey (Allen & Anderson, 1984; Sherratt & Macdougall, 1995). Thus, the antiapostatic seed selection detected in our study may be consequence of phenotypic variation within and among predator species, where those that prefer the rarer prey (for reasons unrelated to rarity) have the greatest influence on preferences at population level (Sherratt & Macdou-
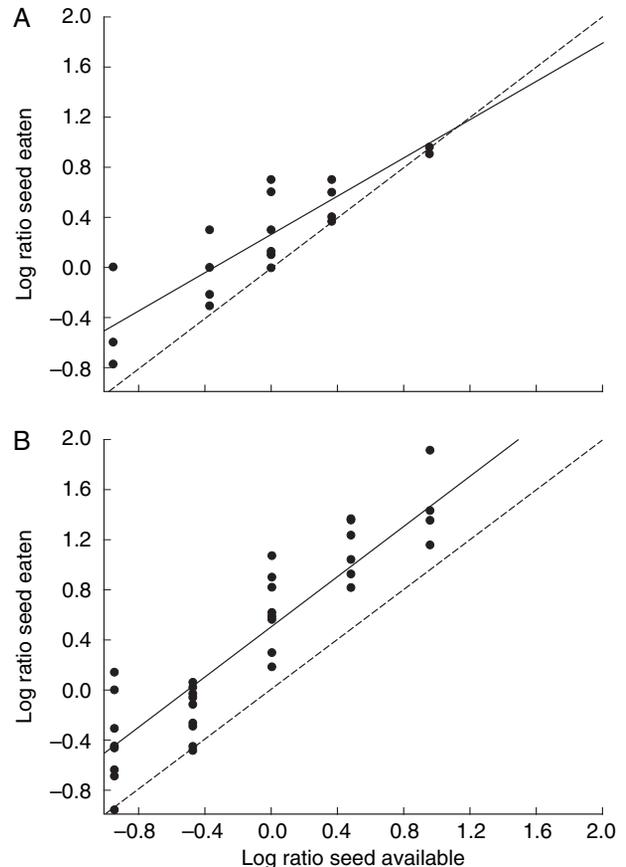
gall, 1995). Another explanation for the unexpected result may be that the seed density used to define the 'low seed density treatment' was still 'high' from the seed predator perspective and thus antiapostatic

selection resulted. However, the low seed density is probably much lower than values observed in the field. Seed predators are commonly faced with seed densities largely higher than the ten seeds per m^2 used in our experiment, ranging from 50 to 200 seeds per m^2 in the ground of forests (Bustamante & Simonetti, 2000).

From the results, we suggest two levels of seed selection. The first level is driven by seed density (among-patch seed selection); when seed density is increased, patches may be detected with greater ease. Much evidence suggests that solitary foragers can estimate patch quality, selecting high quality ones and thus maximizing energetic intake (Stephens & Krebs, 1986; Price & Reichman, 1987). A second level of seed selection is driven by seed size (within-patch seed selection). Independent of their frequency, large seeds were selected under all conditions, a response that can be explained if large seeds have a higher energetic content (Tripathi & Khan, 1990) and/or lower chemical defences compared to smaller ones (Janzen, 1978).

ECOLOGICAL IMPLICATIONS

A persistent preference for large seeds has important consequences for plant regeneration processes. Firstly, the advantages of a large seed to plant reproductive success is widely recognized, and is associated with higher germination probability (Weis, 1980; Zimmerman & Weis, 1983; Stanton, 1984), higher seedling vigour (Cipollini & Stiles, 1991; Weis, 1980), greater competitive abilities in late successional habitats (Salisbury, 1942) and higher herbivory resistance (Janzen, 1969). For example, the large seeds of *C. alba* have been demonstrated to produce larger seedlings with a higher recruitment probability (Chacón, Bustamante & Henríquez, 1998). We propose that seed predators, by preferring large seeds, have the potential to reduce the quality of the progeny and predict that the size and vigour of seedlings in the presence of seed predators should be significantly lower when compared with an environment without seed predators.

