Use of *Quercus* acorns and leaf litter by North African *Thorectes* species (Coleoptera: Scarabaeoidea: Geotrupidae)

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Acorn burial and consumption by geotrupid dung beetles is an interesting trophic interaction recently reported for Iberian *Thorectes* and North American *Mycotrupes* species. In Iberian *Thorectes* species, this interaction provides not only ecophysiological and reproductive advantages to the beetles but also more effective dispersal for *Quercus* acorns. The genus *Thorectes* is particularly diverse in the Iberian Peninsula and North Africa, where most species of the genus occur. Due to the high diversity of *Thorectes* in North Africa, especially in Morocco, where *Quercus* forests are widely distributed, we investigated whether acorn burial and consumption by *Thorectes* beetles also occurred in this region. For this, field sampling was conducted in northern Morocco by searching for beetles buried and consuming acorns within 1 m^2 quadrats in areas where *Thorectes* species and *Quercus* forests occur jointly. Three beetle species (*T. distinctus, T. laevigatus* and *T. trituberculatus*) were found consuming buried acorns of *Q. suber* in the field. Most of the beetles were found feeding on acorns, while only 20 % were found in dung-provisioned burrows. These results suggest that acorns constitute the staple food of some North African *Thorectes* species. In addition, we found *T. trituberculatus* and *T. distinctus* burrows and nests provisioned with oak leaf litter. Burrows and nests provisioned with *Quercus* litter also suggest a tighter interaction of *Thorectes* beetles with oaks. Feeding and nesting with relatively predictable and abundant resources in oak forests, such as acorns and leaf litter, may be especially important to explain the diversification and success of flightless *Thorectes* species in Mediterranean ecosystems such as those of the Iberian Peninsula and North Africa.

Key words: plant–animal interaction, dung beetles, seed-feeding beetles, saprophagy, leaf-litter nesting.

INTRODUCTION

Dung beetles in the families Scarabaeidae (including Scarabaeinae and Aphodiinae) and Geotrupidae comprise a diverse array of species which exploit faeces, mainly from large herbivores (Hanski & Cambefort 1991). Although there are often local preferences for different types of excrement (Hanski & Cambefort 1991; Martín-Piera & Lobo 1996; Finn & Giller 2002; Tshikae *et al*. 2013), many of these beetles are not specialised in the use of a specific type of dung. Furthermore, many species can feed on carrion, decaying plant material, and fungi (Halffter & Matthews 1966; Hanski 1983; Walter 1983; Philips *et al*. 2004; Halffter & Halffter 2009). Trophic generalism is especially widespread in Geotrupidae, as many species feed on different dung types, plant detritus, and fungus (Howden 1955, 1964; Palestrini & Zunino 1985; Martín-Piera & López-Colón 2000).

An interesting trophic interaction in geotrupid dung beetles involves acorn consumption, which provides ecophysiological and reproductive advantages to the beetles and has implications in the dynamics and regeneration of Mediterranean *Quercus* forests (Verdú *et al.* 2010, 2011; Pérez-Ramos *et al.* 2013). Feeding on acorns has been reported in two Iberian species of the genus *Thorectes* (*T. lusitanicus* (Jekel, 1866)) and *T. baraudi* López-Colón, 1981; Verdú *et al*. 2007, 2011] and in one North American species of the genus *Mycotrupes* (*M. lethroides* (Westwood, 1837); Beucke &

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Received 20 October 2017. Accepted 6 June 2018

ISSN 1021-3589 [Print]; 2224-8854 [Online]
DOI: https://doi.org/10.4001/003.027.0010

Choate 2009). In the case of Iberian species, acorn consumption by *T. lusitanicus* increases the ingestion of fatty acids, which in turn provides an ecophysiological advantage to the beetles, allowing them to withstand more extreme cold conditions and, consequently, to maintain a broader activity period during winter (Verdú *et al*. 2010). At the same time, because acorn production and consumption by *T. lusitanicus* coincides with the reproduction period of the beetles, acorn feeding increases the reproductive potential because of enhanced ovarian development due to the higher metabolic reserves of the fat body (Verdú *et al*. 2010).

