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**TAMAÑO DE SEMILLAS EN *Cryptocarya alba* (MOL.) LOOSER
(LAURACEAE) Y CONDUCTAS SELECTIVAS DE SUS GRANÍVOROS EN EL
MATORRAL DE CHILE CENTRAL.**

Tesis

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Universidad de Chile

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Para optar al grado de

Magíster en Ciencias Biológicas con Mención en Ecología y Biología Evolutiva



Facultad de Ciencias

Por

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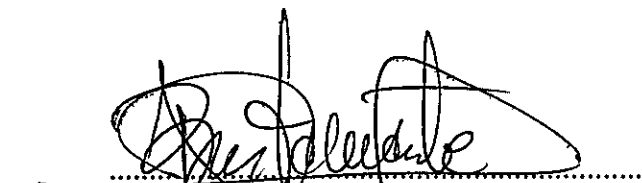
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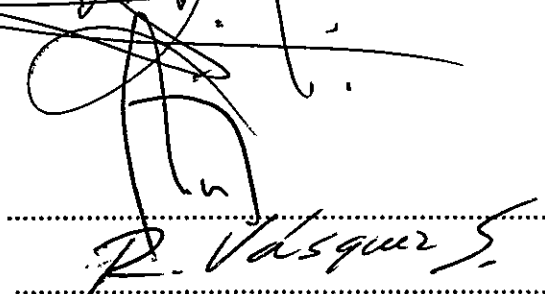
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RESUMEN

El tamaño de semillas afecta la probabilidad de ser depredadas. Semillas grandes serían preferentemente consumidas respecto de semillas más pequeñas. Sin embargo, la frecuencia relativa de los diferentes tamaños, podría modificar estas respuestas selectivas. Así, los depredadores de semillas podrían preferir tamaños más frecuentes. Por otro lado, la densidad de semillas puede modificar las conductas selectivas. Densidades muy altas, producen un efecto de fondo, estimulando el consumo de tamaños menos abundantes. Pusimos a prueba esta predicción, realizando un experimento de campo con semillas de *Cryptocarya alba*, en el P.N. La Campana.

Se dispusieron semillas pequeñas y grandes (percentil 15% superior e inferior) en dos densidad extremas (10 y 100 semillas/m²), en proporción de semillas grandes: 0.1, 0.25, 0.5, 0.75 y 0.9. Luego de 28 días, se evaluó la proporción de semillas remanentes.

Los resultados indican que en todos los tratamientos, las semillas grandes son preferentemente consumidas aún en bajas abundancias relativas, favoreciendo la adecuación de las de menor tamaño. A densidades bajas el consumo es de tipo anti-apostática. Cambios en la densidad de semillas, modifica el tipo de selección desde selección anti-apostática hacia selección frecuencia-independiente, pero con un fuerte sesgo hacia las semillas grandes.

INTRODUCCIÓN GENERAL

La granivoría, constituye una de las causas principales de mortalidad de semillas (Janzen, 1969; 1971; Harper, 1977; Crawley, 1992), pudiendo afectar el éxito reproductivo de las plantas, los patrones de reclutamiento poblacional (Wilson & Whelan, 1990; Crawley, 1992; Myster y Pickett, 1993), así como la distribución espacial de las plantas y la estructura comunitaria (Hulme & Hunt, 1999). La mortalidad de semillas por granivoría puede estar determinada por diversos factores tales como el tipo de hábitat (Webb & Willson, 1985; Bustamante & Vásquez, 1995), la riqueza, abundancia y eficiencia de los consumidores (Willson & Whelan, 1990) y la distribución y abundancia de las semillas en el espacio (Harper, 1977; Schupp, 1992; Nathan, & Muller-Landau, 2000).

Atributos fenotípicos de las semillas, tales como tamaño, coloración y contenidos químicos, constituyen otro importante factor que podría afectar la intensidad en el consumo de semillas (Hare, 1980; Hulme, 1994; Moegenburg, 1996). Por ejemplo, insectos granívoros, son particularmente selectivos frente a semillas rugosas y grandes (Gómez & Zamora, 1994 en Moegenburg, 1996), sin embargo, otros insectos, seleccionan preferentemente semillas pequeñas para alimentarse, debido a que serían más blandas que las semillas grandes (Hare, 1980).

El tamaño de semillas producidas por una especie de planta, puede variar significativamente, tanto a nivel individual como poblacional (Winn, 1988; Silvertown, 1989; Moegenburg, 1996; Mojonnier, 1998). La existencia de esta variación fenotípica, sugiere que los granívoros podrían expresar conductas de forrajeo selectivo en función

del tamaño de las semillas. Al respecto, algunos estudios, han evidenciado que los mamíferos granívoros tienden a consumir frecuentemente semillas de mayor tamaño (Vander Wall, 1990). Este tipo de semillas tendrían un mayor valor energético, por lo que constituiría un foco de atracción para los consumidores (Molau et al. 1989). Sin embargo, debido a que existen semillas de otros tamaños en el suelo, las preferencias de los granívoros sobre las semillas grandes podrían verse afectadas por la existencia de recursos alternativos, determinando por ejemplo, que el consumo se concentre preferentemente sobre tamaños de semillas menores, si estos son más frecuentes. En este caso, un alto consumo de semillas de tamaños pequeños, compensan así un menor retorno energético por unidad de presa (Greenwood, 1984).

Un marco teórico apropiado para estudiar estas conductas selectivas de los depredadores lo constituyen los modelos de selección frecuencia-dependiente. Estos modelos intentan describir por ejemplo, que los depredadores pueden modificar sus preferencias sobre ciertas presas en función de las abundancias de las presas alternativas. Por ejemplo, ellos podrían concentrar su consumo sobre una presa cuando ésta es común y tenderían a rechazarla cuando ésta es rara (selección "pro-apostática", Greenwood, 1984; Allen, 1988). Contrariamente, su consumo preferente podría ser sobre las presas raras, ignorando las presas más comunes (selección "anti-apostática", Greenwood, 1984; Allen, 1988). Así, la selectividad de presas se hace frecuencia-dependiente, y por ende tiene el potencial para constituirse en una presión selectiva que modifica las frecuencias fenotípicas de un rasgo, como una consecuencia de sobrevivencia diferencial de fenotipos (Clarke, 1962 en Allen, 1988; Murdoch, 1969). No existen estudios de

depredación de semillas en el marco de la selección frecuencia-dependiente que evalúen mortalidad de semillas según tamaño.

La densidad de las presas podría modificar la magnitud y el sentido de la selección frecuencia-dependiente por parte de un depredador (Clarke, 1962 en Allen, 1988). Así, la selección apostática debería ser más fuerte ante densidades intermedias y muy débil ante densidades extremas (bajas y altas): resultado que es explicado sobre la base de la conspicuidad de la presa, ya que a una densidad de presas muy alta, las presas más comunes o de mayor abundancia producen un efecto de fondo o "background" sobre las presas raras o menos comunes, haciendo resaltar su presencia. Algunos resultados de experimentos sobre depredación de presas coloreadas artificialmente y dispuestas a distintas densidades han evidenciado que la selección pro-apostática, ante un aumento en la densidad de presas, se invierten hacia selección anti-apostática (Cook & Miller, 1977). Este efecto de fondo o "background" ha sido trabajado empíricamente considerando solo presas que difieren en color, sin embargo, podría ser relevante también si consideramos otros atributos de las presas, en los cuales la percepción visual por depredadores es importante para su localización. En el caso de semillas de diferente tamaño, los depredadores podrían también distinguir sus presas preferidas por la vista, más aún si éstas no difieren químicamente de las no preferidas como es el caso de semillas de una misma especie. A la fecha, no existen estudios que examinen si existe selección frecuencia dependiente por parte de los depredadores en relación al tamaño de semillas y si esta selección puede ser modificada por la densidad de las semillas.

