Behav Ecol Sociobiol (2008) 62:913–922
DOI 10.1007/s00265-007-0515-y

ORIGINAL PAPER

Seed choice by rodents: learning or inheritance?

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Received: 28 February 2006 / Revised: 27 September 2007 / Accepted: 24 October 2007 / Published online: 22 November 2007

Abstract Learning plays a central role in animal life, and it has received special attention in the context of foraging. In this study, we have tested whether learning operates in seed choices by rodents using the Algerian mouse (*Mus spretus*) and Holm oak (*Quercus ilex*) acorns as a model. At the laboratory, those rodents captured in the field during the acorn fall period (experienced individuals) rejected weevil-infested acorns, presumably because of their lower energetic value. By contrast, rodents born in captivity and reared without any contact with acorns (naïves) predated weevil-infested acorns at similar rates than sound ones. After exposing naïves to infested and sound acorns during 15 days, they rejected infested acorns as the experienced individuals. In the field, predation on weevil-infested acorns was lower than on sound ones. Predation rates on infested acorns were lowest at the end of the acorn fall season, whereas predation rates of sound acorns increased along the same period. This might be explained by the improved ability to reject infested acorns because of the accumulated experience acquired by the initially naïve rodents along the acorn fall season. We show that learning shapes strongly seed choices by rodents, and it may be advantageous over inherited behaviors in variable unpredictable situations, such as acorn infestation rates that vary strongly between years and trees. We consider that the role of learning has to be taken into account in future studies on seed predation by rodents.

Keywords Acorns · Learning · Rodents · Seed predation · Weevils

Introduction

Learning plays a central role in animal life (Gagliardo et al. 2001; Kelley et al. 2003; Qvarnstrom et al. 2004; Alves et al. 2007). Recent research considers that learning has a significant evolutionary meaning (ten Cate 2000; Lachlan and Servedio 2004; Beltman et al. 2004). However, the evolutionary and ecological aspects of learning are still less understood compared to other noncognitive behaviors (review in Dukas 2004), although current approaches to cognitive processes under ecological contexts go deep into the evolutionary ecology of animal cognition (Real 1993; Dukas 1998; Shettleworth 1998, 2001; Caldwell and Whiten 2002; Emery et al. 2004; Leduc et al. 2007).

Learning has received considerable attention in the context of foraging (Galef and Giraldeau 2001; Shettleworth 2001). For example, it has been demonstrated that learning influences food choices in a wide range of animals (Estes et al. 2003; Darmaillacq et al. 2004; Villalba et al. 2004; Bernays and Bright Bernays and Bright 2005). In particular, laboratory experiments, using Norway rats *Rattus norvegicus* as a model, have provided insights into the mechanisms underlying the role of learning in food preferences (Galef 1996; Galef and Whiskin 1998, 2001, 2004). However, little

Communicated by T. Czeschlik

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is known about the ecological and evolutionary aspects of learning in food choices by rodents under natural conditions.

Rodents are primarily granivorous; however, they also disperse and cache seeds, thus shaping the natural regeneration of many plant species (Vander Wall 1990; Brewer 2001; Jansen et al. 2002; Roth and Vander Wall 2005). For this reason, seed choice by rodents has been studied in many occasions. Seed choices by rodents has shown to be influenced by the size of the seed (Alcántara et al. 2000; Brewer 2001; Jansen et al. 2002), the plant species (Blate et al. 1998; Steele et al. 2006), the chemical composition of the seeds (Steele et al. 1993; Guimaraes et al. 2003), or the infestation of seeds by insect larvae (Steele et al. 1996). Nevertheless, little is known on the role of learning in seed choices by rodents. There is a single study showing a strong innate basis in the hoarding decisions of grey squirrels (*Sciurus carolinensis*) foraging on red and white oak acorns (Steele et al. 2006). In that study, the authors argue that the behavior observed suggests some level of adaptation by squirrels to the oaks. This level of adaptation assumes an evolutionary scenario where squirrel predation on acorns has been maintained in a stable manner for a long enough time so as to allow the genetic fixation of this behavior. However, this situation may not be true in less predictable environments where, by contrast, learning could be favored (see Dukas 1998, 2004).

In the present study, we hypothesize that learning could influence seed choices by the Algerian mouse (*Mus spretus*) foraging on Holm oak (*Quercus ilex*) acorns. If learning is operating, naïve rodents are expected to differ in their seed choices with respect to the experienced ones. Because this rodent species has a short lifespan and a high reproductive rate and because acorns are available once a year and during a short period (i.e., acorn fall season), a high proportion of the individuals of a rodent population probably have never faced seeds when acorns begin to fall (see Brewer and Webb 2001). In that case, the ecological significance of learning would be positively correlated with (1) the disparity in seed choices between naïve and experienced individuals and (2) the time needed by a naïve to become an experienced individual.