In summary, our results suggest that large seeds of *Cryptocarya alba* are an attractive resources for seed predators, especially when they are at a low frequency in the environment. These preferences are more persistent at high seed density, where large seeds are preferred independently of their frequency in the field. We propose that, by preferentially selecting large seeds, seed predators have the potential to modify the quality of the progeny. Further experiments are needed to elucidate whether seed predation has the potential to affect microevolutionary processes in *C. alba* populations, both within or between generations.

REFERENCES

Allen JA. 1968. Evidence for apostatic selection by wild passerines. *Nature* **220:** 501–502.

Allen JA. 1988. Frequency-dependent selection by predators. *Philosophical Transaction of the Royal Society of London* **319:** 485–503.

Allen JA, Anderson KP. 1984. Selection by passerine birds is anti-apostatic at high prey density. *Biological Journal of the Linnean Society* **23:** 237–246.

Allen JA, Raison HE, Weale ME. 1998. The influence of density on frequency-dependent selection by wild birds feeding on artificial prey. *Proceedings of the Royal Society of London B* **265:** 1031–1035.

Armesto JJ, Martínez J. 1978. Relations between vegetation structure and slope aspect in the mediterranean region of Chile. *Journal of Ecology* **66:** 881–889.

Brewer S. 2001. Predation and dispersal of large and small seed of a tropical palm. *Oikos* **92:** 245–255.

Bustamante RO, Simonetti JA. 2000. Seed predation and seedling recruitment in plants: the effect of the distance between parents. *Plant Ecology* **147:** 173–183.

Bustamante RO, Vásquez RA. 1995. Granivoría en *Cryptocarya alba* (Mol.) Looser (Lauraceae): los efectos del tipo de hábitat y la densidad de semillas. *Revista Chilena de Historia Natural* **68:** 117–122.

Celis-Diez JL. 2002. Tamaño de semillas y depredación frecuencia-dependiente. MSc Thesis, Facultad de Ciencias, Universidad de Chile.

Celis-Diez JL, Bustamante RO, Vásquez RA. 2004. Assessing frequency-dependent seed size selection: a field experiment. *Biological Journal of the Linnean Society* **81:** 307–312.

Chacón P, Bustamante RO, Henríquez C. 1998. The effect of seed size on germination and seedling growth of *Cryptocarya alba* (Lauraceae) in Chile. *Revista Chilena de Historia Natural* **71:** 189–197.

Church SC, Jowers M, Allen JA. 1997. Does prey dispersion

affect frequency-dependent predation by wild birds? *Oecologia* **111:** 292–296.

Cipollini M, Stiles E. 1991. Seed predation by the bean weevil *Acanthoscelides obtectus* on *Phaseolus* species: consequences for seed size, early growth and reproduction. *Oikos* **60:** 205–214.

Cook L, Miller P. 1977. Density-dependent selection on polymorphic prey – some data. *American Naturalist* **111:** 594–598.

Endler JA. 1988. Frequency-dependent predation, crypsis and aposematic coloration. *Philosophical Transactions of the Royal Society of London* **319:** 505–523.

Fernandez-Juricic E, Sanz R, Sallent A. 2001. Frequency-dependent predation by birds at edges and interiors of woodland. *Biological Journal of the Linnean Society* **73:** 43–49.

Geritz SA. 1998. Co-evolution of seed size and seed predation. *Evolutionary Ecology* **12:** 891–911.

Greenwood JJD. 1969. Apostatic selection and population density. *Heredity* **24:** 157–161.

Greenwood JJD. 1984. The functional basis of frequency–dependent food selection. *Biological Journal of the Linnean Society* **23:** 177–199.

Greenwood JJD. 1985. Frequency–dependent selection by seed predators. *Oikos* **44:** 195–210.

Greenwood JJD, Elton R. 1979. Analysing experiments on frequency–dependent selection by predators. *Journal of Animal Ecology* **48:** 721–737.

Greenwood JJD, Blow C, Thomas G. 1984. More mice prefer rare food. *Biological Journal of the Linnean Society* **23:** 211–219.

Greenwood JJD, Johnston JP, Thomas G. 1984. Mice prefer rare food. *Biological Journal of the Linnean Society* **23:** 201–210.

