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Do empty *Juniperus communis* seeds defend filled seeds against predation by *Apodemus sylvaticus*?[1]

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Abstract: The juniper *Juniperus communis*, a dominant plant in the high mountains of SE Spain, produces a high proportion of empty seeds within well-developed cones. We tested the hypothesis that the production of empty seeds by juniper reduces seed predation by the woodmouse *Apodemus sylvaticus*, thereby benefitting the plant. We performed laboratory and field experiments to determine *i)* woodmouse discrimination ability between filled and empty seeds, and *ii)* woodmouse response to changes in the proportion of empty *versus* filled seeds and in the seed density in seed clusters. In addition, we estimated, for six juniper populations over three years, whether plants or populations showing a higher proportion of empty seeds suffered reduced woodmouse predation. Experiments showed that woodmice can eventually discriminate externally between filled and empty seeds, but in most cases had to bite the seeds to identify and reject empty ones. The probability of predation for filled seeds was independent of changes in the proportion of empty *versus* filled seeds and in seed density per cluster. Seed predation suffered by plants in the field was unrelated to the proportion of empty seeds per plant for all populations and years. The presence of empty seeds did not benefit juniper against woodmouse predation, either in terms of individual reproductive output or in terms of offspring escape probability. Our study suggests that the effect of empty seeds on seed predation should be rare in plant-seed predator interactions where predators are polyphagous and eventually able to discriminate against empty seeds, and therefore suffer a low cost when coping with empty seeds.

Keywords: *Apodemus*, empty seeds, *Juniperus*, plant defence, seed predation.

Résumé : Le genévrier, *Juniperus communis*, une plante dominante dans la haute montagne du sud-est de l'Espagne, produit plusieurs graines vides dans des cones bien développés. Dans cette étude, on vérifie l'hypothèse selon laquelle, avec la production de graines vides, le genévrier réduit la prédation de graines par la souris sylvestre *Apodemus sylvaticus*, obtenant ainsi un bénéfice. On a fait des expériences sur le terrain et en laboratoire pour déterminer : *i)* la capacité de la souris sylvestre de discriminer les graines vides des graines pleines et *ii)* évaluer la réponse de la souris sylvestre face aux changements dans la proportion de graines pleines et dans la densité de graines. On a également estimé, dans six populations de genévrier et pendant trois ans, si les plantes ou les populations ayant une plus grande proportion de graines vides étaient moins attaquées par les rongeurs. Les souris sylvestres pouvaient, occasionnellement, distinguer par l'aspect extérieur les graines pleines des graines vides. Dans la plupart des cas, il leur fallait mordre les graines pour discriminer et rejeter les graines vides. La probabilité de prédation de graines pleines est indépendante des changements dans la proportion de graines pleines et de la densité. La prédation subie par les plantes sur le terrain est indépendante de la proportion de graines vides par plante, chez toutes les populations et toutes les années. La présence de graines vides n'est pas bénéfique au genévrier face à la prédation de la souris sylvestre, ni en termes de succès reproductif individuel ni en termes de probabilité d'évasion à la prédation. La production de graines vides ne peut donc pas être considerée comme une stratégie de défense face aux rongeurs. Cette étude suggère que l'effet des graines vides sur les prédateurs est faible dans les interactions plante-prédateur où les prédateurs sont polyphagues, capables de distinguer occasionnellement les graines pleines des graines vides; ces herbivores subissent un faible coût énergétique à cause des graines vides.

Mots-clés : *Apodemus*, défense des plantes, graines vides, *Juniperus*, prédation de graines.