En esta tesis, se pretende examinar si bajo condiciones naturales los depredadores de semillas expresan conductas selectivas en función del tamaño de semillas, frecuencia

relativa según tamaño y densidad de semillas. Se propone que desde una aproximación de la teoría de forrajeo óptimo, el consumo de semillas grandes, debiera ser pro-apostática es decir, desproporcionadamente alta cuando estas son abundantes y desproporcionadamente baja cuando estas son poco abundantes. En tanto, se propone que las semillas más abundantes pueden generar un efecto fondo o “background” y por lo tanto aumentos en la densidad total de semillas debieran modificar la intensidad y dirección de la selección frecuencia-dependiente desde una selección por-apostática a una selección anti-apostática.

Se utilizará como sujeto de estudio a *Cryptocarya alba* (Lauraceae), una de las especies más abundantes del matorral de Chile central, de la cual se conocen aspectos poblacionales de su historia natural, y sus interacciones biológicas con organismos dispersores y depredadores de semillas (ver apéndice 1; Bustamante y Vásquez, 1995), antecedentes generales que la hacen un sujeto apropiado para este tipo de estudios.

El objetivo general de esta tesis es evaluar si los depredadores de semillas expresan conductas selectivas en función del tamaño, frecuencia relativa y densidad de semillas.

Los objetivos específicos son:

- Determinar si el tamaño de semillas per se es un atributo seleccionado por los depredadores de semillas.
- Determinar si existe selección frecuencia-dependiente en el consumo de semillas de distintos tamaños.
- Determinar si la densidad de semillas modifica el resultado de la selección frecuencia-dependiente ejercida por los depredadores de semillas.

CAPITULO I

SEED PREDATION AND FREQUENCY-DEPENDENT SEED SIZE
SELECTION IN *Cryptocarya alba* (MOL.) LOOSER (LAURACEAE): TESTING
THE BACKGROUND EFFECT

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ABSTRACT

Seed size affects the probability of seed predation. Large seed should be more preferred than small seeds. Nevertheless, the relative frequency of different sizes could modify selective responses of seed predators. This implies that seed predators could prefer more common seed sizes. Moreover, if seed densities modify selective behaviors of seed predators, we expect that at high seed density, seed consumption will be concentrated on rare seed sizes. We tested this prediction, doing a field experiment with *Cryptocarya alba* seeds at PN La Campana.

We disposed of large and small seeds (percentile 15 % upper and lower of the seed size distribution) in two contrasting extreme seed densities (10 and 100 seeds/m²), in five proportion of large seeds: 0.1, 0.25, 0.5, 0.75 and 0.9. After 28 days we evaluated the proportion of remnant seeds.

Our results indicated that in all treatments of large seeds were preferred and more consumed than small seeds, even when they were at low relative abundance, favoring fitness of small seeds. At low seed density, consumption was in an anti-apostatic manner. Changes in seed density, from low to high seed density; modify the kind of anti-apostatic selection towards frequency-independent selection.

Keywords: Anti-apostatic selection, frequency-independent selection, background effect, seed predation, seed density, Mediterranean shrubland, La Campana National Park, Chile.

INTRODUCTION

Frequency-dependent prey selection refers to a selective foraging response of predators faced to alternative preys that differs in relative abundance (Greenwood, 1984; Allen, 1988). Pro-apostatic selection occurs when predators consume disproportionately common prey types. Anti-apostatic selection occurs when predators consume disproportionately rare preys and no prey selection as a function of relative abundance of prey (i.e. frequency-independent selection) may also occur (Sherratt & Harvey, 1993).

Optimal foraging theory predicts pro-apostatic selection by predators as in this way they minimize the searching time and/or maximize their energetic intake (Hubbard et al. 1982; Visser 1981 in Weale 1992; Greenwood 1984; Allen 1988). This selective behavior has the potential to modify the phenotypic distribution of surviving preys, thus being a potential selective force (Clarke, 1962 in Allen, 1988, Murdoch, 1969, Allen 1988; Endler 1988; Rodríguez-Gironés & Vásquez, in press). Prey density plays a mayor role in the decision-making of a predator as well. Moreover, prey density may change the magnitude and directions of frequency-dependent prey selection (Clarke 1962 in Allen 1988; Weale et al. 2000; Allen 1988; Sherratt & Harvey 1993). Effectively, at high densities, common prey enhances the conspicuity of rare preys, making them more attractive relative to a situation of a lower prey density ("background effect" *sensu* Greenwood, 1984; Greenwood et al. 1984a, b; Church et al. 1997; Allen et al 1998). In this case, changes from a pro-apostatic to anti-apostatic prey selection are predicted and rare preys become more vulnerable to predators when they are increased at high densities. The few studies conducted to test the background effect, have effectively

demonstrated an over-consumption of rare preys at high prey densities, using wild birds as predators and artificial preys that differed in colors (see Cook & Miller, 1977; Allen, 1988; Allen et al. 1998).

Selective responses of seed predators are regarded appropriate to examine frequency-dependence prey selection (Greenwood, 1985). Phenotypic attributes of seeds such as colors and odors have often been examined to determinate the quantity and quality of seed predation (Janzen, 1971; for experimental data see Hare, 1980; Hulme, 1994; Moegenburg, 1996; Hulme & Borelli, 1999). Although seed size is regarded a key signal used by predators to orient their preferences (Price & Reichman, 1987), up to date, it has never been examined in seed predation in the context studies of frequency-dependent selection. This fact is curious as it is largely known, that large seeds are presumably preferred over small seeds (for experimental data see Molau et al. 1989; Vander Wall, 1994, 1995; Mojonier, 1998; Hulme, 1993). In this study, we examined frequency-dependent seed size selection upon seeds of *Cryptocarya alba* (Mol.) Looser (Lauraceae), a common endemic tree of Central Chile. We conducted a field experiment considering two contrasting seed densities, under the assumption that change in seed density will change the magnitude and sign of frequency-dependent seed size selection.

MATERIALS AND METHODS

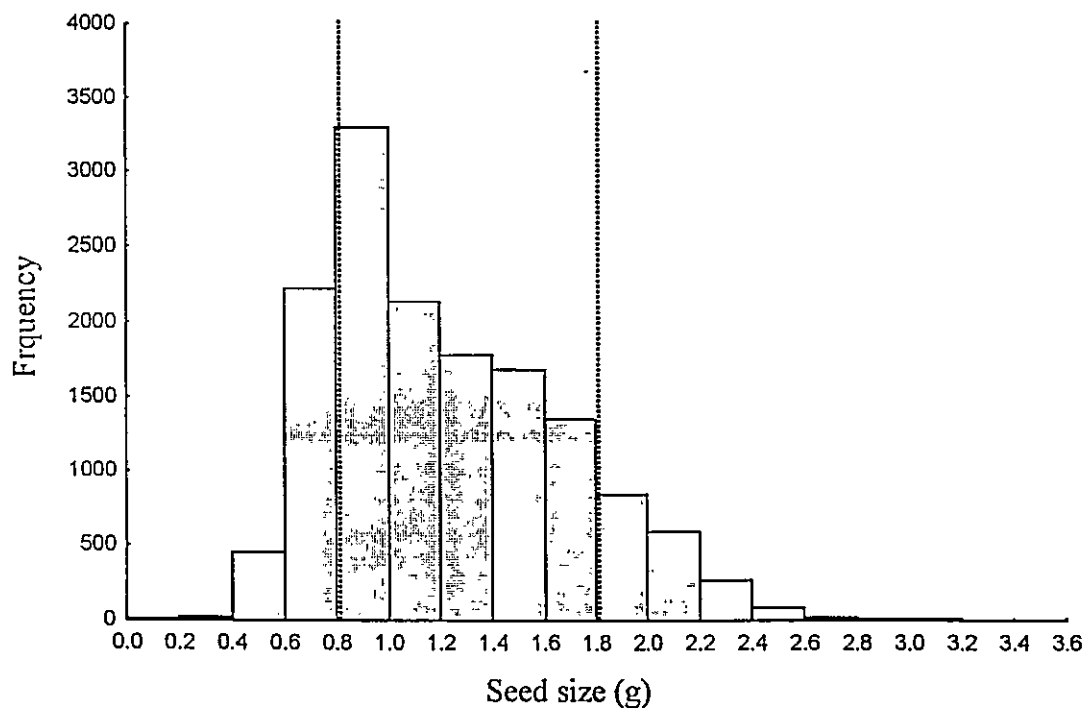
Study site:

