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Acorn preference under field and laboratory conditions by two flightless Iberian dung beetle species (*Thorectes baraudi* and *Jekelius nitidus*): implications for recruitment and management of oak forests in central Spain

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Abstract. 1. Recently, a mutualistic relationship has been described between some dung beetles (*Thorectes lusitanicus* and *Mycotrupes lethroides*) and oak species (*Quercus suber*, *Q. canariensis*, and *Q. rubra*), which could be crucial for ensuring seedling recruitment and sustaining the equilibrium of oak populations. For *T. lusitanicus*, a diet based on acorns during the reproductive period improved resistance to low-temperature conditions and improved ovarian development.

2. In this paper, we conducted field and laboratory experiments to investigate the interaction between two potential acorn-eating beetles, *Thorectes baraudi* and *Jekelius nitidus*, with *Quercus suber*. We determined the feeding preferences of both beetle species and estimated the rates of acorn manipulation by beetles according to habitat structure and several characteristics of the acorn, such as seed size and acorn infestation by weevils.

3. Results demonstrated the positive interaction between the dung beetle *Thorectes baraudi* and *Quercus* trees. *Thorectes baraudi* was clearly more attracted to volatiles of acorns than to dung. *Jekelius nitidus*, on the contrary, was either not or anecdotally attracted to acorns. On the contrary, in the case of *Jekelius nitidus*, the acorn attraction could be considered anecdotal or even accidental. Our field results demonstrated the acorn burying behaviour of *T. baraudi* in the oak forests of the Cabañeros National Park (Spain), suggesting a potential role of this beetle species as an active secondary acorn disperser.

4. This unexpected behaviour could be particularly important in Mediterranean oak forests and savannahs, where most *Quercus* species are strongly recruitment limited because of serious overgrazing problems.

Key words. Acorn removal, Cabañeros National Park, deer grazing, dietary shift, Mediterranean ecosystems, oak recruitment, *Quercus*, seed dispersal.

Introduction

Plant-disperser mutualism is hypothesised to be crucial for long-term viability of tree populations (Díaz, 1992, Purves *et al*., 2007). Most studies on seed dispersal in oak forests have focused on the interactions between *Quercus* species and small vertebrates, especially rodents (Pulido & Díaz, 2005; Gómez *et al*., 2008) and jays (Gómez, 2003; Pons & Pausas, 2007). Recently, two novel interactions have been described between dung beetles and oak species. In oak forests of the southeastern Iberian Peninsula, an endemic Geotrupidae dung beetle species, *Thorectes lusitanicus*, buries and feeds on

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acorns of two coexisting *Quercus* species (Pérez-Ramos *et al*., 2007). Laboratory bioassays have confirmed their feeding preferences for acorns in comparison with the main type of food previously described for this beetle species (dung of large herbivores) (Verdú *et al*., 2007). The same behaviour has been observed in *Mycotrupes lethroides* (Beucke & Choate, 2009), another Geotrupidae dung beetle species restricted to the southeastern coastal plain of the United States. This surprising dietary shift confers clear ecophysiological and reproductive advantages for the beetle (Verdú *et al*., 2010). This interaction also implies a potential benefit for natural regeneration of the tree because *T. lusitanicus* acts as a post-dispersal seed predator and an authentic secondary seed disperser. A proportion of the acorns buried by beetles are abandoned or not completely consumed by them, which enables a higher survivorship of the seeds and increases their protection from more efficient seed predators (Pérez-Ramos *et al*., 2007). However, this type of oak–beetle mutualism, which could be crucial to ensure seedling recruitment and sustain oak population equilibrium, has not yet been documented in other similar forest ecosystems.