Introduction

Seed predation by animals negatively affects reproductive success and population dynamics of many plant species (see reviews in Janzen, 1971; Louda, 1989; Crawley, 1992; Hulme, 1996). To avoid this mortality factor, plants have presumably evolved different traits, such as secondary seed compounds, hard seed coats, smaller seeds and masting behaviour (Crawley, 1992; Hulme, 1993; Kelly, 1994). The production of parthenocarpic fruits (seedless fruits without fertilization) and aborted or otherwise empty seeds has also been considered to be a defensive trait against predators. According to this hypothesis, the presence of empty seeds should improve the survival probability of filled ones by increasing the cost for predators wanting to exploit these rewarding (filled) seeds (Janzen, 1971; Stephenson, 1981; Willson & Burley, 1983; Crawley, 1992). The kind of cost suffered by seed predators depends on several factors. Some insect predators suffer a reproductive cost, quantified as the number of seed predator offspring failing to develop inside empty seeds (Traveset, 1993; Verdú & García-Fayos, 1997). In addition, Zangerl, Berenbaum & Nitao (1991) have shown that empty fruits may act as decoys that divert herbivores away from fruits containing filled seeds, although predators feeding on empty fruits may experience reduced growth. Finally, the cost can be expressed in terms of foraging efficiency, quantified as the increase in time necessary to find a filled seed as a function of the number of empty seeds surrounding the filled seed within the fruit, the individual plant, or the cluster of dispersed seeds (Mustart, Cowling & Wright, 1995; Ziv & Bronstein, 1996; Fuentes & Schupp, 1998).

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The hypothesis of empty seeds as a defensive trait has been supported mainly for insect seed predators, with most studies finding a significant negative relationship between the number of empty seeds produced by the plants and the proportion of seeds attacked by insects (Zangerl, Berenbaum & Nitao, 1991; Traveset, 1993; Ziv & Bronstein, 1996; Verdú & García-Fayos, 1997; but see Mustart, Cowling & Wright, 1995). However, in the case of vertebrate seed predators, the scant evidence available is equivocal. For example, seed predation by birds on *Juniperus osteosperma* depends on the proportion of empty seeds per tree (Fuentes & Schupp, 1998). Similarly, differences in seed predation by rodents between plant species can be driven by the differences in the proportion of empty seeds per species (Kollmann, Comes & White, 1998). In contrast, predation on *Cryptantha flava* seeds by rodents is independent of the proportion of empty seeds per fruit (Casper, 1988).

Here, we investigate in juniper, *Juniperus communis* L. (Cupressaceae), the hypothesis that empty seeds serve as a defence mechanism against predation by negatively affecting the main seed predator, the woodmouse *Apodemus sylvaticus*. Juniper bears a high proportion of externally well-developed but empty seeds (García, 1998a, García *et al.*, 2000). Using an approach which included laboratory and field experiments, we tested the specific mechanisms determining the interaction between the seed predator and empty seeds, including: *i*) how the woodmouse can differentiate between empty and filled juniper seeds, *ii*) whether filled seeds are selectively depredated by the woodmouse in relation to empty seeds, and *iii*) whether the predation probability for filled seeds is influenced by the proportion of empty seeds and by the density of seeds in the cluster. In addition, over a wide range of juniper populations and years, we determined the patterns of relationship between empty seeds and seed predation, in order to determine whether individual plants suffered a reduced predation rate when they increased their proportion of empty seeds.

Material and methods

NATURAL HISTORY OF THE SYSTEM

Juniperus communis is a main component of the high-mountain shrublands of southeast Spain at altitudes from 1500 to 2500 m a.s.l. (Molero, Pérez & Valle, 1992). This dioecious stunted shrub bears fleshy spherical cones (*ca* 6.5 mm diameter) containing 1-3, and rarely 4, seeds. Many seeds within well-developed cones are empty, showing an undeveloped embryo which did not fill the seed coat, due to pollination failure or seed abortion during development (García, 1998a, García *et al.*, 2000). Furthermore, more than 70% of ripe cones contain no filled seeds (average for six populations and three years; García, 1998b). Healthy (filled) seeds show a white, oily embryo and nucella, entirely filling the seed coat. Externally, empty seeds are indistinguishable from filled seeds, since the seed coat grows normally irrespective of the embryo development. The only apparent difference between the two types of seeds is the weight, aborted seeds being significantly lighter than filled ones (García, 1998b).

The woodmouse *Apodemus sylvaticus* L. (Muridae) is the main vertebrate seed predator of juniper in the Mediterranean high-mountains. This rodent acts both as a pre- and postdispersal seed predator, consuming juniper seeds from green and ripe cones still attached to the plants and from those fallen beneath plants, but also scavenging seeds from bird faeces after dispersal (mainly by *Turdus torquatus* and *T. viscivorus*; García *et al.*, 1999a). When presented with entire cones and dispersed seeds, detached from the pulp, woodmice do not show preference between these food items and attack them with the same intensity (García, 1998b). The ecological importance of woodmouse predation for juniper regeneration is strengthened by the fact that *J. communis* reproduces only by seeds and lacks a persistent soil seed bank in these areas (García, 1998b).