This study was carried out at La Campana National Park (32° 57'S 71° 08'O), Ocoa sector, coastal range, Central Chile. The vegetation is characterized by a Mediterranean shrubland where tree species such as *Cryptocarya alba*, *Peumus boldus* Mol., *Quillaja saponaria* Mol. and *Litrhaea caustica* (Mol.) H. et A. are dominant (Villaseñor & Serey, 1980/81). *Cryptocarya alba* (Lauraceae), is a 4 – 30 m height, shade-tolerant evergreen tree (Armesto & Pickett, 1985), living in 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 between populations (0.1 a 3.4 g, see appendix 2). The main seed predators are rodents (including *Abrothrix longipilis* (Waterhouse), *Abrothrix olivaceus* (Waterhouse), *Oligoryzomys longicaudatus* (Bennett), and *Phyllotis darwini* (Waterhouse)) and birds (such as *Lophortyx californica* (Shaw) and *Diuca diuca* (Molina)), (Bustamante & Vásquez, 1995, see appendix 1).

Seed size distribution:

We collected 15.000 seeds from 50 individual trees; 300 randomly selected seeds per tree. In this study, a seed was operationally defined as a whole dispersal unit: the seed plus its pericarp. We obtained the fresh weight to represent the seed size distribution (Fig. 1). We defined a “small seed”, if it was within the lower 15% of the distribution (i.e., range 0.01–0.81 g, Fig.1), and a “large seed”, if it was within the higher 15% of the population distribution (i.e., 1.81–3.6 g, Fig. 1).

Figure 1. Seed size distribution of *Cryptocarya alba* at La Campana National Park (2001). Data were obtained from 50 parental trees (300 seed per individual). Dotted lines represent percentile 0.15 and 0.85 respectively.



Experimental design:

During June and August 2001 we set up a field experiment with five treatments, each with different frequencies of large seeds: 0.1, 0.25, 0.50, 0.75 and 0.9. We disposed ten replicates per treatment at two contrasting seed densities, simulating the extremes variations observed in the field: 10 seeds/m² and 100 seeds/m² (Bustamante & Simonetti, 2000). For each combination of density and frequency, 100 stations (1 m²) were arranged in a rectangular grid (i.e., 290 x 30 m, 1,14 hectares), located 10 m apart. Each treatment of frequency and seed density was disposed at random but preventing to install three neighbor stations with equal frequency and seed densities. We evaluated the

number of seeds removed after 28 days. Lately, no significative seed removal has been observed (see appendix 2).

Statistic analysis:

We conducted the following analysis:

a) Seed survival curves using Log Rank analysis to compare two samples (Lee, Desu, & Gehan, 1975) to examine if seed predators prefer large over small seeds. For this analysis, we used treatment of large seeds at the proportion 0,5.

b) Seed size selection analysis following the model 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 large / small seeds present in the environment and e_L / e_S , is the ratio of large / small seed present in the diet. The parameter b evaluates the type of frequency-dependence. If $b > 1$, then the selection is pro-apostatic; if $b < 1$, then the selection is anti-apostatic; if $b = 1$, then there exist no seed selection (frequency-independent). The parameter V evaluates the bias of seed predators with independence of frequency. If $V > 1$, there is a bias to large seeds; if $V < 1$, there is a bias to small seeds; if $V = 1$, there is no bias at all. To test the statistical significance of b and V , we conducted a log-log regression analysis (Greenwood & Elton 1979). The parameter b was docimated through $t = (b^{\wedge} - 1) / \text{S.E.} (b^{\wedge})$. The parameter V was docimated through $t = b \log V / \text{S.E.} (b \log V)$ with $n - 2$ d.f.

c) ANOVA, to evaluate the effect of either seed density and the frequency of large seeds on seed consumption by seed predators. The response variable was the ratio e_L/e_S .

d) We conducted an ANCOVA to compare the frequency-dependent seed size selection between the two contrasting seed densities.

Data correction

As the experiment was conducted during the months of maximal precipitations (July-August), we corrected possible effects of run-off by water. We installed additional five experimental units (protected by a metallic fence, to avoid seed predation) at a proportion 0.5: 0.5 large: small seeds. The five experimental units were disposed at low and high seed density respectively. After 28 days, we evaluated the number of removed seeds.

RESULTS

Run-off effects:

Run-off effects were detected only at low seed density. About 4% of large seeds and 12 % of small seeds were removed by water. With this information, all experimental data were corrected before analysis

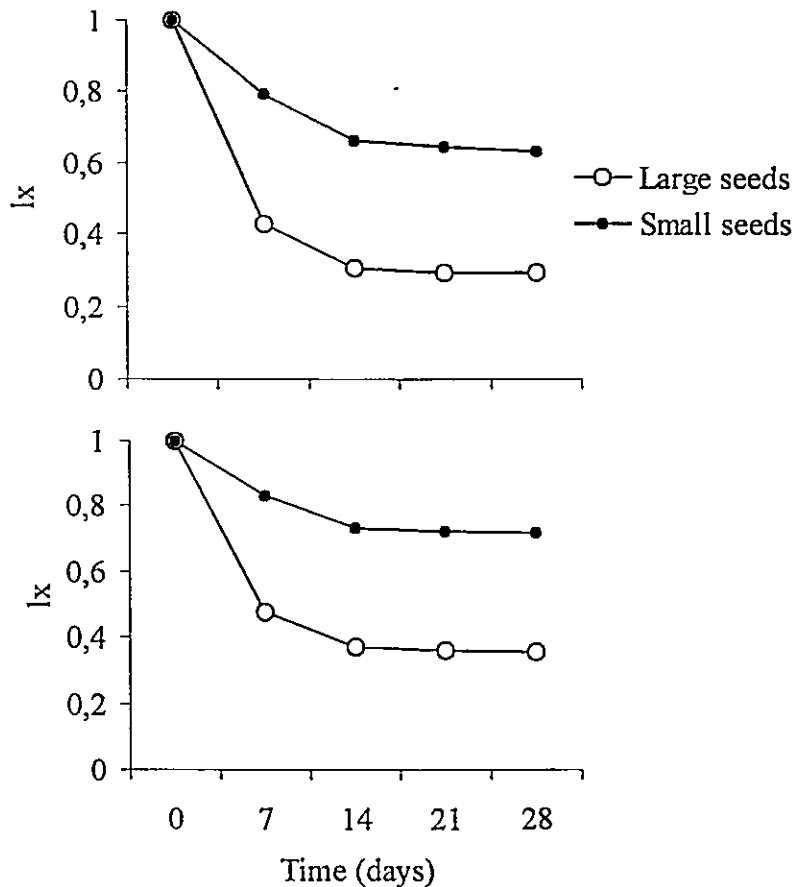
Seed survival:

Seed survival was significantly lower in large seeds at both seed densities (Table 1). These differences were significant (Log Rank L = 8.194; $P < 0.0001$ for low density see Fig. 2a; Log Rank L = 24.788; $P < 0.0001$ for high density see Fig. 2b).

Table 1. Survival of large and small seed at equal relative abundance, with two contrasting seed density.