Acorn burial and consumption not only affects the ecophysiology of *Thorectes* species, but also has an important role in acorn dispersal (Pérez-Ramos *et al*. 2007; Verdú *et al*. 2007, 2011). Because *T. lusitanicus* individuals bury a large number of acorns that are partially consumed without damaging the cotyledons, feeding on acorns by the beetles does not negatively affect seedling germination. As a result, the beetles are more effective dispersers than rodents, which generally consume the whole acorn (Pérez-Ramos *et al*. 2013). These results suggest an interesting ecological interaction between *Thorectes* beetles and *Quercus* species, which are key components of the Mediterranean forest vegetation. This interaction has further connections to the vertebrate herbivores, whose faeces are buried by these beetles for feeding and nesting, indirectly favouring acorn dispersal (Verdú *et al*. 2007) and likely enhancing soil-nutrient cycling (Nichols *et al.* 2008).

The genus *Thorectes* (excluding species belonging to genera *Jekelius* López-Colón, 1989 and *Silphotrupes* Jekel, 1866 (López-Colón 1989, 1996; Cunha *et al*. 2011; Lobo *et al*. 2015; Schoolmeesters 2016) is particularly diverse in the Iberian Peninsula and North Africa, where 16 out of the 22 species of the genus occur (Schoolmeesters 2016). Within North Africa, the highest diversity of *Thorectes* is found in Morocco, where seven out of the 11 North African species of the genus are distributed: *T. laevigatus* (Fabricius, 1798), *T. distinctus* Marseul, 1878, *T. trituberculatus* Reitter, 1893, *T. coloni* Ruiz, 1998, *T. armifrons* Reitter, 1893, *T. coiffaiti* Baraud, 1969, and *T. variolipennis* Marseul, 1876 (Baraud 1985; Ruiz 1998; Schoolmeesters 2016; see also http://www.biogeografia.org/). The diversity of the genus *Thorectes* in Morocco, where six species of *Quercus* also occur (Shay 2001) and oak forests are widely distributed, raises the question of whether the interaction between the beetles and *Quercus* occurs in this region. Finding this interaction in North African *Thorectes* species is relevant for conservation and management of Mediterranean ecosystems in the region. On the one hand, apterism and low dispersal ability of these beetles would explain the high vulnerability of *Thorectes* species from a conservation perspective (see Verdú & Galante 2006 for factors threatening the Iberian species). Thus, due to restricted distributions and habitat fragmentation, six out of 22 species belonging to the genus *Thorectes* have been catalogued as threatened (IUCN 2016). On the other hand, the high degree of endemism of *Thorectes* species increases the need to study this interaction because of its effects on *Quercus* dispersal and recruitment, especially in the Iberian Peninsula and northern Morocco where *Thorectes* registers its highest diversity.

In this study we report the use of *Quercus* acorns by *Thorectes* beetles in North Africa and the novel finding of nesting with *Quercus* leaf litter in these geotrupid dung beetles.

MATERIAL AND METHODS

Study area

Sampling was conducted in January 2014 in northern Morocco (Fig. 1, Table 1), in areas where *Thorectes* species may be found within forests of *Quercus ilex*, *Q. suber, Q. faginea* and/or *Q. canariensis*. All the surveyed sites registered high sheep and cattle densities and thus high dung availability. Due to acorn consumption by livestock and, in some cases, gathering by local people, acorns seldom appeared on the ground surface, preventing estimations of acorn availability.

Sampling

A total of 17 sites were sampled within the study area (Fig. 1), but only nine corresponded to *Quercus* forests inhabited by *Thorectes* species (Table 1). To determine whether *Thorectes* species buried and fed on acorns, at each site we looked for buried beetles (either with or without acorns and/or excrement) as well as for nests provisioned with litter (see below) or excrement under *Quercus* trees. To find buried beetles and nests, we exhaustively searched under the leaf litter and up to 25 cm depth in the soil within randomly