LABORATORY EXPERIMENT

We performed a laboratory experiment to test whether rodents are able to discriminate between empty and filled seeds, examining the mechanism used by the rodent for this discrimination. For the experiment, seven adult woodmice were captured with live-traps in the locality of Campos de Otero (2300 m a.s.l., Sierra Nevada, Granada) and maintained in individual laboratory cages of 40 cm × 25 cm × 25 cm made of wire mesh and with plastic soil. Woodmice were acclimated for one month, given *ad libitum* access to a mixture of rolled cereals, nuts, and fresh carrot, and kept under a daylight/darkness ratio of 12:12 at 18°C. During October 1994, we carried out a seed-selection experiment in which 10 filled plus 20 empty juniper seeds were simultaneously offered to each one of seven woodmice (see Jennings, 1976, and Jensen, 1993 for similar procedures with this species). Seeds were presented in a Petri dish of 9 cm diameter together with a piece of fresh carrot. All the seeds came from bird droppings, where they appeared intact and free of pulp remains, and were collected in September 1994 in Campos de Otero. Filled and empty seeds were externally distinguished by a floating method of 95% accuracy (García, 1998b). The experiment spanned the 12-hour period of darkness, after which we collected the contents of the dishes and the seed remains from cage soil. In the survey, we classified seeds as "unattacked" when they appeared intact; "rejected" when the seed coat was bitten by woodmouse but rejected without opening the seed; and "consumed" when the seed coat had been vigorously gnawed and the internal content had been eaten. Seeds were used only once, to avoid tainting with woodmouse odour during the trial. The experiment was repeated three times (trials) separated by at least 12 hours minimum. Woodmice did not suffer significant weight loss over the experiment and all were released in their original habitat after the experimental trials.

FIELD EXPERIMENTS

Field experiments were performed during October 1997 in the locality of Boleta (2000 m a.s.l., Sierra de Baza, Granada). Experiments consisted of offering to woodmice combinations of filled and empty juniper seeds, in Petri dishes of 9 cm diameter located in the surroundings of junipers, separated 5-10 m from one another, filled with soil, and fixed, by a central nail, flush with the ground surface. These combinations of seeds represented different proportions of filled *versus* empty seeds and different seed densities, these variables always comparable to values found for the seeds appearing under natural conditions, both in mother plants and in the seed rain generated by dispersers (García, 1998b). Filled and empty seeds came from bird droppings collected at the site before the beginning of the experiment and were externally identified using the flotation procedure. Dishes were revisited seven days after the addition of seeds, and the seeds were classified in the laboratory as unattacked, rejected, or consumed, following the above procedure. By adding insecticide to all the dishes (CHAS® 5G - Agrodan, chlorpyrifos 5% w/w) we avoided possible seed losses due to insects, and the insecticide did not deter woodmice from eating seeds from dishes. We detected no sign of seed consumption or removal by birds nor the presence of other potential vertebrate granivores of *J. communis*, and all the feeding traces and faeces found in the dishes were attributable to *A. sylvaticus*. We performed the following experiments:

EXPERIMENT #1

We tested whether the predation probability of seeds changed when the ratio of filled to empty seeds varied while keeping the seed density constant. For this, we compared woodmouse predation between two treatments: "low proportion," composed of one filled and nine empty seeds per dish; and "high proportion," composed of five filled and five empty seeds. The experiment consisted of 15 dishes for each treatment and was repeated twice (two trials). For each trial, we used 20 dishes that excluded predators using wire cages of 1.3 cm mesh and insecticide, in order to control the possible effect of abiotic factors over seed removal from dishes. Predator-exclusion dishes contained 10 seeds randomly chosen from natural seed rain, showing 22% of filled seeds.