In the Iberian Peninsula, there are three flightless Geotrupidae genera (*Jekelius*, *Silphotrupes*, and *Thorectes*) that could potentially behave as acorn consumers. Recent molecular studies (R. L. Cunha, J. R. Verdú, J. M. Lobo, and R. Zardoya, unpublished results) have clearly demonstrated that these three genera of dung beetles, considered by some authors (Löbl & Smetana, 2006) as belonging to the same genus (*Thorectes sensu lato*), are monophyletic and sister groups. The western Mediterranean Basin and, in particular, the Iberian Peninsula constitutes the main diverse region of diversification for these three genera. Nineteen of the 39 world species belonging to these genera (Schoolmeesters, 2010) occur in the Iberian Peninsula, a territory which harbours the greatest proportion of *Thorectes* (*s.l.*) endemic species in the Palaeartic Region (Baraud, 1992; Verdú & Galante, 2000). One of the most representative Iberian reserves in Mediterranean ecosystems is the Cabañeros National Park, a protected region where the vegetation is characterised by a mosaic of grassland (Mediterranean savannah), dense scrubland, and mixed oak forests. Previous studies in this reserve have documented serious problems with natural regeneration for the main co-existing *Quercus* species (Muñoz & Bonal, 2007; Smit *et al*., 2009). The high pressure of seed and seedling consumers along with the high rate of seedling mortality as a result of the summer water stress and the low density of small acorn dispersers, such as rodents or jays (Muñoz & Bonal, 2007; Smit *et al*., 2009), have been identified as the main limiting factors for oak seedling recruitment in these forest sites. Two species of flightless Geotrupid beetles, *Thorectes baraudi* and *Jekelius nitidus*, which are commonly considered as dung-fibre consumers of several mammal species such as cows, sheep, red deer, and rabbits (López-Colón, 1989, 2000), have large populations in this natural reserve (Numa *et al*., 2009). However, the potential role of these two beetle species as acorn consumers and dispersers still remains unknown.

In this paper, we conducted field and laboratory experiments to investigate the interaction between two Iberian dung beetle species, *Thorectes baraudi* and *Jekelius nitidus*, with *Quercus suber*. We determined the feeding preferences of both beetle species and estimated the rates of acorn manipulation by beetles according to habitat structure and several characteristics of the acorn, such as seed size and acorn infestation by weevils. The results will outline the potential role of these *Quercus*–beetle interactions for the oak forest regeneration in the Cabañeros National Park.

Materials and methods

Study area

The study area is located in the Cabañeros National Park in the centre of the Iberian Peninsula (39°24′N; 0°35′W) within the Iberian Mediterranean region. The climate is Mediterranean with cool, wet winters alternating with warm, dry summers. Annual rainfall ranges from 500 to 750 mm. Annual temperature varies from 18 to 21 °C with a maximum value of 40 °C and a minimum of −12 °C. The landscape is composed of a mosaic of forest, dense scrubland and savannah-like habitats. The dominant vegetation is mainly constituted by oak trees such as *Quercus suber*, *Q. pyrenaica*, *Q. faginea* and *Q. ilex* (Vaquero de la Cruz, 1997). The availability of trophic resources (mainly red deer droppings) for dung beetles can be considered to be homogenously distributed across the different habitats and landscapes (Numa *et al*., 2009). The availability of acorns in the soil, however, can vary according to the habitat structure and the density of acorn consumers, such as red deer (*Cervus elaphus*), wild boar (*Sus scrofa*), roe deer (*Capreolus capreolus*), wood mouse (*Apodemus sylvaticus*), Algerian mouse (*Mus spretus*), Iberian hare (*Lepus granatensis*), wood pigeon (*Columba palumbus*), and the European jay (*Garrulus glandarius*).

Habitat preference by dung beetles

Habitat preference of both dung beetle species was estimated by exploring the variation in the number of collected individuals in 27 sampling sites distributed across the three main landscapes of the study area (forest, scrubland, and grassland). The abundance of both beetle species was estimated in each sampling site by placing 12 pitfall traps baited with *c*. 100 g of sheep dung. All pitfall traps, which remained active from March to November 2004, were removed every 2 weeks and the number of the collected individuals was recorded (see Numa, 2008 for methodological details).