Seed size	Seed density	
	Low	High
Large	0.30 ± 0.11	0.47 ± 0.07
Small	0.66 ± 0.09	0.82 ± 0.05

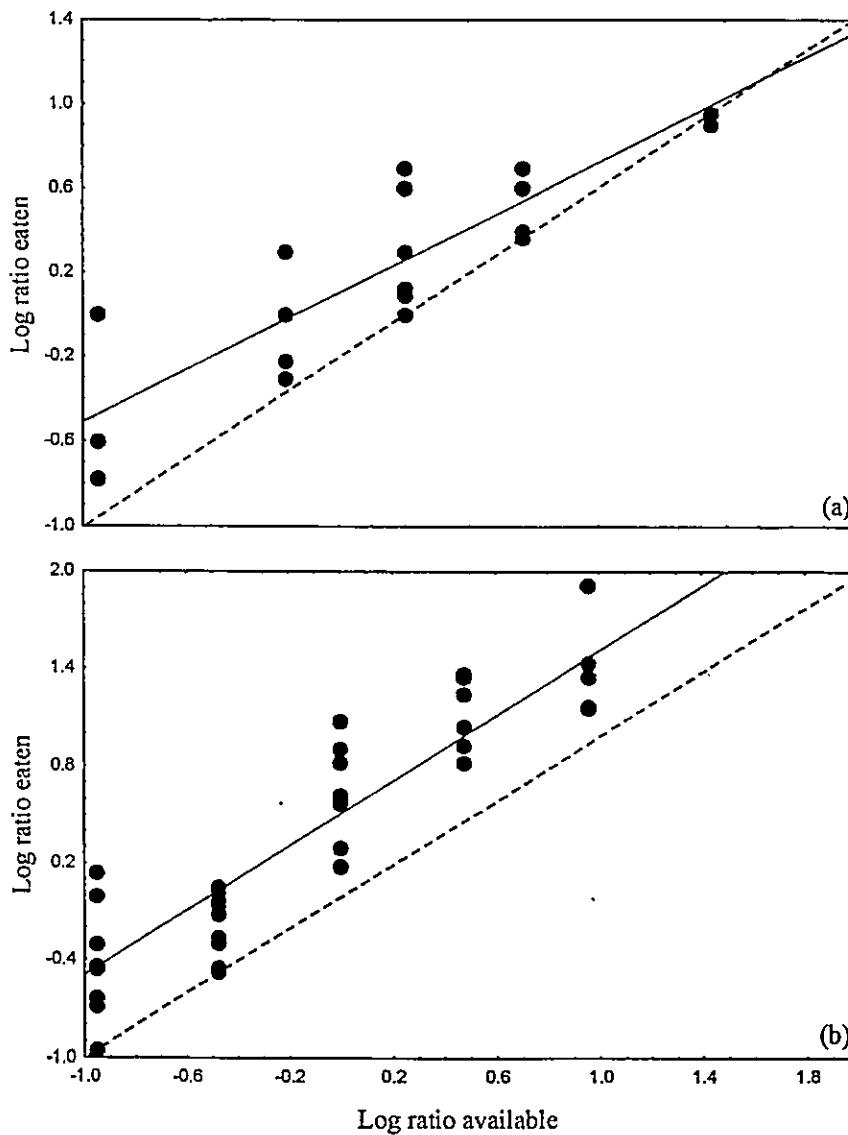
Figure 2. Seed survival of large and small seeds at equal relative abundance in *Cryptocarya alba* at La Campana National Park. (a) Low density (i.e. 10 seed / m²) and (b) High density (i.e. 100 seed / m²),.



Frequency-dependence:

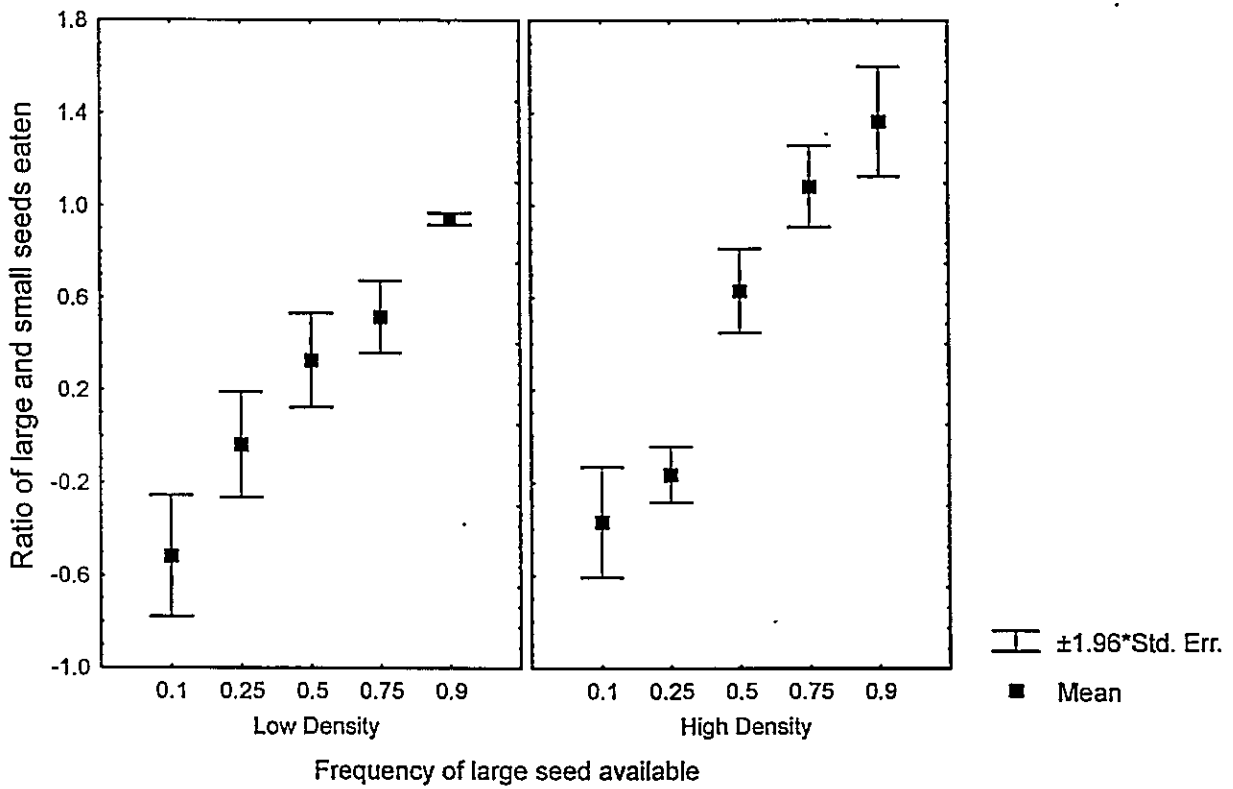
At low seed density, we detected anti-apostatic seed size selection ($b = 0.77$; $t = -2.91$; d.f. = 1, 25; $P = 0.008$; Fig. 3a), being $b \log V$ significantly higher than 0 ($t = 5.42$; d.f. = 25; $P < 0.05$). At high seed density, we detected frequency-independent seed size selection ($b = 1.03$; $t = 0.02$; d.f. = 1, 39; $P = 0.50$; Fig. 3b), being $b \log V$ significantly higher than 0 ($t = 10.81$; d.f. = 39; $P < 0.05$). We also detected significant slope differences between high and low seed densities (ANCOVA $F_{1,64} = 4.24$; $P < 0.04$).

Figure 3. Seed consumption of large seeds in *C. alba* as a function of the frequency of large seeds available in the field, at La Campana National Park. (a) Low seed density (i.e. 10 seed / m²) and (b) high seed density (i.e. 100 seed / m²). For comparison, dotted lines represent no selective response ($b = 1$).



We detected a significant effect for the frequency of large seeds on e_L/e_S (ANOVA, $F_{4, 58} = 66.89$, $P \gg 0.001$; Table 2), and for seed density (ANOVA, $F_{1, 58} = 14.59$, $P = 0.00033$; Fig. 4). Moreover, significant interaction was detected between these two factors (ANOVA, $F_{4, 58} = 3.07$, $P = 0.023$; Fig. 4).

Figure 4. Effect of the frequency of large seeds and seed density over the ratio of large and small seeds removed by seed predators.