The main aim of the present study is to assess the role of learning in seed choice by rodents and the ecological consequences that this may have. The study was done in laboratory and field conditions. In the laboratory, we tested whether acorn choices regarding acorn size and weevil infestation are inherited or learned by *M. spretus* by comparing the seed choices of experienced and naïve individuals and subsequently by testing seed choices with the formerly naïve individuals after being offered different types of seeds. In the field, we estimated the relative abundance of naïve and experienced rodents in a *M. spretus* population at the beginning of the acorn fall season, and we measured the effects of acorn size and weevil infestation on seed predation patterns. We assessed whether the patterns of predation changed along the acorn fall season, as would be expected if naïves are developing progressively into experienced individuals (Brewer and Webb 2001). Based on our laboratory and field studies, we discuss why the evolution of learning might have been favored in seed choices by rodents and the ecological significance of such behavior.

Materials and methods

Study area, species, and ecological context

Field work was conducted at the Cabañeros National Park (Ciudad Real province, Central Spain, 39°24′N, 3°35′W) during autumn to winter of 2003. The study site is a Holm oak forest, with a shrub cover of *Cistus ladanifer*, *Phillyrea angustifolia*, and *Erica arborea*. The Algerian mouse (*M. spretus*) is by far the most abundant rodent at the study area, but the wood mouse (*Apodemus sylvaticus*) is also present (Muñoz and Bonal 2007). *M. spretus* is a small species (8–20 g) that inhabits the Iberian Peninsula and Northern Africa (Blanco 1998). Its lifespan is 12–14 months, and it typically breeds all year round (Blanco 1998). Females give birth to three to seven young that reach sexual maturity and reproduce in 4–5 weeks (Blanco 1998; own data). *M. spretus* consume a high proportion of the acorn crop, as acorns constitute the bulk of their diet during autumn to winter (Leiva and Fernández-Ales 2003; Muñoz and Bonal 2007).

In the study area, the acorn fall starts in September and lasts till January (Bonal and Muñoz 2007). Up to that date, acorns are available on the ground for postdispersal consumers, mainly small rodents and ungulates (Pulido and Díaz 2005; Bonal and Muñoz 2007; Muñoz and Bonal 2007). The acorn size of Holm oaks is extremely variable, ranging from 0.5 to 20 g (Pulido and Díaz 2005; Bonal and Muñoz 2008; Bonal et al. 2007). The chestnut weevil, *Curculio elephas* (Coleoptera: *Curculionidae*), is the most common predispersal acorn predator of Holm oaks. At the study site, half of the acorn crop is attacked by these insects on average, but between trees it may range from 0 to 100% (Bonal et al. 2007). Female weevils use a specialized tiny snout to perforate the acorn coat and deposit an egg inside (Desouhant et al. 2000). Attacked acorns are abscised a few days later, and the larvae continue growing inside, feeding on the cotyledons, after the acorn has fallen to the ground. Once their development is finished (on average 21.5 days after the acorn is dropped; Bonal and Muñoz 2007), they drill a circular exit hole of approximately 1.5 mm of diameter through the acorn coat, leave the acorn, and burrow underground for diapause. In this ecological scenario, rodents may encounter a wide range of acorn sizes, either sound or infested, and the latter either with the larva still inside or with a larval exit hole.

Field work

Rodent samplings We performed rodent censuses using standard Sherman live traps to determine the abundance of *M. spretus* at the study area and to estimate the proportion of naïves in the population at the beginning of the acorn fall season. We estimated the reproductive activity at the population level by recording the proportion of *M. spretus* less than 2 months old (easily identifiable by their gray coat and small size, usually less than 10 g) and also the proportion of males with scrotal testes. Two rodent censuses were carried out during 2003. One was performed in late April, as individuals born up to 2 months earlier are naïves. Acorns are available on the ground until February, when they are completely consumed by acorn predators (Bonal and Muñoz 2007). From April to the beginning of the acorn fall in autumn, all new individuals recruited into the population would be naïves, as no acorns are available during this period. Hence, a second census was performed in November, to estimate to what extent the number of naïves increased. We placed 32 trapping stations in the study site distributed over an area of approximately 50 ha. Traps were placed randomly but in such a fashion as to represent the entire study area. Each trapping station consisted of ten traps laid out in two parallel lines of five traps with 10 m between traps. Trapping sessions lasted for three nights (960 trap nights). Each trap was baited with an apple and a paste made of tuna fish in oil and flour. A piece of waterproof cotton was added to protect the captured rodents from cold and rain. At the point of capture, rodents were aged, sexed, weighted, and marked by cutting a small piece of hair from their head, which would make each individual easily recognizable in case of recapture. After being measured, rodents were released immediately at the point of capture.