Hoffmann A. 1998. *Flora Silvestre de Chile, Zona Central*, 4th edn. Chile: Ediciones Fundación Claudio Gay.

Horsley DT, Lynch BM, Greenwood JJD, Hardman B, Mosely S. 1979. Frequency-dependent selection by birds when the density of prey is high. *Journal of Animal Ecology* **48:** 483–490.

Hubbard SF, Cook RM, Glover JG, Greenwood JJD. 1982. Apostatic selection as an optimal foraging strategy. *Journal of Animal Ecology* **51:** 625–633.

Hulme P. 1993. Post-dispersal seed predation by small mammals. *Symposia of the Zoological Society of London* **65:** 268–287.

Hulme P, Borelli T. 1999. Variability in post-dispersal seed predation in deciduous woodland: relative importance of location, seed species, burial and density. *Plant Ecology* **145:** 149–156.

Janzen D. 1969. Seed eaters vs seed size, number, toxicity and dispersal. *Evolution* **23:** 1–27.

Janzen D. 1978. The ecology and evolutionary biology of seed chemistry as relates to seed predation. In: Harborne JB, ed. *Biochemical aspects of plant animal interaction*. New York: Academic Press.

Lee ET, Desu MM, Gehan EA. 1975. A Monte-Carlo study of the power of some two sample tests. *Biometrika* **62:** 425–532.

Moegenburg S. 1996. *Sabal palmetto* seed size: cause of variation, choice of predators and consequences for seedlings. *Oecologia* **106:** 539–543.

Notman E, Gorchov D, Cornejo F. 1996. Effect of distance, aggregation, and habitat on levels of seed predation for two mammals–dispersed neotropical rain forest tree species. *Oecologia* **106:** 221–227.

Price M, Reichman O. 1987. Distribution of seeds in Sonoran desert soils: implications for heteromid rodent foraging. *Ecology* **68:** 1797–1811.

Rodríguez-Gironés MA, Vásquez RA. 2002. Selección dependiente de la frecuencia. In: Soler M, ed. *Evolución: la base de la biología*. Granada, España: Editorial Proyecto Sur.

Salisbury EJ. 1942. *The reproductive capacity of plants*. London: Bell & Sons.

Sherratt TN, Harvey IF. 1993. Frequency-dependent food selection by arthropods: a review. *Biological Journal of the Linnean Society* **48:** 167–186.

Sherratt TN, Macdougall AD. 1995. Some population consequences of variation in preference among individual predators. *Biological Journal of the Linnean Society* **55:** 93–107.

Stanton M. 1984. Seed size variation in wild radish: effect of seed size on components of seedling and adult fitness. *Ecology* **65:** 1105–1112.

Stephens DW, Krebs JR. 1986. *Foraging theory*. Princeton, NJ: Princeton University Press.

Tripathi RS, Khan ML. 1990. Effects of seed weight and microsite characteristics on germination and seedling fitness in two species of *Quercus* in a subtropical wet hill forest. *Oikos* **57:** 289–296.

Vander Wall S. 1995. The effect of seed value on the catching behavior of yellow pine chipmunk. *Oikos* **74:** 533–537.

Villaseñor R, Serey I. 1980/81. Estudio fitosociológico de la vegetación del cerro La Campana (Parque Nacional La Campana en Chile central). *Atti Istituto Di Botanica Laboratorio Crittogamica Università Di Pavia, Serie 6* **XIV:** 69–91.

Weale ME, Whitwell D, Raison HE, Raymond DL, Allen JA. 2000. The influence of density on frequency-dependent food selection: a comparison of four experiments with wild birds. *Oecologia* **124:** 391–395.

Weis IM. 1980. The effects of propagule size on germination and seedling growth in *Mirabilis hirsuta*. *Canadian Journal of Botany* **60:** 1868–1874.

Willis A, McEwan J, Greenwood JJD, Elton R. 1980. Food selection by chicks: effect of color, density, and frequency of food types. *Animal Behavior* **28:** 874–879.

Zimmerman J, Weis IM. 1983. Fruit size variation and its effect on germination and seedling growth in *Xanthium strumarium*. *Canadian Journal of Botany* **61:** 2309–2315.