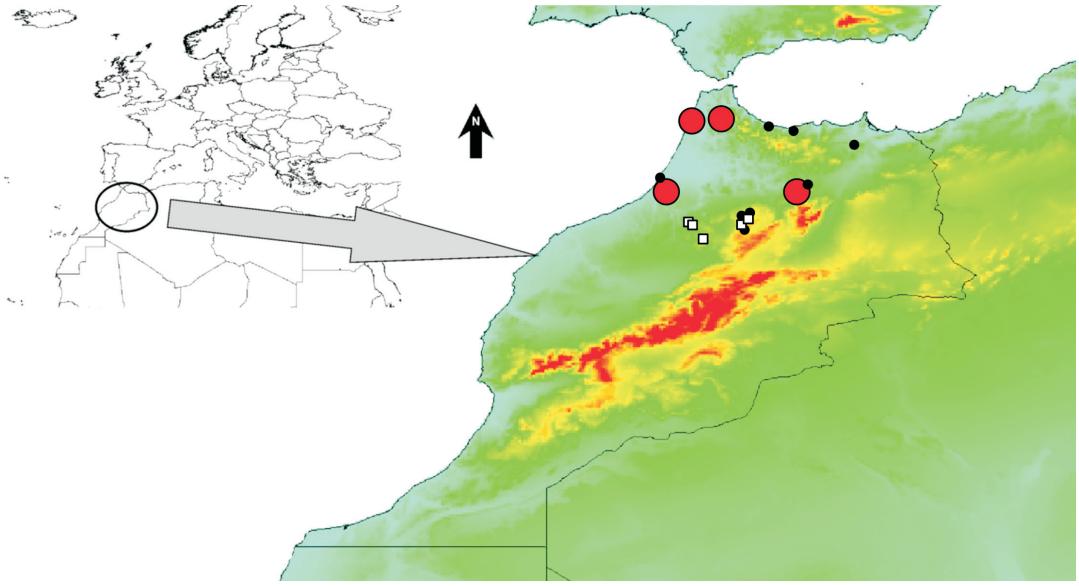

Fig. 1. Location of sampling sites in northern Morocco. Sites where both *Thorectes* and *Quercus* species were found are showed as large circles (see Table 1), while white squares represent sites with *Quercus* species in which no evidence of *Thorectes* species burying or consuming acorns was found. Black dots represent the location of the remaining surveyed sites.

selected 1 m^2 quadrats under tree canopies of *Q. suber*, *Q. ilex*, *Q. faginea* and *Q. canariensis*. At each site, we searched 6–15 quadrats 100 m apart in a total of 88 plots at the nine sites where both *Quercus* and *Thorectes* species occurred. The beetle occurrence recorded in the sampling are available at http://biogeografia.org/ clicking in 'Información taxonómica y biogeográfica sobre los Scarabaeoidea coprófagos de Marruecos'.

Differences between the two most abundant species in the proportion of beetles found with buried acorns were analysed using a Chi-square test.

RESULTS

Four species of the genus *Thorectes* were found: *Thorectes laevigatus, T. trituberculatus*, *T. armifrons,* and *T. distinctus*. All four *Thorectes* species were found in *Quercus* forests, although most *T. armifrons* were observed in pasture habitats. A total of 61 individuals of *Thorectes* species were collected in the 88 quadrats under *Quercus* tree canopies (Table 2). A total of 23 individuals belonging to three species (15 *T. trituberculatus*, 5 *T. distinctus*, and 3 *T. laevigatus*) appeared with buried acorns. The beetles were usually hidden inside the acorn

Table 1. List of sites sampled for the use of *Quercus* acorns by *Thorectes* species in Northern Morocco.