Acorn manipulation by beetles

As a result of the high acorn removal rates previously detected in the study area by other seed predators (especially large herbivores), the oak–beetle interactions were examined by an exclusion field experiment. In November 2006, a total of 32 wire cages (1 × 1 × 0.3 m; see Fig. 1) were randomly distributed within the study area, covering the two

Fig. 1. Predator exclusion cage designed for the field experiment directed to estimate the acorn manipulation rates by *Thorectes baraudi* and *Jekelius nitidus*. These cages are wooden squares (1 × 1 × 0.3 m) covered with a protective stainless steel mesh (0.25-cm grid size) that hinder acorn predation by rodents, birds, and other insects. The cages were placed within wider fenced areas to exclude red deer, roe deer, and wild boar.

most contrasting habitats along the landscape. A total of 16 wire cages were set up in a forest locality and another 16 cages were placed in a savannah locality. The mesh size of the cages (0.25 cm × 0.25 cm) was selected to exclude other acorn predators such as large herbivores, birds, and rodents. Five pairs of beetle specimens (five males and five females) were introduced within each cage together with a fixed quantity of acorns three times greater than their population ($n = 30$). Half of the cages were filled with individuals of *T. baraudi* and the other half with individuals of *J. nitidus*. To evaluate the effect of seed size and acorn infestation by weevils on oak–beetle interactions, three types of acorns were used in each replicate: 10 large acorns (more than 3 cm in length), 10 small acorns (~2 cm in length), and 10 acorns infested by weevils (particularly by *Curculio elephas*). Acorns of *Quercus suber* were collected from various trees (at least 10 of each species) in the surroundings of the study area during the fruiting season (October to December 2006). The individuals of the two beetle species were also manually collected and returned to the study area at the end of the experiment.

All acorns were periodically monitored from autumn 2006 to spring 2007, recording the number of them buried by beetles, the percentage of seed mass consumed and the number of seedlings established.

Feeding preferences

Behavioural experiments under laboratory conditions were conducted from November to December 2006 on beetles collected in the Cabañeros National Park to test the response of both beetle species to different food sources. Two four-arm olfactometers were used to test the effects of different volatiles emitted by acorns of *Q. suber* and two types of dung (cow and rabbit). The olfactometer consisted of a central arena with sterile dry leaves as a substrate and four 5-cm diameter hole exits to attach the tubes (arms) containing the plastic containers with the test samples at the ends. These plastic containers were designed to capture the beetles that positively responded to the tested resources. The olfactometers were developed and described in detail by Verdú *et al*. (2007). The temperature in the bioassay room was maintained at 25–27 °C. Odour sources were randomly placed in the olfactometers in each trial.

Odour source preference was tested using the following four odour sources: (i) 50 g of fresh cow dung, (ii) 50 g of fresh rabbit dung, (iii) 50 g of mature *Q. suber* acorns, and (4) a control consisting of an empty container. For this bioassay, a total of 100 males and 100 females were used in 10 separate trials for each beetle species (20 beetles per session and olfactometer).

Data analyses

In the field experiment, differences in the number of acorns buried by beetles were examined using the non-parametric Mann–Whitney (MW) test for habitat comparisons and the Kruskal–Wallis (KW) test for comparisons among the three types of acorns. The Conover–Inman post-hoc test was additionally used for pair-wise comparisons. The KW test was also used to compare habitat preferences as well as the number of beetles attracted to the different odour sources under laboratory conditions. Possible differences between sexes were investigated using Wilcoxon's signed-rank test (W). All analyses were conducted using Statistica 6.0 software (StatSoft, 2001) and StatsDirect 3.0 (StatsDirect, 2005).

Results

Habitat preference by dung beetles

In total, 673 individuals of *T. baraudi* and 2,122 of *J. nitidus* were collected in the pitfall traps. The number of collected individuals of *T. baraudi* differed significantly among the three types of habitats (KW = 8.26, $P = 0.02$), appearing at a higher abundance in the forest and in the scrubland habitats compared with the open grasslands (savannahs). However, no significant difference among the habitats was found for *J. nitidus* (KW = 4.10, $P = 0.13$).