We analysed whether woodmice discriminated between filled and empty seeds in the field, comparing the proportion of attacked seeds between filled and empty seeds within the high-proportion treatment, because in this latter treatment both types of seeds had the same probability of being randomly chosen by woodmice.

EXPERIMENT #2

We tested whether the predation probability of seeds changed when seed density varied, while keeping the ratio of filled to empty seeds constant. For this we used three treatments: "low density," consisting of one filled and four empty seeds per dish; "medium density," consisting of two filled and eight empty seeds; and "high density," consisting of four filled and 16 empty seeds. The experiment was performed twice (two trials), each one consisting of 15 dishes for each treatment and 30 predator-exclusion dishes, the latter containing the number and proportion of filled/empty seeds described above.

RELATIONSHIP BETWEEN EMPTY-SEED PROPORTION AND MAGNITUDE OF SEED PREDATION PER PLANT

To gather an observational database broad enough to analyse the relationship between the frequency of empty seeds per plant and the intensity of woodmouse predation, we made a three-year study of the following juniper populations (see García *et al.*, 1999b, for a extensive description of these localities): Boleta (2000 m a.s.l., Sierra de Baza), Campos de Otero, Dornajo, Trevenque and Maitena (respectively 2300, 2000, 1800, and 2100 m a.s.l., Sierra Nevada), and Collado Cabañas (1800 m a.s.l., Sierra de Cazorla, Jaén). During the autumns of 1994, 1995, and 1996, we chose 20 female plants in each population (except Campos de Otero, where $n = 75$ plants). Most of the plants showed large accumulations of cone and seed fragments dropped on the ground beneath the crown. These fragments were remains of *A. sylvaticus* predation on juniper cones and seeds and belonged to the corresponding plant. To test whether woodmice concentrate their activity on those plants with higher proportions of empty seeds, we collected 30-40 ripe cones per plant ($n = 11\ 352$ cones) in September, opening all the seeds in the lab to determine the number and proportion of empty seeds per plant sample. In November, we determined in the field the intensity of woodmouse predation on the same plants, looking for remains of cones and seeds attacked by woodmice in 10 sampling quadrats of 0.04 m^2, randomly placed beneath plants. We used the proportion of quadrats showing remains of mouse predation (cones or seeds) in relation to the total number of quadrats sampled per shrub as an estimate of the intensity of mouse predation per plant. Although this method did not allow calculation of the percentage of seed loss relative to cone crop, this estimate correlates positively to predator activity per individual plant (see Fuentes & Schupp 1998, for a similar procedure). During our sampling, we detected no sign of seed predation attributable to vertebrates other than *A. sylvaticus*.

STATISTICAL ANALYSIS

The data were analysed using non-parametrical tests, due to the lack of normality of most variables (Zar, 1996). The Wilcoxon test was used to compare the proportion of seeds attacked by the woodmouse between filled and empty seeds in the laboratory experiment, with each individual ($n = 7$) as a replicate and pooling the results of trials for each individual. The χ^2 test was used to compare: *i*) the proportion of seeds attacked by the woodmouse between treatments of the field experiments, first considering all the seeds in the cluster and then only the filled seeds; and *ii*) the proportion of rejected and consumed seeds among filled and empty seeds, both for the laboratory experiment and the high-proportion treatment of field experiment #1. During the field experiments, the percentage of seed loss in the predator-exclusion dishes was in all cases negligible (< 5%) and therefore these dishes were not considered in the data analysis (see Kelrick *et al.*, 1986, for a similar procedure). The relationship between the proportion of empty seeds per plant and predation by the woodmouse in the field was tested first, for each population and year, with a logistic regression considering the intensity of predation as a categorical dependent variable with four categories (no predation, low: > 0-0.33, medium: > 0.33-0.66, and high: > 0.66). Second, the proportion of empty seeds and the intensity of predation were correlated (Spearman rank test) using the mean values per population and year for both variables. Most of the statistical analyses were fixed to the standard significance level $\alpha < 0.05$ (Zar, 1996). However, when statistically analyzing more than one related variable, and to avoid the increase of probability of making a type-I error, we chose the sequential Bonferroni test for fitting the significance level (* indicates $p < 0.05$ after Bonferroni hereafter; see also Rice, 1989).