Site	Coordinates	Altitude (m a.s.l.)	*Quercus* species	*Thorectes* species
Road Khènifra-Khemisset	N33.17759, W5.87785	1403	*Q. ilex*	*T. trituberculatus*
Road Cedar Forest-Azrou	N33.42741, W5.17505	1694	*Q. faginea*	*T. armifrons*
Road Khènifra-Khemisset	N33.44722, W6.07690	982	*Q. suber*	*T. trituberculatus*
Road Khènifra-Khemisset	N33.48130, W6.13555	862	*Q. suber*	*T. trituberculatus*
South of Lake Aoua	N33.55417, W5.07701	1647	*Q. ilex*	*T. armifrons*
Mâmora forest	N34.04963, W6.54914	111	*Q. suber*	*T. distinctus*
Tazzeka National Park	N34.05243, W4.18517	1375	*Q. suber*	*T. trituberculatus*
North of river Loukus	N35.29146, W6.06440	283	*Q. suber*	*T. distinctus*
Moulay Abdeselam	N35.33866, W5.54281	873	*Q. suber*, *Q. canariensis*	*T. laevigatus*

Table 2. Number of sampled quadrats (N), total number of beetles found in the quadrats (NBe), and total number of beetles with acorns (NAc) for the different *Thorectes* and *Quercus* oak species.

	Q. faginea[(1)]/ *Q. canariensis*[(2)]			*Q. ilex*			*Q. suber*		
	N	NBe	NAc	N	NBe	NAc	N	NBe	NAc
T. armifrons	8[(1)]	1	0	8	3	0	–	–	–
T. distinctus	–	–	–	–	–	–	29	16	13
T. laevigatus	3[(2)]	0	0	–	–	–	9	6	3
T. trituberculatus	–	–	–	7	3	0	24	32	7

(Fig. 2). By contrast, we found individuals with buried dung in only seven cases (four *T. armifrons* and three *T. trituberculatus*). In addition, four *T. trituberculatus* adults were found inside burrows containing packed *Quercus* leaf litter. The remaining 27 individuals were found buried in the soil, without any kind of trophic resource. Outside the quadrats, we found a further 12 nests of *T. trituberculatus* provisioned with *Quercus* leaf litter, some with larvae. We also observed *T. distinctus* nests provisioned with leaf litter.

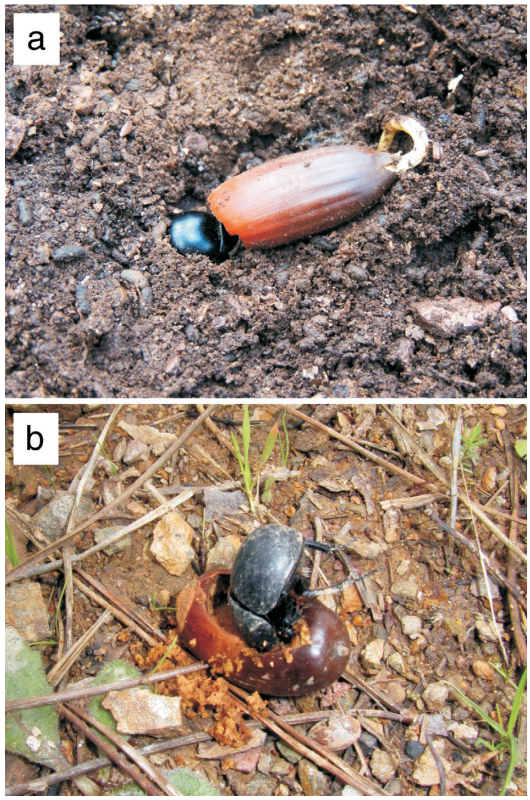

Fig. 2. **a**, Acorn buried and consumed by *Thorectes trituberculatus* (Tazeka National Park). Notice that the beetle has fed on the basal part of the acorn and that the epycotyl appears in its apex, showing that acorn consumption by the beetle left the cotyledons intact. **b**, *T. laevigatus* feeding on a *Q. suber* acorn on the ground (Monte del Renegado, Ciudad Autónoma de Ceuta; N35.5405, W5.2145; 280 m altitude; 25 November 2012; J.L. Ruiz).

The mean density of *Thorectes* spp. in *Quercus* forests was 0.69 ± 0.14 individuals/m^2 (mean ± standard error), ranging from 0.17 ± 0.17 individuals/m^2 to 3.17 ± 1.25 individuals/m^2 (both extreme values corresponding to sites with *Q. suber* forests inhabited by *T. trituberculatus*).