Acorn choices in the field Acorn choices by rodents were studied during the acorn fall season of 2003 by monitoring the predation of marked acorns at feeding plots (50×50 cm) settled under the canopy of 45 Holm oaks. Selected oaks were sparsely distributed along the study area, with a minimum distance between each other of 35 m. This distance ensured that the same rodent was not feeding under different selected trees, according to home range sizes of radio-tracked *M. spretus* at the study area (90–130 m^2, with maximum linear displacements of 25 m; unpublished data). This was confirmed because we did not recapture the same rodent in different study trees during our trappings. The number of feeding plots per tree (two to four) was proportional to its canopy surface. Feeding plots were protected from other postdispersal acorn consumers (mostly ungulates) by means of 50×50×20 cm wire cages with a mesh size of 5×5 cm, which permitted the entrance of rodents. At each feeding plot, we placed six acorns of two types from the tree, half sound and half infested with the weevil larvae still inside. These acorns are easily identifiable because of the small perforation by the ovipositing female (Bonal et al. 2007, Bonal and Muñoz 2007, 2008). Acorns were individually weighed (to the nearest 0.01 g) and marked with 20 cm of fluorescent fishing line with 5 cm of fluorescent pink flagging tape at the end, to locate them in case they had been moved from the plots. This method of marking seeds is not considered to influence rodent foraging behavior (Jansen et al. 2002; Muñoz and Bonal 2007). Feeding plots were monitored every 10 days along the acorn fall season (November 2003–January 2004). At each monitoring, marked acorns were classified as not predated, partially predated, or completely predated. In addition, we noted whether the weevil larvae had exited from the infested acorns by checking for the presence of an exit hole. Acorns partially or completely predated were replaced by fresh ones in the feeding plots. Acorns were manipulated using fresh gloves to avoid human odor effects on seed choices by rodents (Wenny 2002).

Laboratory work

Capture and maintenance of rodents Laboratory experiments were carried out at the University of Castilla-La Mancha facilities. In December, we captured 19 adult *M. spretus*, 7 males and 12 females, using Sherman live traps from areas surrounding the study site of field work. These rodents were considered the 'experienced individuals,' as they had fed on acorns during the major part of the acorn fall season. Each mouse was housed individually in 60×32×30 cm terraria filled with a layer of sand 5 cm deep and provided with a piece of waterproof cotton for use as nesting material. Food for hamsters, fruits, and water were provided ad libitum. Terraria were placed indoors under natural photoperiodicity with no visual contact among individuals to avoid stress. In December, we additionally captured 15 pregnant females that gave birth to three to seven young each (mean±SE=4.8±0.3). Once the lactation period had finished, we randomly selected one young of each litter (15 mice) and another four randomly chosen from all litters. Finally, we had 8 males and 11 females that were 'naïves,' as they had no experience in feeding on acorns. Each naïve was individually housed the same as the adults captured in the field and fed with hamster food, fruits, and water ad libitum. Experienced rodents were held in their home terraria for at least 10 days before testing so that they had become familiarized with their new environment before the onset of the experiment. The naïves were maintained approximately 7 months in the laboratory before testing to reach a similar age than experienced individuals. Rodents were captured and maintained in laboratory under license from the Junta de Comunidades de Castilla-La Mancha. All the animals were healthy during the trials, and they were released at the exact capture sites at the end of the experiments.