Results

SELECTION BETWEEN FILLED AND EMPTY SEEDS

In the laboratory, woodmice heavily attacked both filled and empty seeds but empty seeds tended to be discriminated against in favour of filled ones ($Z = -2.20$, $p = 0.027$, $n = 7$, Wilcoxon test; Figure 1). When offered the same number of filled and empty seeds in field experiment #1 (high-proportion treatment), woodmice attacked filled seeds at a higher rate than empty ones, for both trials (trial I: $\chi^2 = 8.38$, $p = 0.0038$*, df = 1,148; trial II: $\chi^2 = 22.51$, $p < 0.0001$*, df = 1,148; Figure 1). In both laboratory and field experiments, almost all filled seeds were consumed after being attacked, whereas most empty seeds were rejected after an initial bite (laboratory: $\chi^2 = 290.33$, $p < 0.0001$*, df = 1,499; field trial I: $\chi^2 = 111.81$, $p < 0.0001$*, df = 1,96; field trial II: $\chi^2 = 91.24$, $p < 0.0001$*, df = 1,83; Figure 1).

EFFECT OF THE PROPORTION OF EMPTY SEEDS AND SEED DENSITY ON SEED PREDATION

In field experiment #1, the attack rate per dish increased significantly only when the proportion of filled seeds per dish was raised in trial #1 (Figure 2). However, changes in the proportion of filled seeds per dish did not significantly change survival probability for filled seeds in any trial of this experiment (Figure 2).

Predation rate was unaffected by seed density, and similar percentages of attacked seeds appeared in the different treatments of field experiment #2, for all the seeds in the cluster as well as only filled seeds (Figure 2).

RELATIONSHIP BETWEEN EMPTY-SEED PROPORTION AND MAGNITUDE OF SEED PREDATION PER PLANT

Figure 3 shows the values of the proportion of empty seeds and the intensity of woodmouse predation for the plants of different populations and years. Woodmouse predation was independent of the proportion of empty seeds per plant for all populations and years ($\chi^2 < 5.89$, $p > 0.05$, logistic regression, for all study cases). Similarly, no dependence was found at the population level when correlating the mean values per population and year of proportion of empty seeds with mouse predation intensity (*Rho* = 0.03, $p = 0.93$, $n = 10$, Spearman rank correlation).

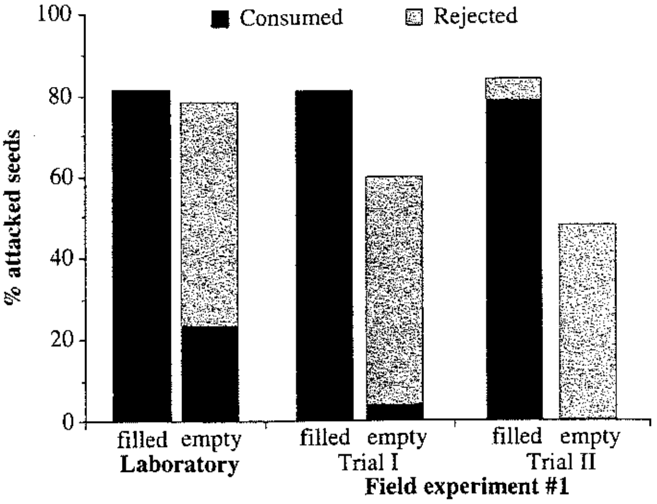

FIGURE 1. Percentage of filled and empty juniper seeds attacked by woodmice in the laboratory and field experiment #1. The percentages of attacked seeds classified as consumed or rejected by woodmice are also differentiated.