DISCUSSION

Seed predators of *C. alba* prefer large seeds, as seed survival and $b \log V$ analysis indicate. These results agree with theoretical and empirical expectations, which predict preferences on large seeds due to its higher energetic content relative to smaller seeds (Janzen, 1969; Hare, 1980; Vander Wall, 1995; Moegenburg, 1996; Geritz, 1998; Brewer, 2001). It has been widely documented that seed density could modify seed consumption (Willson & Whelan, 1990; Notman et al. 1996; Hulme & Borelli, 1999). Moreover, in this study, we found that seed density increased consumption of large seeds and changed the intensity and direction of frequency-dependent selection from anti-apostatic to frequency-independent seed size selection. These results do not agree with theoretical expectations: a) we expected pro-apostatic seed size selection (Allen, 1968; Hubbard et al, 1982) and we observed anti-apostatic selection. b) we expected that seed density modifies seed selection from pro-apostatic to anti-postatic (background effect, *sensus* Horsley et al. 1979; Willis et al. 1980; Church et al. 1997; Allen et al. 1998; Fernandez-Juricic et al. 2001), and we observed that seed density modifies seed selection from anti-apostatic to frequency-independent selection.

We suggest the existence of two levels of seed selection. The first level is affected by seed density (between patch selection); when we increased seed density, the patch was detected easily and seed consumption of large[†] seeds was significantly enhanced. Numerous evidence suggest that solitary foragers can estimate patch quality, thus maximizing the energetic intake in high quality patches (Stephens & Krebs, 1986; Price & Reichman, 1987). A second level is affected by seed size (intra-patch selection).

Independent of their frequency, large seeds were always selected. This selective response may be explained because large seeds have a higher energetic content and /or lower chemical defenses compared to small seeds (Janzen, 1978). In summary, a patch of high seed density could attract a higher number of seed predators than a patch of low seed density. Once patch selection has occurred predators will select larger seeds inside patches at every frequency. This bias may be the result of a search image on predators generated by a previous experience (Krebs & Davies, 1981).

Frequency-independent selection has been detected in many studies of predation, assuming $V = 1$ (see Sherratt & Harvey, 1993). However, no studies have detected the case $V > 1$ (i.e. $b \log V > 0$). Although this situation has been theoretically proposed (Greenwood 1985), to our knowledge, this is the first study that detected empirically frequency-independent selection biased to one specific prey phenotype.

It is possible that the rejection of the background hypothesis is explained because others factors rather than seed size modifies the selective responses of predators. Such as, for instance, the chemical substances of seeds may affect seed predators preferences (see Janzen, 1978, Blate et al, 1998). We suggest that chemical substances may be involved in seed selection. Thus, at high seed density, the existence of a dilution effect (Krebs & Davies, 1981) is possible, where rare seeds (i.e. large seeds) are "diluted" inside the common seed (i.e. small seeds). This effect has been widely documented in prey-predator dynamics (Landeau & Terborgt, 1986), and supports the adaptive advantage to live in groups (Watt & Chapman, 1998; Landeau & Terborgt, 1986). By analogy, this may be the case of seeds.

Ecological implications:

A persistent preference on large seeds, favoring the escape of small ones, implies important consequences for plant regeneration processes. Firstly, the advantages of large seed on plants reproductive success is widely recognized, expressed as a higher germination probability (Schaal, 1980; Weis, 1980; Zimmerman & Weis, 1982; Dolan, 1984; Stanton, 1984; Vera, 1997), higher seedling vigor (Cipollini & Stiles, 1991; Weis, 1980; Bonfil 1998), greater competitive abilities in late successional habitats (Salisbury, 1942) and higher herbivory resistance (Janzen, 1969, 1971; Baker, 1972; Bonfil, 1998), and finally in plant recruitment (Harper 1977; Shaal 1980; Winn 1988; Silvertown 1989). This is the case of *C. alba*, as well, where it has been demonstrated that large seeds have a greater recruitment probability (see Chacón et al 1998; Chacón and Bustamante 2001). Therefore, seed predators, by preferring large seeds, are indirectly reducing the quality of the progeny. Through this result, seed density should be an important factor that modulates predators seed selection. In addition, it has been documented a wide variation for *C. alba* in seed density (Bustamante & Simonetti 2000): a) with high density under parental and perch trees and low density towards edges or gaps at the end of seed shadow and b) high temporal variation among individual seed production (Bustamante, unpublished data). This variation could imply that there may exist spatial zones with higher selective pressures favoring small seeds relative to the zones of lower seed density (the tail of the seed shadow).

In summary, our results suggest that large seeds of *Cryptocarya alba* are extremely attractive resources for predators, probably because of its higher energetic content. These preferences are reinforced at high seed density where they are preferred across different frequencies of large seeds. Therefore, we rejected the background effect and we detected changes from anti-apostatic to frequency-independent seed size selection.

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Appendix 1. Granivores assemblage of PN La Campana, including birds and rodents. We include additional information of diet and habitat use. **Diet:** G: Granivores; F: Frugivores; I: Insectivores; H: Herbivores; M: Micofagus; O: Omnivorous. **Wta:** Weight of the adult. **Habitat:** M: Matorral; G: Grassland; F: Forest; HD: Human Dwelling, ni: No information. (Redford & Eisenberg, 1992; Araya & Millie, 1998; Riveros & Thiele, 1982).

a) Small mammals	Diet	Wta (gr)	Regime	Habitat	Freq. (%)
<i>Akodon</i>					
<i>longipilis</i> (Waterhouse)	G	38.2	Nocturnal	M, G, F	5.6 *
<i>Mus musculus</i> (Linnaeus)	G, I, H (O)	17–25 ‡	Nocturnal	M, G, HD	5.5 *
<i>Octodon degus</i> (Molina)	H, G	215	Daily	M, G	§ *
<i>Olygoryzomys</i>					
<i>Longicaudatus</i> (Bennet)	G	23.8	Nocturnal	M, G, F	22.2 *
<i>Ratus ratus</i> (Linnaeus)	G, F (O)	200	Nocturnal	M, G, F, HD	66.7 *
b) Birds					
	Diet	Body size (cm)	Habitat	Frequency (%)	
<i>Anairetes parulus</i>	I	11	F, M	5.66	
<i>Aphastura spinicauda</i>	I	14	F	10.38	
<i>Asthenes humicola</i>	I	16,5	M	1.89	
<i>Callipepla californica</i>	G, H	26	M, G	9.43 *	
<i>Carduelis barbatus</i>	G, M	13,5	M, G, F	0.94	
<i>Columba araucana</i>	F, G	38	F	1.89 *	
<i>Columbina picui</i>	G	19	M, G	1.89	
<i>Curaeus curaeus</i>	G, I (O)	28	F, M, G	16.04 *	
<i>Diuca diuca</i>	G, F, I	17,5	M, G	3.77 *	
<i>Leptasthenura aegithaloides</i>	I	16	M, G	1.89	
<i>Mimus thenca</i>	G, F, I	29	M, G	1.89 *	
<i>Nothoprocta perdicaria</i>	G, I (O)	30	M, G	0.94 *	
<i>Phytotoma rara</i>	G, F, H	20	M, G	0.94	
<i>Pygarrhichas albogularis</i>	I	16	F, M	3.77	
<i>Pyrope pyrope</i>	I, F	21	F, M	0.94	
<i>Scelorchilus albicollis</i>	I, F	19	F, M	1.89	
<i>Troglodytes aedon</i>	I	12	M, G, F	8.49	
<i>Turdus falcklandii</i>	I, F	28	F, M	7.55	
<i>Zenaida auriculata</i>	G	27	M, G	1.89	
<i>Zonotrichia capensis</i>	G, I, F, H	15	M, G	17.92	

For small mammals we set up a grid of 120 Sherman traps for four days and three nights, using sunflowers seeds and oat baits as artificial food. We checked traps early in the morning for nocturne mammals and in the afternoon for diurnal mammals. To evaluate the composition of potential seed predators, we set up 4 linear transect (400 m long) with stations every 100 m (16 stations in total), in each station we observed birds for 5 minutes inside a circle of 20 m radius.

§ Not captured, but observed at daily time rounding experimental units and near its borrows, we found remains of *Cryptocarya alba* seeds.