Acorn choices in the laboratory We collected acorns from Holm oaks at the study area and weighed them to the nearest 0.01 g. In each trial, we placed 12 acorns at random in a 3×4 grid with a distance of 2 cm among them at the center of the home terrarium. Acorns were divided into three categories of size: large (>6 g), medium-sized (4–5 g), and small (<2 g). Each category included four types of acorns: one sound, one infested with the weevil larva still inside, one with a larval exit hole, and one sound with an artificial hole perforated by us simulating a larval exit hole. This latter category (sound-artificially perforated acorns) allowed us to test whether rodents use the hole perforated by the larva as a single cue, or they use other cues in their acorn choices. As *M. spretus* show nocturnal activity, acorns were placed at 18:00 GMT and revised at 9:00 GMT in the next morning. Then, we noted whether each acorn had been partially or completely predated and weighed the acorns that were partially predated to estimate the amount of cotyledon eaten. Before each trial, we eliminated remains of commercial food from the terrarium to ensure that experimental acorns were the only food source available. We performed one trial per mouse. Once naïves had completed their test, they were fed exclusively with a mixture of sound and both types of infested acorns (i.e., with the larva still inside and with a larval exit hole) during 15 days. During this ‘training period,’ they had the opportunity to learn to discriminate among acorns. Thus, when the training period had finished, the test was repeated to examine whether they had changed their initial feeding choices.

Data analyses

Acorn choices in the field were analyzed using repeated-measures analysis of variance (ANOVA) with angular-transformed proportion of acorns predated as the dependent variable, type of acorn as a between-subjects factor, and date as the within-subjects factor to test for the changes in the predation patterns during the acorn fall season. Logistic regressions were performed to analyze the effects of acorn mass on the probability of predation in the field. Data from laboratory tests were analyzed in two hierarchical steps (Sallabanks 1993). In the first step, rodents must decide which acorn to eat. In the second step, rodents must decide how much to eat from the selected acorn. Examining feeding decisions during the first step allowed us to determine whether rodents were able to reject the acorns without eating them. We analyzed the frequencies of acorns eaten (partially or completely) using log-linear models (Heisey 1985), with acorn size and acorn type as classification factors. In the second step, we analyzed the amount of cotyledon consumed from the eaten acorns using factorial ANOVA. The amount of cotyledon consumed was estimated as the weight of each intact acorn minus its weight after consumption. Post-hoc comparisons were made with Tukey honestly significant differences tests in all cases. In the case of naïves, we performed a repeated-measures ANOVA with individual as the within-subjects factor and type and size of acorns as the between-subjects factors to search for differences in the amount of cotyledon consumed before and after the training period. The amount of cotyledon consumed was log transformed to conform to the assumption of normality (Kolmogorov–Smirnov test, $d=0.06$, $P>0.2$) and homocedasticity (Barttlet test, $P>0.2$).

Results

Rodent samplings

M. spretus was by far the dominant species in the study area. Overall, we trapped 92 *M. spretus* and 11 *A. sylvaticus*. In April, we captured 40 *M. spretus* (20 males and 20 females); 30% of them were less than 2 months old, and the 40% of adult males had scrotal testes. In November, we trapped 52 *M. spretus* (28 males and 24 females); 27% of them were less than 2 months old, and 35% of the adult males had scrotal testes. Given the high reproductive rate and the short lifespan of the species, our trappings suggest that more than 90% of rodents of the population studied were naïves at the beginning of the acorn fall season. Moreover, as *M. spretus* reproduces all year long, additional naïves are recruited into the population during the acorn fall season.

Acorn choices in the field

Every 10 days, we monitored 566 marked acorns on average and found more than 94% of them. Acorn predation was strongly influenced by acorn type. Sound acorns were predated at higher rates than both types of infested acorns ($F_{2,\ 106}=56.42$, $P<0.0001$; Fig. 1). Moreover, predation rate on sound acorns increased along the acorn fall period, whereas predation rates on both types of infested acorns were constant or slightly decreased over

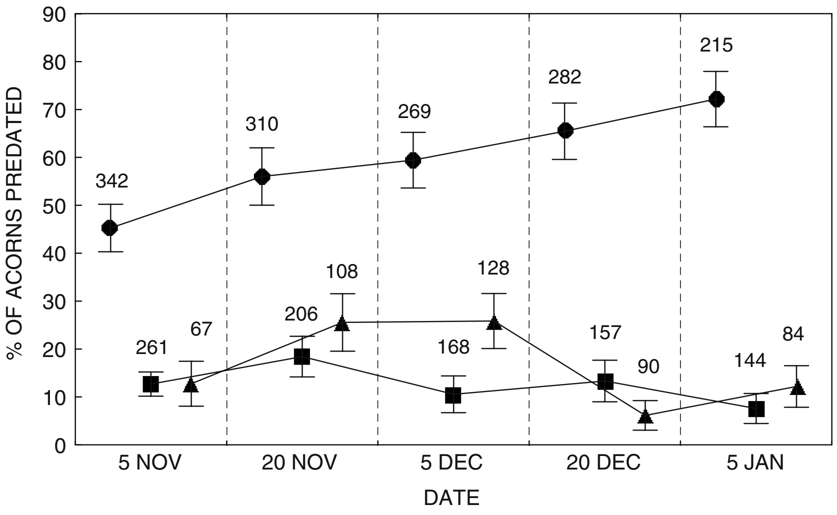

Fig. 1 Predation rates of sound acorns (*circles*), infested acorns with the weevil larva still inside (*squares*), and acorns with a larval exit hole (*triangles*) along the acorn drop season in the field. Values on *whiskers* show the number of marked acorns placed in the feeding plots