Discussion

Woodmouse seed predation was independent of the number of juniper seeds per cluster. *A. sylvaticus* did not show density-dependent seed predation over the range

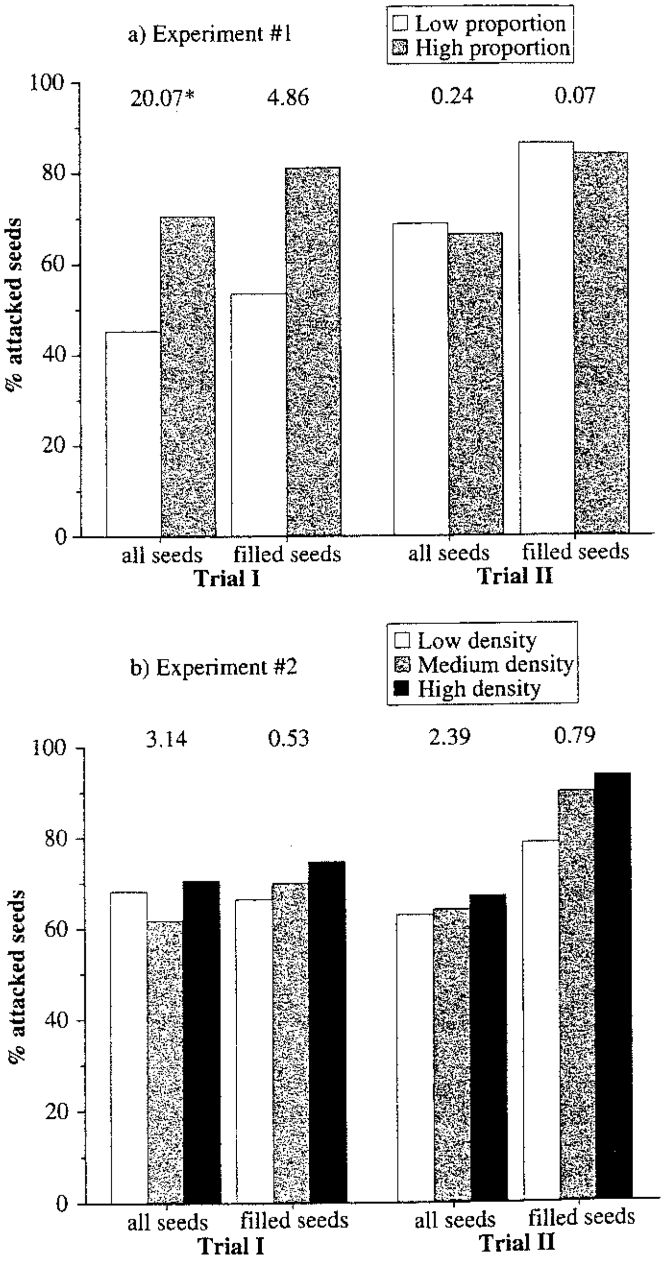

FIGURE 2. Percentage of juniper seeds attacked by woodmice in field experiments testing a) the effect of the proportion of empty *versus* filled seeds (Experiment #1), and b) the effect of seed density (Experiment #2), on woodmouse predation. For each experiment and trial, the percentages for all the seeds in the cluster (all seeds) and the filled seeds (filled seeds), as well as the χ^2 test-values comparing the treatments within each experiment are shown (* = $p < 0.05$ after Bonferroni).