* Potential predators of *C. alba* seeds

‡ The Mammals of Texas - Online Edition; http://www.nsr.ttu.edu/tmot1/mus_musc.html

APÉNDICE 2

**SOME METHODOLOGICAL ISSUES RELATED WITH FREQUENCY-
DEPENDENT SEED SIZE SELECTION UNDER FIELD CONDITIONS**

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ABSTRACT

Seed predation is one of the major causes of plant mortality, thus affecting plant fitness. Seed size is a life history attribute that affects the probability of seed predation; larger seeds should be more attractive prey to predators compared to smaller seeds, because they constitute more profitable prey with higher energetic and/or nutrient content. However, predator preferences may be modulated by the relative abundance of alternative seeds of different sizes. We set up a field experiment to evaluate frequency-dependent seed predation using seeds of *Cryptocarya alba* (Mol.) Looser (Lauraceae), at La Campana National Park (Mediterranean zone of Chile). Predators always consumed large seeds preferentially regardless of their relative frequency in a patch. These results suggest that seed predators might be a selective force against large seeds.

Key words: anti-apostatic selection, seed predation, *Cryptocarya alba*, Mediterranean shrubland, La Campana National Park.

INTRODUCTION

Seed predation is a major cause of mortality in plant populations (Janzen 1971, Harper 1977, Crawley 1997). Hence, it is commonly regarded as a selective force able to drive the evolution of seed traits such as seed size, color and chemical content, among others (Janzen 1969, Hare 1980, Smith 1973, Hulme 1994, Moegenburg 1996, Geritz 1998, Hulme and Borelli, 1999). Seed size is a trait related consistently with plant fitness, with larger seeds being frequently more successful than smaller seeds in terms of seedling recruitment and/or plant competition (Harper 1977, Fenner 1985, Silvertown 1989, Chacon and Bustamante 2001). Seed size varies considerably both between and within populations and adult individuals (Janzen 1969, Winn 1988, Silvertown 1989, Willson and Whelan 1990, Moegenburg 1996, Mojonnier 1998), and explanations for such variability have relied on plastic responses of adult plants to environmental conditions (Silvertown 1989). In the face of this phenotypic variation of seed size, seed predators might express selective consumption responses over particular phenotypes. It is expected that larger seeds are preferred, because of their higher profitability in energetic and/or nutrient content (Horsley et al. 1979, Mojonnier 1998, for supporting empirical evidence see e.g., Molau et al. 1989, Vander Wall 1990, Moegenburg 1996, Brewer 2001).

If the intensity of seed predation depends on the relative abundance of different seed sizes, then predation is frequency-dependent (Greenwood 1984a, Allen 1988). Thus, seed predation can be apostatic (*sensu* Greenwood 1984a), when it concentrates on large seeds when they are frequent in the environment, or it can be anti-apostatic (*sensu* Greenwood 1984a), if predators prefer larger seeds when they are scarce. Seed

predation is frequency-independent when predation upon large seeds varies in direct proportion to their relative abundances.

Frequency-dependent prey selection has been particularly fruitful for understanding the ecological and evolutionary consequences of predator-prey interactions (Allen 1988, Endler 1988, Rodríguez-Gironés and Vásquez, in press). However, this approach has been scarcely utilized to understand the evolutionary relationship between seeds and their predators. Moreover, the majority of studies on frequency-dependent predation have been conducted under laboratory or semi-natural conditions, with commercial or artificial prey, and have focused on the foraging behavior of predators rather than on the consequences for prey populations (see Greenwood 1984a, b, c, 1985, Allen 1988, Endler 1988). To our knowledge, this is the first study addressing frequency-dependent seed predation under field conditions using different phenotypes of a native seed.

We studied frequency-dependent seed size predation upon seeds of *Cryptocarya alba* (Mol.) Looser (Lauraceae), a common endemic tree of the Mediterranean region of central Chile. We carried out a field experiment to answer the following questions: (i) Do seed predators express frequency-dependent seed size selection? An answer to this question is crucial to elucidate if seed predators have the potential to drive, at least partially, the evolution of seed size; (ii) For how long is it possible to detect a selective predatory response given an initial relative frequency and seed density? An answer of this question is critical to assess the temporal consistency of patterns of frequency-dependent predation. Further, it will allow us to detect the temporal scale on which predation actually affects a given prey distribution. This issue is also linked to a third question: (iii) How a certain pattern of frequency-dependent predation is affected by

previous predation? This issue connects with a fundamental and recognized methodological difficulty in empirical studies: the fact that animals themselves to some extent create their own ecological circumstances (see e.g., Vásquez and Kacelnik 2000).

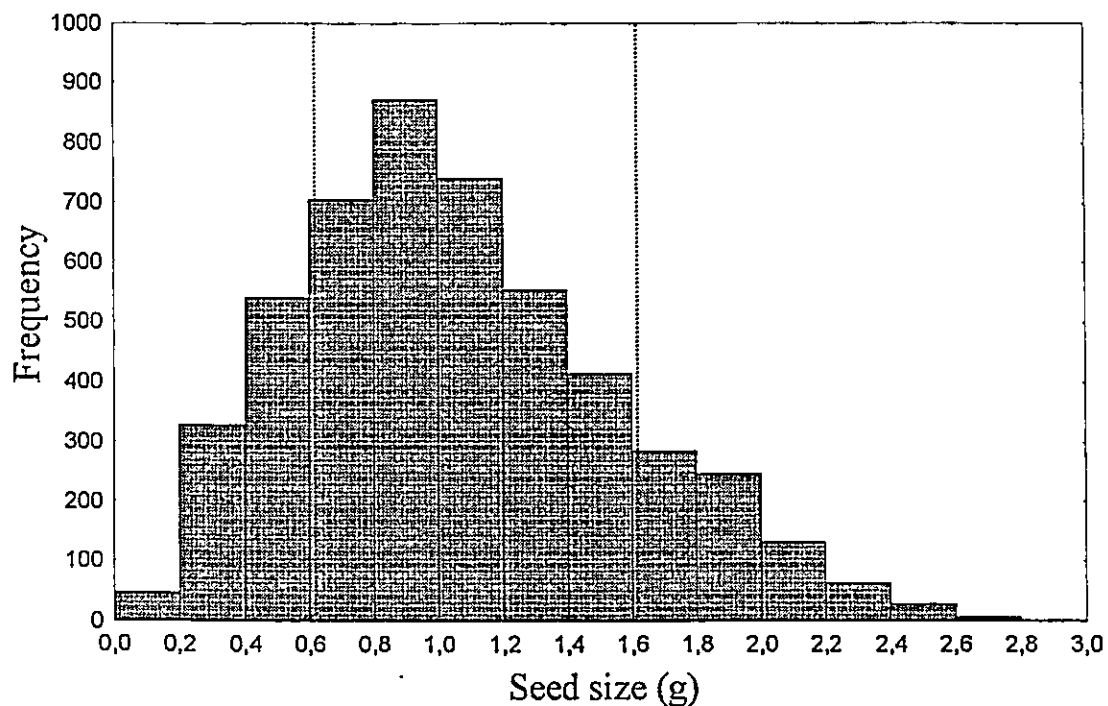
MATERIALS AND METHODS

This study was carried out at La Campana National Park (32° 57'S 71° 08'O), coastal range, Central Chile. The vegetation is characterized by a Mediterranean shrubland where tree species such as *Cryptocarya alba*, *Peumus boldus* Mol., *Quillaja saponaria* Mol. and *Litrhaea caustica* (Mol.) H. et A., are dominant (Villaseñor and Serey 1980/81). *Cryptocarya alba* is a 4–30 m height, shade-tolerant evergreen tree (Armesto and Pickett 1985), living in south-facing slopes and humid ravines (Armesto and Martínez 1978). Its fruits are red to pink one-seeded drupes (Hoffmann 1998) that varies in seed size both within parental tree and at the population level (0.1 to 3.3 g, see Chacón and Bustamante 2001). The main seed predators are rodents (including *Abrothrix longipilis* (Water), *Abrothrix olivaceus* (Water), *Oligoryzomys longicaudatus* (Bennett), and *Phyllotis darwini* (Water)) and birds (such as *Lophortyx californica* (Shaw) and *Diuca diuca* (Molina)) (see Bustamante and Vásquez 1995).