time (acorn type×date, $F_{8,\ 424}=5.33$, $P<0.0001$; Fig. 1). Sound acorns were completely predated more often (94.55%) than infested ones with the larva inside (68.17%) and those with larval exit holes (77.98%; $P<0.001$ in both cases). No relationship was found between predation likelihood of sound acorns and acorn size (Wald Statistic=2.55, $P=0.11$), but predation on infested acorns, with the larva still inside and with larval exit holes, was positively correlated with acorn size (Wald Statistic=31.96, $P<0.001$ and 82.19, $P<0.001$, respectively).

Acorn choices in the laboratory

What to eat? The frequencies of acorns eaten by experienced and naïve rodents (before and after the training period) are shown in Fig. 2. Acorn type had an effect on the number of acorns eaten by experienced individuals (Table 1). Acorns with larval exit holes were rejected without being eaten more frequently than the other acorn types in all acorn sizes ($P<0.01$ in all cases), and sound acorns that were artificially perforated were eaten at similar frequency to sound intact acorns (Fig. 2). By contrast, naïves did not discriminate between acorns with a larval exit hole from the rest of acorn types before the training period (Table 1; Fig. 2). The frequency of acorns eaten by naïves was significantly lower for large- than for small- and medium-sized acorns before the training period ($P<0.01$ in both cases; Table 1). However, after the training period, naïves significantly rejected the acorns with a larval exit hole without being eaten ($P<0.01$ in all cases, Fig. 2) but did not reject sound acorns with artificial holes. The frequencies of eaten acorns were not influenced by acorn size ($P=0.38$; Table 1).

How much to eat? Only one acorn out of the 684 eaten in the laboratory trials was completely consumed. In the

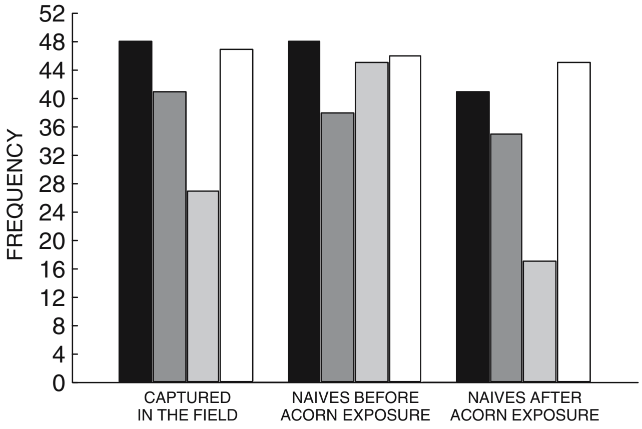

Fig. 2 Frequencies of eaten acorns of each type (*solid bar*, sound; *dark gray bar*, infested with the larva still inside, *light gray bar*, infested with a larval exit hole; and *empty bar*, sound but artificially holed) by rodents of each experimental group

Table 1 Results of the fitting of log-linear models to the three-way contingency tables generated by the factors acorn size, acorn type, and whether acorns were eaten or not for each group of rodents

Factors	*df*	E		NB		NA	
		G^2	*P*	G^2	*P*	G^2	*P*
Size	2	0.01	0.99	0	>0.99	0	>0.99
Type	3	0.01	0.99	0	>0.99	0	>0.99
Eaten	1	42.27	<0.001	69.58	<0.001	9.66	<0.001
Ea×si	2	2.85	0.24	18.39	<0.001	1.93	0.38
Ea×ty	3	22.90	<0.001	5.48	0.14	32.42	<0.001
Ty×si	6	0.24	0.99	0.44	0.99	0.26	0.99
Ea×ty×si	6	4.77	0.59	3.12	0.79	8.55	0.21

E Experienced, *NB* naïves before training them with a mixture of acorns, *NA* naïves after training

Table 2 Results of factorial ANOVA comparing the mass of cotyledon eaten by experienced and naïve rodents among acorn types (sound, infested with the weevil larva inside, infested with a larval exit hole, and sound artificially holed) and acorn sizes (small, medium-sized and large)