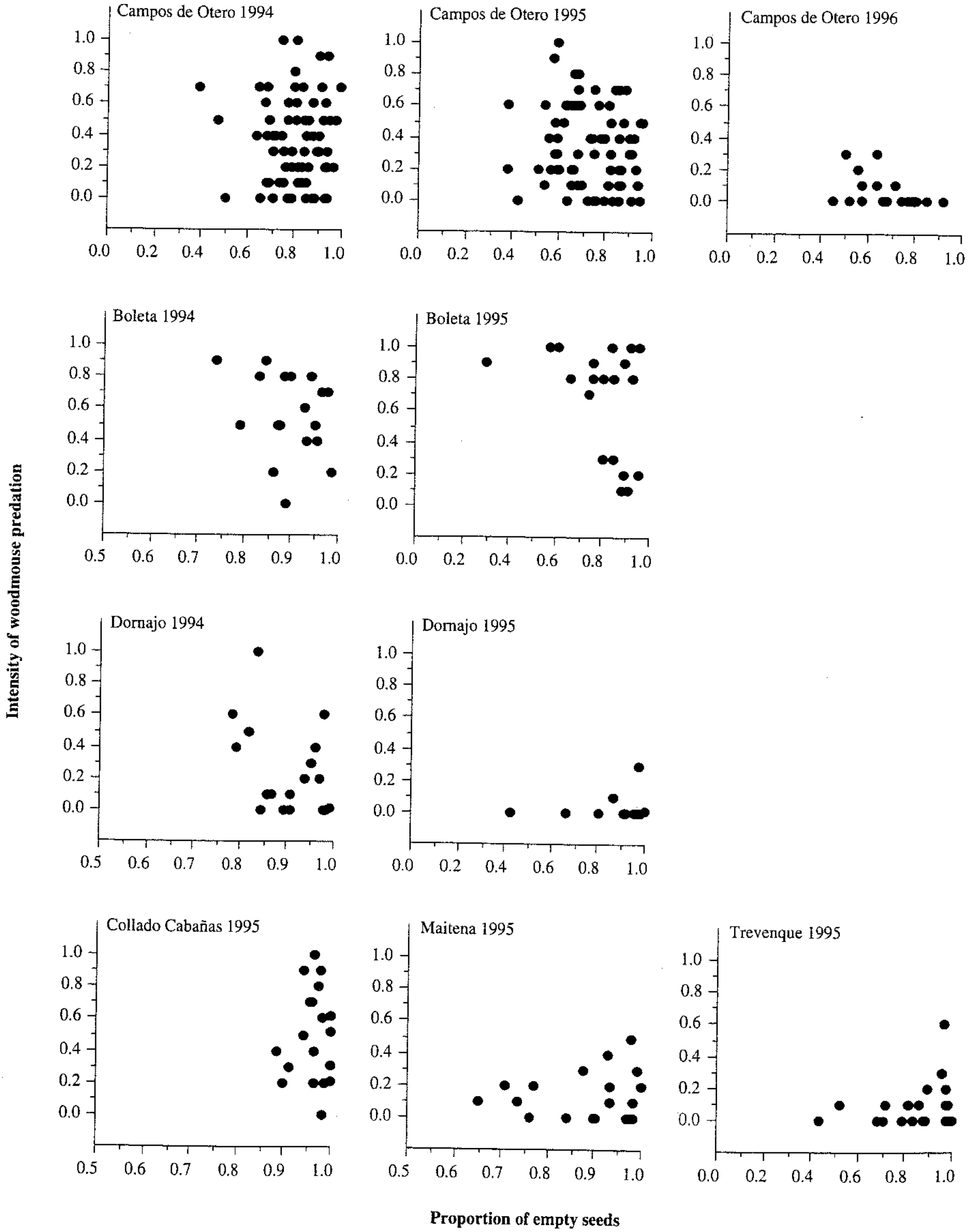

FIGURE 3. Intensity of woodmouse predation on different plants in different populations and years, in relation to the proportion of empty seeds per plant ($n = 75$ plants for Campos de Otero 1994-1995 and 20 plants for the rest of the study cases).

of seed densities used in our experiments (but see Casper, 1988; Willson & Whelan, 1990; Hulme, 1994; 1997). The independence between seed density and predation may be related to the juniper seed size (seed weight = 12.47 ± 0.15SE mg), because large seeds (> 10 mg) attract rodents even in clusters containing very few seeds, density-dependence being rarely found above this threshold size (Hulme, 1993; 1994). The fact that seeds in clusters differing in seed number had similar probabilities of predation suggests that the seed clump, and not the individual seed, was the predation target for the woodmouse (Mittelbach & Gross, 1984; Webb & Willson, 1985; Willson & Whelan, 1990; Hulme, 1994; Hulme & Hunt, 1999).