We collected 5000 seeds from 50 individual trees; 100 randomly selected seeds per tree. For the purposes of this study, we defined a seed as the whole dispersal unit, that is, the seed plus the pericarp that covers it. We expressed seed size through seed fresh weight. The size distribution of collected seeds is shown in Figure 1. We operationally defined as a “small seed” those seeds included within the lower 15% of the distribution (i.e., range 0.01–0.61 g), and a “large seed”, those seeds included within the higher 15% of the population distribution (i.e., 1.61–2.8 g). Our aim was not the assessment of the impact of frequency-dependent selection on real seed distributions, but the analysis of

the potentiality of seed predator to exert frequency-dependent selection and infer seed population consequences.

Figure 1. Seed size distribution of *Cryptocarya alba* at La Campana National Park During 2000. Data were obtained from 50 parental trees (100 seed per individual) Dotted lines represents 0.15 and 0.85 percentile respectively.



During July and August 2000 we set up a field experiment comprising five treatments that varied in the available proportion of large seeds (in relation to small seeds): 0.1, 0.25, 0.50, 0.75 and 0.9. We disposed five replicates per treatment at a constant seed density (50 seeds/m²; see Bustamante 1992, Bustamante and Simonetti 2000). Replicates were arranged in a 60 x 60 m grid with stations located 15 m apart each, making a total of 25 experimental stations. Seed frequency at each station was selected at random with

the restriction of not allowing three equal frequencies being at neighboring stations. We observed the number of removed seeds after 7 and 14 days. After two weeks seed consumption was negligible (Fig. 2). In order to answer the three questions addressed in this study, we conducted the following analysis:

- a) We made seed survival curves using Log Rank analysis to examine if seed predators prefer large over small seeds independently of their relative abundance. For this analysis, we used only data obtained from the 0.5:0.5 large:small treatment.
- b) In order to analyze the temporal consistency of frequency-dependent predation, we compared seed predation between day 0 to day 7 with seed predation between day 0 and day 14.
- c) To evaluate if frequency-dependence is affected by previous seed consumption, we compared seed predation between the periods from day 0 to day 7 with the period from day 7 to day 14.

The analysis of frequency-dependent seed size selection was performed following the model of Greenwood and Elton (1979):

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

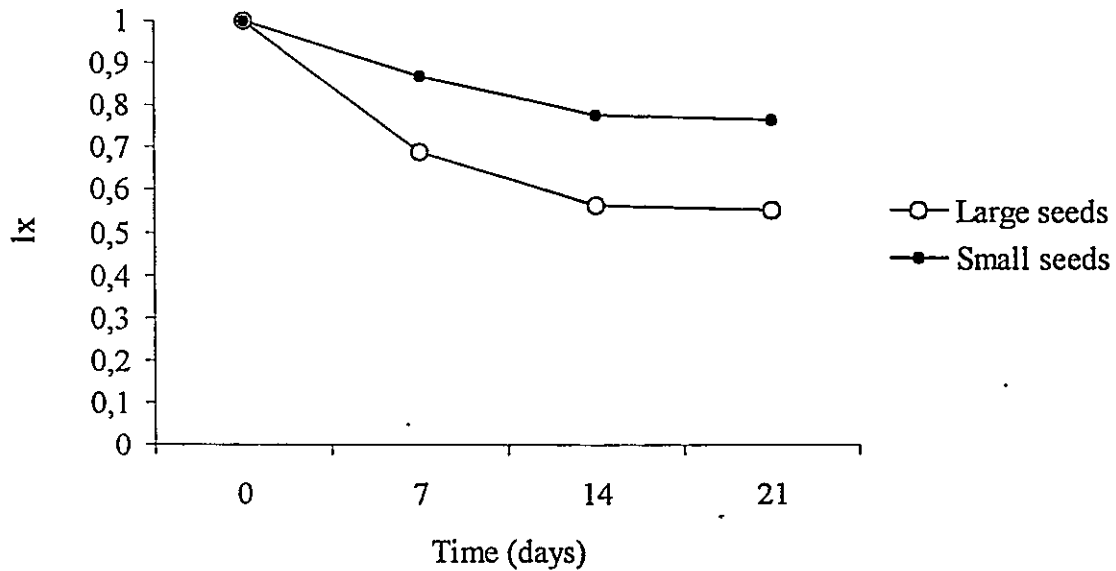
In our case, A_L/A_S is the ratio large/small seeds present in the environment and e_L/e_S , the ratio large/small seeds consumed by predators. The parameter b evaluates the frequency-dependence. If $b > 1$, then selection is pro-apostatic (negative frequency-dependence); if $b < 1$, then selection is anti-apostatic (positive frequency-dependence); if $b = 1$, then selection is frequency-independent (no selection). The parameter V evaluates the bias of seed predators with independence of the frequency. If $V > 1$, there is a bias to

large seeds; if $V < 1$, there is a bias to small seeds; if $V = 1$, there is no bias. To test the statistical significance of b , we conducted a log-log regression analysis (Greenwood and Elton 1979). The parameter b was documented through $t = (b^{\wedge} - 1) / \text{S.E.}(b^{\wedge})$.

RESULTS

The proportion of seed survival was in average 0.5 ± 0.08 (mean \pm SE, $n = 5$) in large seeds and 0.77 ± 0.11 ($n = 5$) in small seeds by the end of the experiment (after 21 days). Seed survival differed significantly between seed sizes (Log Rank L = -8.36; $P < 0.0001$; see Fig. 2).

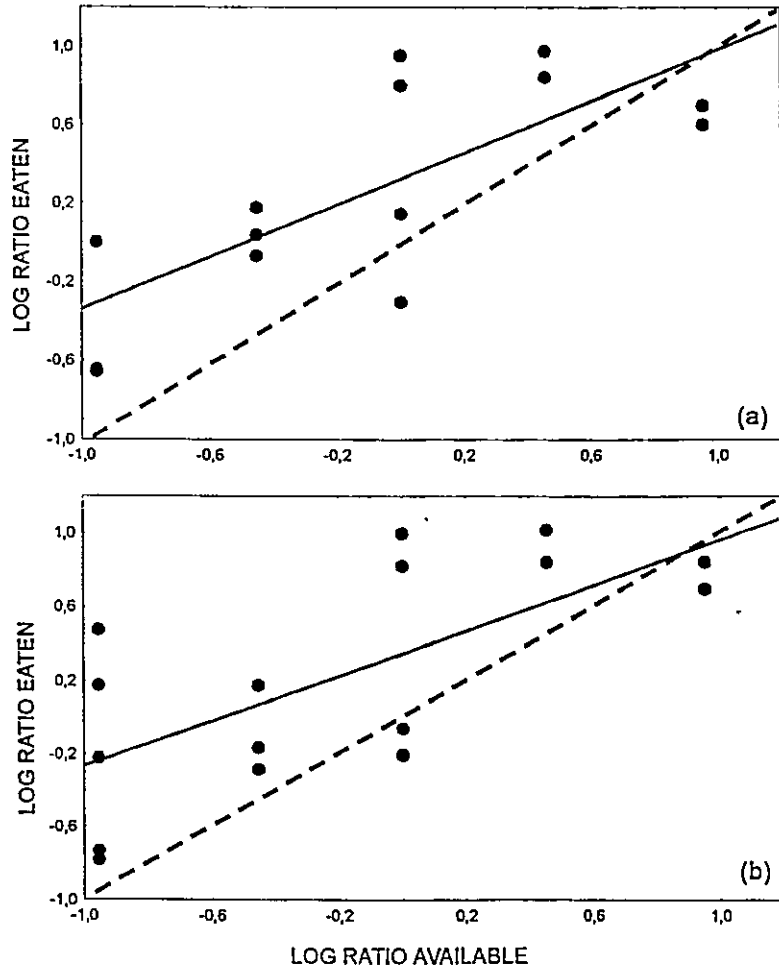
Figure 2. Seed survival of large and small seeds of *Cryptocarya alba* at equal relative abundance in at La Campana National Park, Ocoa location.