Only *Q. suber* acorns were found buried by the beetles (0.37 ± 0.10 acorns/m^2). *Thorectes* species inhabiting *Q. suber* forests buried from 0.30 ± 0.13 acorns/m^2 for *T. trituberculatus* and *T. laevigatus* to 0.45 ± 0.15 acorns/m^2 in *T. distinctus*. The proportion of beetles with buried *Q. suber* acorns (42.6 % for the three acorn burying species in total) differed between the two most abundant species in our sampling, *T. distinctus* showing a higher proportion of individuals buried with acorns (81.3 %) than *T. trituberculatus* (21.9 %) ($\chi^2 = 15.471$, $P < 0.0001$; Chi-square test).

DISCUSSION

Our results show that some North African species of the genus *Thorectes* (*T. laevigatus, T. trituberculatus, T. distinctus*) bury and feed on *Quercus* acorns, similarly to the Iberian species *T. lusitanicus* and *T. baraudi* (Verdú *et al*. 2007, 2011). Further observations of *T. laevigatus* consuming *Q. suber* acorns both directly on the ground (Fig. 2b) and buried in the soil in Ceuta (a Spanish city on the North African side of the Strait of Gibraltar) (J.L.R., pers. obs.) corroborates the use of acorns as a food resource in this North African species. The absence of acorn-feeding observations for *T. armifrons* may

be related to the low abundance of this species in *Q. ilex* and *Q. faginea* oak forests during the sampling. This beetle species occurs in higher numbers in cedar forests and pasture habitats (Romero-Samper & Lobo 2008; F. Sánchez-Piñero and J.L.R., pers. obs.). Thus, a larger sampling effort in oak forests will be necessary to ascertain whether this species actually feeds on acorns.

Thorectes species in this study were found consuming only *Q. suber* acorns. Although two acorn-consuming species (*T. laevigatus*, *T. trituberculatus*) also inhabit *Q. ilex* forests and *Q. suber* + *Q. canariensis* mixed forests, only *Q. suber* acorns were found to be eaten by these beetles. This finding coincides with the preference for *Q. suber* acorns shown by the Iberian *T. lusitanicus* (Verdú *et al*. 2007). However, laboratory experiments by other researchers have indicated that *T. lusitanicus* similarly selected acorns of *Q. suber* and *Q. rotundifolia* (= *Q. ilex* ssp. *ballota*) over acorns of *Q. canariensis* (Verdú *et al*. 2007). These authors indicate that acorn characteristics such as size, shell hardness, and tannin level could be involved in acorn selection by the beetles. Differences in consumption of acorns from the different *Quercus* species by *Thorectes* species could not be assessed in this study due to the small sample size for *Quercus* species other than *Q. suber,* the dominant oak species in the sampling area. Thus, field and laboratory research will be necessary to clarify whether acorns of different *Quercus* species are consumed by North African *Thorectes* species as well as the factors involved in acorn selection.

Acorns appear as the staple food of some North African *Thorectes* species. Two thirds of the individuals found within the quadrats with some kind of resource were buried with acorns (and were usually inside the partially consumed acorn), while only seven beetles (20 % of the individuals) were feeding on dung. Observations of acorn consumption by *T. laevigatus* in cork oak forest patches with available dung from livestock (mainly sheep and goats) as well as wild boars and rabbits in the environs of Ceuta (J.L.R., pers. obs.) also support the importance of acorns in the diet of some *Thorectes* species. These results indicate the relevance of acorns as a food resource for these beetles, generally regarded as mainly coprophagous species (Palestrini & Zunino 1985; Ruiz 1995; Martín-Piera & López-Colón 2000). Acorn consumption has been shown to provide advantages to the beetles due to the increase of fat reserves, with positive effects on thermal tolerance, ovarian production, and immune-system health (Verdú *et al*. 2010, 2013). Feeding on acorns could be especially important for flightless *Thorectes* species with limited dispersal ability, allowing the use of a relatively predictable and abundant food resource in oak forests during the breeding season of the beetles, ultimately explaining the long-term maintenance of these geotrupids in climatically fluctuating Mediterranean ecosystems of both the Iberian Peninsula and North Africa (Cunha *et al*. 2011).