Acorn manipulation by beetles

The proportion of acorns manipulated by *Thorectes baraudi* was significantly higher than those manipulated by *Jekelius nitidus* (MW = 409, $P < 0.01$). *Thorectes baraudi* buried the 5.8% of the experimental acorns (1.75 ± 0.52 acorns/cage; mean ± SE), whereas *J. nitidus* buried only 0.7% (0.21 ± 0.08 acorns/cage). Both beetle species buried a higher quantity of acorns in the forest site than in the savannah habitat (*T. baraudi*: MW = 30, $P = 0.01$; *J. nitidus*: MW = 42, $P = 0.04$) (Fig. 2A and C). No significant differences in acorn

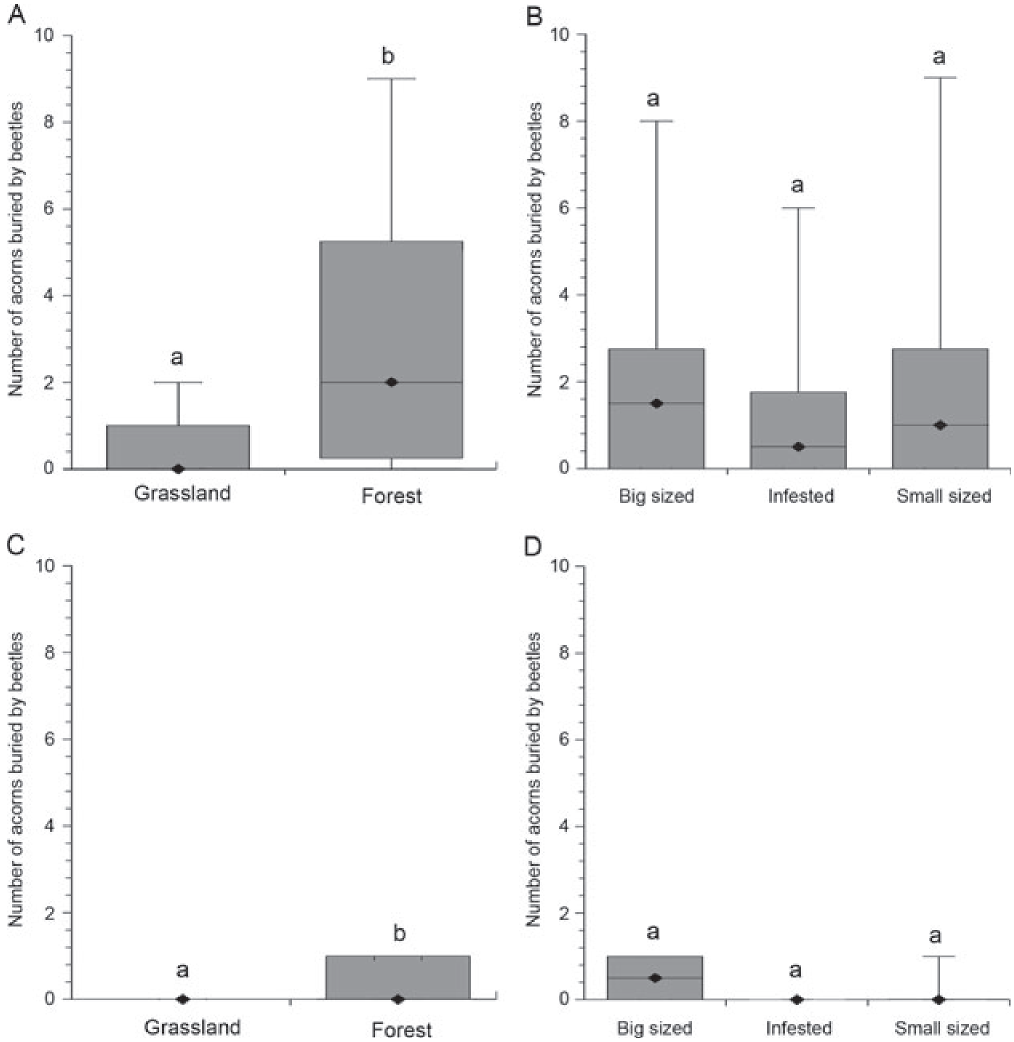

Fig. 2. Acorn burial rates for *Thorectes baraudi* (A, B) and *Jekelius nitidus* (C, D) according to the type of habitat (grassland and forest) and acorn characteristics (seed size and infestation by weevils). Horizontal lines and rhombuses within each box represent medians, boxes show quartiles and whiskers represent the extreme values. Treatments with the same letter did not differ from each other for the sum of both sexes per bar ($n = 10$; Kruskal–Wallis test with the Conover–Inman post-hoc test for pair-wise comparisons, $\alpha = 0.05$). Possible differences between sexes are explained in the text.

manipulation rates were detected as a function of the seed size and the acorn infestation by weevils (*T. baraudi*: KW = 0.50, $P = 0.78$; *J. nitidus*: KW = 3.12, $P = 0.21$; Fig. 2B and D).

Feeding preferences under laboratory conditions

Thorectes baraudi showed a positive response to acorns that was significantly higher (KW = 28.82, N = 10, $P < 0.0001$) compared with the other available odour resources (Fig. 3A). A significant feeding preference for rabbit dung versus cow dung was also observed for this species ($P < 0.001$). The response to cow dung was not significantly different to the control conditions ($P = 0.086$). Additionally, there were no differences between males and females in odour responsiveness ($P = 0.480$).

For *J. nitidus*, the most preferred odour resource was the rabbit dung although no significant differences were found compared with cow dung ($P = 0.250$) (Fig. 3B). Contrary to *T. baraudi*, *J. nitidus* did not show a higher positive response to acorns than to the other odour resources including the control ($P = 0.884$). Similar to *T. baraudi*, no significant differences between males and females in odour responsiveness were observed for this species ($P = 0.980$).

Discussion

Inter-specific differences in acorn preferences

Results from the present study unequivocally demonstrate the existence of a positive interaction between the dung beetle