Our experiments, especially those in the field, have also shown that the proportion of filled seeds attacked by the woodmice was higher than that of empty seeds (Figure 1), indicating that *A. sylvaticus* can partially distinguish empty juniper seeds from filled ones before biting them. Discrimination ability among seeds of different profitability has been frequently evidenced for vertebrate seed predators (*e.g.*, among seed species, Kelrick *et al.*, 1986; Kerley & Erasmus, 1991; Hulme, 1993; between filled and empty seeds, Vander Wall & Balda, 1977; Jensen, 1985; Obeso, 1998; between sound seeds and seed damaged by predispersal insects, Sallabanks & Courtney, 1992; Forget, Munoz & Leigh, 1994). In our case, the woodmouse may discriminate between filled and empty seeds using cues such as seed weight, which is significantly higher in filled than in empty seeds of *J. communis*, (see also Vander Wall & Balda, 1977; Senar, 1983; Jensen, 1985; Jordano, 1990; Obeso, 1998), or olfactory cues, with filled juniper seeds rich in scented compounds (Jennings, 1976; Jensen, 1985; Vander Wall, 1998). However, this discrimination ability is far from perfect, since in most cases the woodmice had to bite the seed coat to discriminate definitively against empty seeds (Figure 1, see also Obeso, 1998). Nevertheless, individual empty seeds take only a few seconds to manipulate (D. García, pers. observ.), suggesting that a woodmouse would expend only slightly greater effort to find filled seeds in a cluster containing many empty seeds (but see Kaufman & Collier, 1981; Jordano, 1990; Fuentes & Schupp, 1998). This implies that the cost to the predator associated with empty seeds is probably not very high, since the woodmouse ultimately identifies the empty seeds easily, before or after biting them.

Woodmice were apparently not influenced by the presence of empty seeds, given that we found no clear seed predation response to the proportion of filled *versus* empty seeds in the experiments. That is, most filled seeds were consumed irrespective of the number of empty seeds surrounding them. This suggests that empty seeds did not dilute woodmouse predation on filled seeds. Experimental results are strongly corroborated by observational data, which showed that woodmouse predation was independent of the proportion of empty seeds per individual plant and per population across sites and years, despite an outstanding within- and among-population variation in both seed viability and woodmouse predation. Furthermore, the lack of woodmouse response to seed viability per plant agrees with the minor effect of other individual plant traits such as plant size, cone crop or cone size on this rodent's predation (García, 1998b).

Our results indicate that the juniper does not benefit from producing more empty seeds, either in terms of reproductive output (individual plant perspective, evidenced by observational data) or in terms of offspring escape probability (seed population perspective, evidenced by experimental data). This finding, which contrasts with most available information (Zangerl, Berenbaum & Nitao, 1991; Traveset, 1993; Ziv & Bronstein, 1996; Verdú & García-Fayos, 1997; Fuentes & Schupp, 1998), is apparently related to some basic characteristics of the *A. sylvaticus-J. communis* system. Most insect seed predators maintain an intimate interaction with host plants, suffering a high penalty when ovipositing in empty seeds, which is quantified as a direct decrease in reproductive success (Traveset, 1993; Ziv & Bronstein, 1996; Verdú & García-Fayos, 1997). This populational effect would be strongest in monophagous insects, especially those unable to discriminate between filled and empty seeds (Traveset, 1993; Mustart, Cowling & Wright, 1995; Verdú & García-Fayos, 1997). In contrast, most granivorous vertebrates are polyphagous, living on several different co-occurring seed species, and therefore they might avoid the populational effect of empty seeds by changing their food habits, even when the plant producing empty seeds is their main resource (woodmice also feed on other woody species in the Mediterranean mountains; Herrera, 1984; Hulme, 1997; García, 1998b; Castro *et al.*, 1999). Additionally, the effect of empty seeds on vertebrate seed predators does not translate directly to a lower reproductive success but rather to lower foraging efficiency (see also Kaufman & Collier, 1981). All of this implies that only when the cost of feeding on empty seeds is very high, whether because the predator cannot distinguish them from filled seeds or because trying empty seeds dramatically increases handling time, can we expect a clear response of vertebrate seed predators to empty seeds (Fuentes & Schupp, 1998). However, this is not the case for woodmice living on juniper seeds, because they might learn to discover empty seeds before gnawing, and in any case can easily bite and reject the culls in a few seconds. This lack of effect of empty seeds on seed-predation rate may be a general pattern for systems in which the seed predators are polyphagous vertebrates, able to learn to discriminate against empty seeds.

In conclusion, this study suggests that empty seeds cannot be considered a defence against rodents in *J. communis*. The consistent production of empty seeds across all studied Mediterranean populations and years should thus be a consequence of other factors, for example, maternal constraints in seed development due to climatic stress and/or inbreeding depression (García *et al.*, 2000). The role of rodent seed predation in the maintenance of this trait is, therefore, negligible.

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