We observed an anti-apostatic pattern of seed size predation from day 0 to 7 ($b = 0.66$; $t = -2.06$; d.f. = 1, 12; $P < 0.05$; Fig. 3a). Similarly, anti-apostatic selection was detected from day 0 to day 14, as well ($b = 0.61$; $t = -2.52$; d.f. = 1, 15; $P < 0.02$; Fig. 3b). No

differences were detected between curves obtained during period from day 0 to day 7 and period from day 0 to day 14 (ANCOVA $F_{1,27} = 0.434$; $P = 0.836$).

Figure 3. Seed consumption of large seeds in *Cryptocarya alba* as a function of the frequency of large seeds available in the field at La Campana National Park. Data represent five proportion of larger seeds: 0.1, 0.25, 0.75 and 0.9 (with constant density = 50 seed/m²), (a) seed consumption from 0 to 7 days ($n = 14$) and (b) seed consumption from 0 to 14 days ($n = 17$), assuming 0 as the original proportion of larger seed,

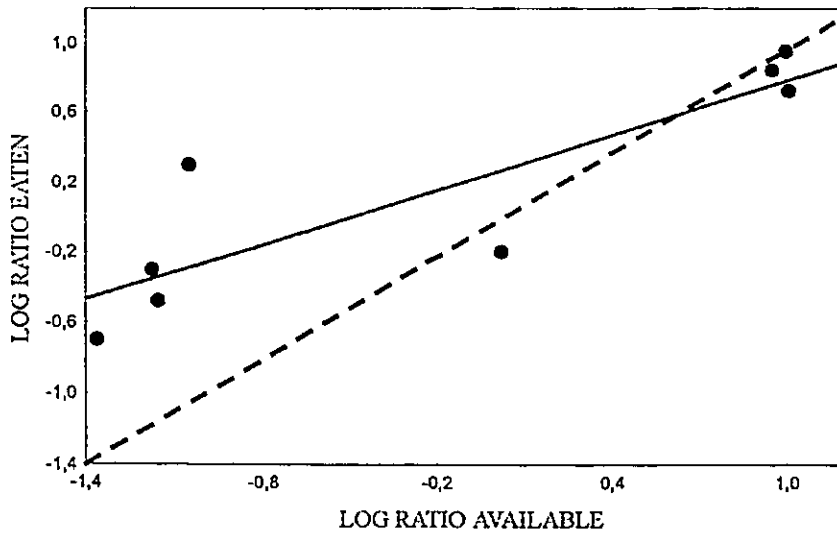


After 7 days of predation, we detected a significant modification of the relative abundances of seeds experimentally offered, particularly when large seeds were scarce (Table 1). However, no significant change in relative abundances was detected on subsequent weeks when considering the remaining availability of the previous week as the initial seed offer (Table 1). We found that the proportion of seed consumption during the whole experimental period (i.e., 21 days) was higher when large seeds were relatively scarce (70% of seed reduction at 0.1 relative availability of large seeds, versus 36% of seed reduction at 0.9 relative availability; see Table 1). Anti-apostatic seed selection was also observed if we consider as initial seed distribution the remaining seed distribution after 7 days of predation, i.e, when analyzing seed selection from day 7 to day 14 ($b = 0.59$; $t = -3.25$; d.f. = 7; $P = 0.02$; see Fig. 4).

Table 1. Modifications of the proportion available of large seed by seed consumption in *Cryptocarya alba* at La Campana National Park, Ocoa location.

Time (days)	Proportion available of large seeds				
	0.1 %	0.25 %	0.5 %	0.75 %	0.9 %
0	0.1	0.25	0.5	0.75	0.9
7	0.05	0.07	0.34	0.5	0.75
14	0.04	0.06	0.26	0.46	0.60
21	0.03	0.06	0.25	0.46	0.58
Proportion of seed reduction to 21 days	0.7	0.76	0.5	0.39	0.36

Figure 4. Seed consumption curve of large seeds in *Cryptocarya alba* as a function of the relative abundance of large seeds available in the field, with five proportion of larger seeds: 0.1, 0.25, 0.75, 0.9 (constant density = 50 seed / m²), from 7 to 14 days (n = 9), at La Campana National Park, Ocoa location. Assuming day 7 as the resulting consumption as the new offer.



DISCUSSION

Results of frequency-dependent selection are commonly interpreted in the context of optimal foraging theory (Hubbard et al. 1982). If a seed predator is an optimal forager, then it will consume large seeds in a pro-apostatic manner. That is, in order to minimize searching time and/or to maximize energetic intake, seed predator will consume large seeds at a disproportionately low rate when they are scarce or it will consume large seeds at a disproportionately high rate when they become abundant (Murdoch 1969, Fulick and Greenwood 1979, Horsley et al. 1979, Hubbard et al. 1982, Greenwood 1984a, b, c, 1985, Allen 1988, Sherratt and Harvey 1993, Allen et al. 1998). The detection of persistent anti-apostatic seed size selection in our study differs significantly from the mentioned theoretical expectation and deserves alternative explanations.

First, individual-based explanations related with optimal foraging theory to understand frequency-dependence selection may be limited when predation is exerted by a guild of different predator species that might follow different cues beyond seed size to select prey optimally. Certainly, *C. alba* seeds in our study were exposed to a guild of predators composed by diverse avian and mammalian species (Bustamante 1996). Our results only detected the net effects produced by this guild. Second; it is possible that when large seeds are scarce they are easily detected because they become conspicuous among the most frequent small size phenotypes (the "background effect"; see Greenwood 1985, Landeau and Terborgh 1986, Allen et al. 1998).

A consistent preference for large seeds implies modifications of the seed size distribution. By favoring the escape of smaller seeds (Winn 1988), seed predators may

exert a directional selective forcing with the potential to reduce the mean size of the seed population. It is largely known that larger seeds germinate in a higher proportion and produce more vigorous seedlings with higher competitive abilities relative to smaller seeds (Harper 1977, Winn 1988, Silvertown 1989; see Chacón et al. 1998, Chacón and Bustamante 2001, for examples in *C. alba*). Therefore, there exist at least two contrasting selective pressures responsible for the evolution of seed size in *C. alba*: seed predation favoring smaller seeds, and abiotic stress favoring larger seeds (Venable and Brown 1988). The extent of these contrasting selective forces in the evolution of seed size is an issue that requires further theoretical and/or empirical research.

The early detection (within 7 days) of anti-apostatic seed size selection and the maintenance of this selective consumption without changes over the rest of the experimental period (Fig. 4), support the assertion that short-term experiments are adequate to examine selective population responses of seed predators. In our study, it is possible that seed predators depressed experimental patches rapidly to a threshold level beyond which seed patches became unattractive and predators switched to alternative resources present in the environment. In our study site there are abundant alternative resources such as seeds of *Persea lingue* Nees (Lauraceae) and *Sophora macrocarpa* J. E. Sm. (Papilionaceae), that coexist in the floor of the forest with seeds of *C. alba*, and are attractive to seed predators (Bustamante 1996).

In studies of predation, have been noted the problem of changes in the initial distribution or abundance of prey due to the own predation being studied, for example, in studies of the predator's functional response (see Hassell 1978). Our results show that we could have assessed frequency-dependence between day 7 and day 21, and the overall results

would have remained unaffected. Despite the fact that we did not assess finer scale changes in prey distribution (i.e., between day 0 and 7), we are confident, due to the constancy of the results, that the predator guild produces positive frequency-dependent selection upon large seeds of *C. alba*.

In order to expect changes of frequency-dependent seed size selection through time, seed predators ought to modify the relative abundance of the preferred seeds (i.e., large seeds). In our experiment, large seeds decreased significantly even when they were scarce. However, large seeds were always consumed preferentially. This result suggests that large seeds of *C. alba* are extremely attractive resources for predators probably because they have a higher energetic content and/or lower chemical defenses compared to small seeds (Janzen, 1978).

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