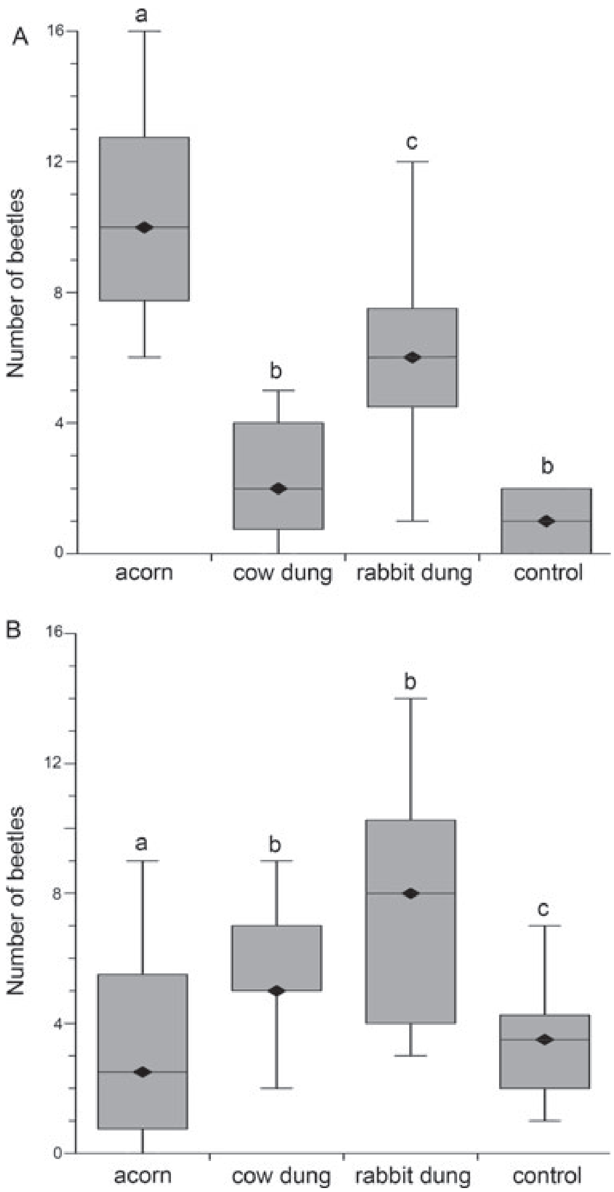

Fig. 3. Olfactory responses of *Thorectes baraudi* (A) and *Jekelius nitidus* (B) to three different odour cues under laboratory conditions. Horizontal lines and rhombuses within each box represent medians, boxes show quartiles and whiskers represent the extreme values. Treatments with the same letter did not differ from each other for the sum of both sexes per bar ($n = 10$; Kruskal–Wallis test with the Conover–Inman post-hoc test for pair-wise comparisons, $\alpha = 0.05$). Possible differences between sexes are explained in the text.

T. baraudi and *Quercus* trees. Both field and laboratory experiments provided similar results to those of the phylogenetically close species *T. lusitanicus* (Pérez-Ramos *et al*., 2007; Verdú *et al*., 2007). The olfactory bioassays showed that *T. baraudi* was clearly more attracted to volatiles of acorns in comparison with the main feeding resource previously described for this beetle species (dung of large herbivores). Interestingly, its feeding preference for acorns was independent of the sex, a finding that is supported by the results of previous studies (Pérez-Ramos *et al*., 2007). However, odour responses in laboratory experiments showed a lower attractiveness for acorns in *T. baraudi* (~50%) than in *T. lusitanicus* (86%) (Verdú *et al*., 2007). These results suggest that this peculiar trophic habit was less remarkable for this beetle species, perhaps because of the lower abundance of acorns in the forest sites where they usually inhabit.

On the contrary, in the case of *J. nitidus*, the attraction to acorns could be considered anecdotal or even accidental. The scarce number of field interactions between *J. nitidus* and acorns in comparison with *T. baraudi*, as well as the absence of acorn attractiveness shown in the olfactometer experiments, indicated a scarce or null feeding preference for acorns in this Geotrupidae species. Therefore, our results suggest that the attraction to acorns in the Iberian Peninsula seems to be exclusive of *Thorectes* species. More analyses are necessary to understand the complex behaviour of food selection towards the diverse supply of resources available in a Mediterranean locality as the Cabañeros National Park. In the same way, further analyses are needed to explore the physiological response of *Thorectes* and *Jekelius* species using a broader range of food types (such as dung of sheep, red deer, wild boar, etc.) and qualities (e.g. different diets, antihelmintic treatments, etc.) by means of techniques such as electroantennography and olfactometry bioassays. Additionally, more studies are needed to explore oak–beetle interactions in other Iberian endemic *Thorectes* species, such as *T. ferreri* and *T. valencianus*, as well as for the species present in the western part of North Africa (Löbl & Smetana, 2006).

Interestingly, habitat preferences by the two studied beetle species could be related to their differential feeding preferences for acorns. Thus, the acorn-eating beetle species, *T. baraudi*, showed more abundant populations in forest habitats compared with savannahs sites, while no significant among habitat preferences were found for *J. nitidus*. Research is still needed to resolve if habitat preference is a consequence of acorn consumption or if both trophic and habitat adaptations are evolutionarily associated.