The interaction between *Thorectes* and *Quercus* species in North African oak forests may have further ecological consequences, since acorn consumption by the beetles has been shown to increase germination rates (Pérez-Ramos *et al*. 2013). In fact, the proportion of beetles found buried with acorns was similar in the North African *Thorectes* species (42.6 % in average, and up to 81 % in *T. distinctus*) and the Iberian Peninsula (44 %, varying between 20 % and 68 % of the individuals found in the two locations surveyed by Verdú *et al*. (2007)). Beetle densities in our sampling (0.2–3.2 individuals/m^2 among sites inhabited by the three acorn burying species) were, in general, lower than the reported density of *T. lusitanicus* in southern Spain (2.5 individuals/m^2) (Verdú *et al*. 2007). However, differences in sampling effort, weather conditions, and phenology do not allow a precise comparison of these results. Nonetheless, we believe that these data point to the fact that *Thorectes* may play a similar role in acorn dispersal in North African *Quercus* forests as *T. lusitanicus* does in the Iberian Peninsula (Pérez-Ramos *et al*. 2007, 2013). Further research is necessary to determine the actual effect of these beetle species in acorn dispersal and germination in North African oak forests.

A remarkable result is the finding of nest provisioning with *Q. suber* leaf litter, obtained here for *T. trituberculatus* and *T. distinctus*, this also occurring in the Iberian species *T. lusitanicus* (Verdú *et al*., unpubl.). Nesting with plant litter has not been previously recorded in *Thorectes*, considered a genus of dung-nesting species (Klemperer & Lumaret 1985, Martín-Piera & López-Colón 2000). However, nesting with plant detritus is known in some Geotrupidae, such as *Anoplotrupes stercorosus* (Scriba, 1791) (Rembialkowska 1982), *Cnemotrupes* Jekel, 1865 species (Howden 1955), *Silphotrupes* (Jekel, 1866) species (J.R. Verdú,

unpubl.) and the speciose genus *Lethrus* Scopoli, 1777 (Schreiner 1906; Kosztolányi *et al*. 2015), as well as in a few, usually very specialised, Scarabaeinae such as *Cephalodesmius* Westwood, 1842 and *Pachysoma* McLeay, 1821 species (Monteith & Storey 1981; Scholtz *et al*. 2004; Halffter & Halffter 2009) and some *Anomiopsoides* Blackwelder, 1944 species (*e.g*. *A. biloba* Burmeister, 1861 and *A. cavifrons* Burmeister, 1861) (J.R. Verdú, unpubl.). The use of plant detritus for nesting in *Pachysoma* is regarded as contributing to a reversion to ancestral conditions in larval morphology (Scholtz *et al.* 2004), suggesting that nesting with plant detritus in these species is a secondary adaptation from dung-nesting ancestors. Geotrupidae phylogeny suggests that this is probably also the case in *Thorectes* species, with acorn use and nesting with oak leaf litter probably being a derived trait from the mainly dung-nesting Geotrupini and the ancestral lineage of genera *Jekelius-Silphotrupes-Thorectes* (Verdú *et al*. 2004, Cunha *et al*. 2011).

In the case of *Thorectes*, feeding on acorns and nesting with leaf litter from the same oak species suggest an ancient evolutionary relationship between these beetles and *Quercus* oaks (see Cunha *et al*. 2011). Feeding on acorns and nest provisioning with leaf litter could be especially important for flightless *Thorectes* species with limited dispersal ability, allowing the use of relatively predictable and abundant resources in oak forests, ultimately explaining the diversification and success of these geotrupids in highly variable Mediterranean ecosystems of the Iberian Peninsula and North Africa (Cunha *et al.* 2011). Additional investigation will be needed to uncover the evolutionary relationship between *Thorectes* and *Quercus* species.

AKNOWLEDGEMENTS

We thank G. Chavanon for his help to obtain permission to conduct the research in Morocco. Two anonymous reviewers provided helpful comments and suggestions on the manuscript. D. Nesbitt revised the English language. This study was funded by research grant IEC-048-05/06/2013 from the Instituto de Estudios Ceutíes (Ciudad Autónoma de Ceuta, Spain).

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