Factors	Experienced			Naïves		
	F	*df*	*P*	*F*	*df*	*P*
Type	5.53	3/151	0.038	10.87	3/176	<0.001
Size	3.33	2/151	0.001	27.64	2/176	<0.001
Type×size	3.11	6/151	0.007	0.94	6/176	0.470

experienced rodents, the amount of cotyledon consumed of each acorn type depended on acorn size (Table 2). In sound acorns, they consumed larger amounts of cotyledon in small acorns than in medium-sized ones ($P=0.036$ Fig. 3). They also consumed larger amounts of cotyledon in small acorns than in large ones (Fig. 3), but in this case, the differences were marginally significant ($P=0.08$). In the infested acorns with the larvae inside, there were no significant differences in the amount of cotyledon consumed between acorn sizes ($P>0.2$ in all cases). Finally, in the acorns with a larval exit hole, experienced rodents consumed more cotyledon of large acorns than either of small- ($P=0.05$) and medium-sized ones ($P=0.02$). The amount of cotyledon consumed by experienced individuals was not significantly different between sound and sound, artificially perforated acorns ($P>0.2$ in all cases; Fig. 3).

In the case of naïves before the training period, both acorn type and size independently affected the amount of cotyledon eaten (Table 2). Naïves ate significantly more cotyledon mass of sound acorns with artificial holes than of both types of infested acorns ($P<0.01$ both cases) and significantly less of infested acorns with the larva inside than from the rest of acorn types ($P<0.01$ in all cases; Fig. 4). Furthermore, they consumed more cotyledon mass from large- than from medium-sized and small acorns ($P<0.01$ in both cases) and more from medium-sized than from small acorns ($P<0.01$; Fig. 4). However, after the training period, naïves changed their decisions in relation to acorn type (Table 3). After the training period, they consumed more cotyledon mass of infested acorns with the larva inside and less of acorns with a larval exit hole than in their previous choices, but they did not change their decisions regarding acorn size (Table 3).

Discussion

Acorn choice by rodents

Weevil-infested acorns were clearly less preferred by rodents than sound ones in the field. This contrasts with those studies showing that squirrels do not discriminate between infested and sound acorns (Semel and Andersen 1988; Weckerly et al. 1989) or that they selectively cache sound acorns but eat weeviled ones because weevil larvae may be a dietary supplement (Steele et al. 1996). However, the costs of opening an infested acorn to consume the larvae, which are usually small sized (Bonal and Muñoz 2007, 2008), may exceed the nutritional gain if other alternative food supplements (e.g., other insects) are available (Semel and Andersen 1988; Dixon et al. 1997).

Our results agree with those studies reporting that infested seeds and fruits are rejected because of the extensive damage caused by larvae, their lower caloric value, or reduced palatability (Christensen and Whitman 1991; Traveset et al. 1995; Dixon et al. 1997; García et al. 2000; Bonal and Muñoz 2007, 2008). Weevil larvae considerably reduce the cotyledon mass, but the larger the size of the acorn, the larger is the amount of cotyledon left by the larvae (Bonal et al. 2007). This may explain why predation on larval-holed acorns was positively correlated with acorn size both in the field and in the laboratory tests. Furthermore, the reduced palatability or the nutritional value of the cotyledon left by larvae may have affected

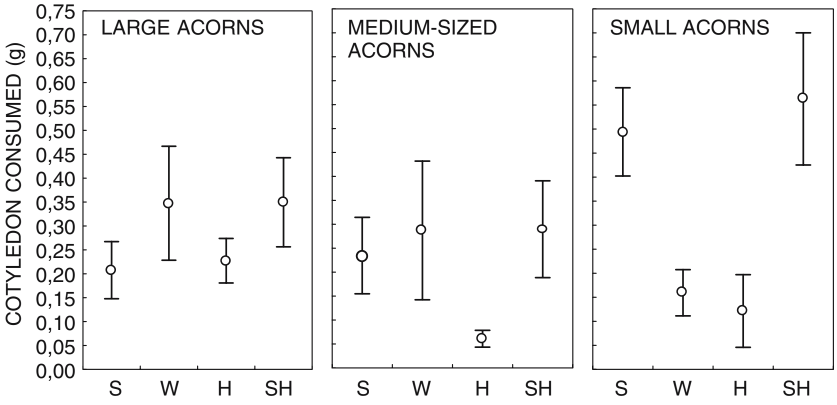

Fig. 3 Comparisons of the mass of acorn consumed by experienced rodents among acorn sizes and acorn types. *S* Sound, *W* infested with the weevil larva inside, *H* infested with a larval exit hole, *SH* sound artificially holed