Ecological implications of oak–beetle interactions for oak seedling recruitment and forest management

Seed dispersion by animals is characterised by a succession of different tasks, including removal of fruits, primary and secondary seed dispersal, predation, and different patterns of seedling establishment (e.g. Janzen, 1971; Howe & Smallwood, 1982). In the case of dung beetles, the secondary dispersal of dung containing seeds of several plants (diplocory) has been already documented, although its effect on seedling establishment remains unknown to date (e.g. Estrada & Coates-Estrada, 1991; Andresen, 2002). In the case of *T. lusitanicus*, the positive consequence for oak recruitment is that a number of these buried acorns are not completely consumed and are left abandoned, while most of them retain the ability to emerge and establish as seedlings (Pérez-Ramos *et al*., 2007; J. R. Verdú, C. Numa, J. M. Lobo and I. M. Pérez-Ramos, unpublished data). The burial of acorns decreases the probability of being found and consumed by other seed predators, thus favouring the seedling recruitment without desiccation as well as stimulating seed germination (Seiwa *et al*., 2002; Gómez, 2004; Pérez-Ramos & Marañón, 2008).

Our results demonstrated the burying behaviour of *T. baraudi* in the forests of the Cabañeros National Park, suggesting a potential role of this beetle species as an active secondary acorn disperser. Thus, the astonishing ecological interaction between *Quercus* and *Thorectes* species could be relevant for ensure seedling recruitment and sustain the oak population equilibrium as documented for *T. lusitanicus* in oak forests of southern Spain (Pérez-Ramos *et al*., 2007) .

Acorn dispersal by beetles could be particularly important in Mediterranean oak forests and savannahs, such as those of central Spain, where most *Quercus* species are strongly recruitment limited (Pulido, 2002; Muñoz & Bonal, 2007; Pérez-Ramos *et al.*, 2008; Smit *et al*., 2009). The high pressure of seed- and seedling-consumers as well as the high rate of seedling mortality as a result of the summer water stress and the low density of small acorn dispersers, such as rodents or jays, have been identified as the main limiting factors for oak seedling recruitment in these type of forest ecosystems (Muñoz & Bonal, 2007; Smit *et al*., 2009). The potential role of *T. baraudi* as an active oak disperser could be especially important in the study area, the Cabañeros National Park, where natural oak recruitment is practically null because of overgrazing (Smit *et al*., 2009). In this park, the high density of *C. elaphus* (12–22 individuals/100 ha) as well as of other large acorn predators such as wild boars (Jiménez, 2005; Jiménez & López-Izquierdo, 2005) hamper acorn persistence in the soil and, thereby, seedling establishment. This could explain the scarce number of direct field observations on the interaction between *T. baraudi* and acorns (e.g., Fig. 4; J. R. Verdú and C. Numa, unpublished data; M. Díaz, personal communication). As a result of the strong spatial dependence of beetles with dung availability (Hanski & Cambefort, 1991), their interactions with large herbivores are very complex. On the one hand, oak forests harbouring higher numbers of ungulates will support larger populations of dung beetles and, in consequence, a higher proportion of acorns could be potentially buried and dispersed by them. On the other hand, when the density of large herbivores is very high, most acorns will be rapidly consumed by them and, thereby, acorn availability for beetles will be very scarce or even null. Thus, we emphasise the need to conduct future studies analysing the potential role of *T. baraudi* as an acorn disperser and its relation with the density of ungulates. Management policies directed to control the problems of overpopulation of large herbivores and to reach their optimal population sizes could favour the positive behaviour of *Thorectes* as an acorn disperser and, thus, promote *Quercus* recruitment.

Further studies are also needed on the evolutionary, physiological, and reproductive advantages of consuming acorns for a dung beetle species obligated to use herbivorous faeces for the building of their nests. In *T. lusitanicus*, we previously demonstrated that the ingestion of acorns during autumn and winter increased its fat body mass and consequently its tolerance to low temperature conditions, as well as the reproductive success of the species (Verdú *et al*., 2010). We hypothesise that this benefit could be minimised because of the low availability of acorns in the study area for *T. baraudi*. For this purpose, a field study focused on the growth and development of the fat body and the ovaries of *T. baraudi* under different conditions of acorn availability could be very useful to elucidate the trade-offs of the interaction between *T. baraudi* and *Quercus* species.

Fig. 4. An individual of *Thorectes baraudi* hibernating inside a germinated cork oak acorn.

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