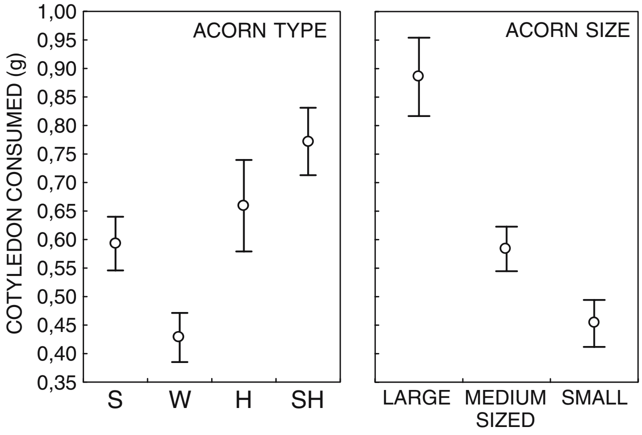

Fig. 4 Comparisons of the mass of acorn consumed by naïve rodents before acorn exposure among acorn types and acorn sizes. *S* Sound, *W* infested with the weevil larva inside, *H* infested with a larval exit hole, *SH* sound artificially holed

acorn choices as well (Sallabanks and Courtney 1992). In fact, the frass of weevil larvae filled the space originally occupied by the cotyledons as they fed (personal observation), making the infested acorns less attractive for rodents. These changes may explain why both types of infested acorns were completely consumed less frequently than sound acorns in the field.

Acorn choice and learning

We found different patterns of acorn predation between experienced rodents (either captured in the field or trained in the laboratory) and naïves. Therefore, individual experience on acorns can influence subsequent acorn choices. Experienced rodents rejected the acorns with a larval exit hole without eating them, but the hole was not the single cue used for rejection, as sound acorns artificially perforated were eaten at similar rates to sound ones. The larval exit holes could facilitate access to olfactory cues derived from weevil activities inside the acorn, providing a possible proximate cause of rejection. Alternatively, the ratio between the size and weight of acorns may have influenced seed choices. This ratio is much lower in acorns with larval exit holes than in sound ones because of cotyledon loss (Bonal et al. 2007; Bonal and Muñoz 2008). Naïves did not reject the acorns with larval exit holes. It is possible that naïves associate the visual and olfactory cues or weight/size ratios of acorns with larval exit holes, with their specific taste and reduced palatability of these acorns (see Rowe and Skelthorn 2005). After the training period, naïves rejected the acorns with larval exit holes. They also consumed less cotyledon mass from these acorns, suggesting that they had learned to recognize this type of acorn as not profitable.

We found differences in the choices between experienced and naïve rodents regarding acorn size. The mass of sound acorns consumed by experienced rodents was negatively related to acorn size. This may be explained by the increased time-spending costs linked to handling large seeds (Jacobs 1992; Hadj-Chikh et al. 1996). Because of their foraging experience in the field, experienced rodents may be able to avoid increased handling costs of larger acorns, which may in turn be associated with increased predation risk (Jacobs 1992). As a matter of fact, handling costs may be particularly important in a small-sized species like *M. spretus* (Muñoz 2005). By contrast, the mass of sound acorns consumed by naïves was positively related to acorn size, possibly because they had not experienced the costs of handling large acorns in the field. This may also explain why they continued to consume larger acorns even after being fed with a mixture of acorns in laboratory, where they never experienced any kind of predation risk.

Learning vs inheritance in acorn choice

In foraging behavior, learning can be especially useful when errors in prey selection can have important negative consequences for predators, such as physiological costs of ingesting certain food items (e.g., toxins, see Galef 1996). Learning may be also useful to save time and energy that could be used for other vital tasks (Stephens and Krebs 1986; Dukas 1998). Learning to recognize infested acorns could maximize net energy intake and may save time that could be devoted to more profitable food sources, reproduction, or predator avoidance. However, if acorn recogni-

Table 3 Results of the repeated-measures ANOVA and Tukey HSD tests for comparisons of the amount of cotyledon (in grams) eaten by naïve rodents before and after being exposed to acorns

Source of Variation	ANOVA			Tukey HSD			
	F	*df*	*P*	Type	Before	After	*P*
Training	0.01	1/215	0.923	S	0.54	0.56	0.862
Training×size	2.06	2/215	0.130	W	0.31	0.54	0.016
Training×type	3.99	3/215	<0.01	H	0.52	0.26	0.023
Training×size×type	0.30	6/215	0.94	SH	0.68	0.67	0.963

S Sound, *W* infested with the weevil larva inside, *LH* infested with a larval exit hole, *SH* sound artificially holed tion is so advantageous for rodents, why has this ability not been genetically fixed in the rodent behavioral repertoire? Learning may be advantageous over genetically fixed traits in variable and unpredictable environments (Dukas 1998, 2004) and acorn infestation rates vary sharply between oaks, sites, years, and also along the acorn drop season (Crawley and Long 1995; Bonal and Muñoz 2007; Bonal et al. 2007). This spatial and temporal variability in the abundance of infested acorns can make optimal foraging decisions dependent on the relative abundances of each acorn type (Emlen 1996). For example, if sound acorns are scarce, rapid recognition of infested acorns may help to balance the costs and benefits of consuming them, thus making learned decisions advantageous over inherited rejection of infested acorns. Steele et al. (2006) documented a strong inherited basis in the hoarding decisions of gray squirrels foraging on red and white oak acorns, suggesting that squirrels have some level of adaptation to the oaks. This assumes that squirrels have fed on acorns in a somewhat stable and predictable environment, which has allowed the genetic fixation of this behavior. Hence, whether learning evolves or not in a species could be mediated by the variability and predictability of food sources. Then, it would be interesting to study explicitly whether the smaller variability and higher predictability in food resources favor inherited behaviors in habitats with variable food resources and with different rodent species.

Ecological implications of learning in acorn choice

In the study area, *M. spretus* behaves mainly as a predator of Holm oak acorns, although a few acorns may be cached for long periods of time (Muñoz and Bonal 2007). In a 2-year study (2003–2004), we found that 50% of the sound acorns were predated at the feeding plots, whereas only 10% of sound acorns were cached and not recovered in the short term (Muñoz and Bonal 2007). Predation at the feeding plots was even higher (80%) and caching rate even lower (5%) in the case of infested acorns (Muñoz 2005). Seed predation has usually been studied at the population level, where the responses of a certain granivorous species to a particular array of seeds have been measured (e.g., Forget 1990; Steele et al. 1996; Garb et al. 2000; Brewer 2001; Jansen et al. 2002; Roth and Vander Wall 2005). Such studies typically do not examine intraspecific variability in foraging responses. We found significant interindividual differences in foraging experience that influence seed choices by rodents. Therefore, intraspecific variability in seed choices by rodents must be considered when developing an ecological theory about the effects of seed choice (see Hayes and Jenkins 1997; Jenkins 1997). Furthermore, patterns of seed predation recorded at the population level may mask patterns of variation in seed predation among individuals. For example, in the field, we found no correlation between sound acorn predation and acorn size at the population level, which might lead us to conclude that there were no significant effects of acorn size on seed predation by rodents (Garb et al. 2000; Kollman et al. 2001). However, the population patterns may combine those of experienced individuals (which preferred small sound acorns) and naïves (which preferred large sound ones). By contrast, population patterns may be in accordance with individual preferences if there is no variability among individuals. For instance, in the case of the infested acorns, we found a positive correlation between acorn predation and acorn size at the population level and also in both naïves and experienced individuals in the laboratory trials. Our laboratory trials suggest that the time necessary for a naïve to discriminate between intact and infested acorns is less than 15 days, explaining the low predation on infested acorns in the field. On the other hand, the increasing acorn predation of sound acorns during the acorn fall season and the very low predation of infested acorns at the end of this period may be explained by naïves becoming more experienced during the acorn fall season, increasing their ability to reject infested acorns.

The present study shows that learning influences seed predation by rodents and suggests that it may have ecological consequences not previously considered. However, we are aware that the results obtained under standardized conditions should be taken cautiously, as multiple variables may act in a natural environment. Indeed, the difficulties of studying the cognitive processes in the field and the ecological processes in the laboratory may be one of the main causes to explain why cognitive and ecological approaches have not been well integrated yet and why the role of learning remains largely unanswered in the ecological context (Dukas 2004).

Acknowledgments We thank B. Nicolau for his assistance in the field and laboratory. M. Díaz, JM Aparicio, T Czeschlik, and three anonymous reviewers provided helpful comments on the manuscript. AM and RB were supported by a fellowship from La Junta de Comunidades de Castilla-La Mancha. This study was supported by the projects REN2003-07048/GLO, CGL2006-06647/BOS, PAC-02-008, 096/2002 and 003/2007. Rodents were captured and maintained in the laboratory under license from the JCCM.

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