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A beetle and a fly: mutualism or parasitism?

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Introduction

Obligate relationships between very different organisms have an enduring fascination to field biologists. While associations between species may be noticed frequently in the field, often there is little or no experimental evidence that explores the nature of the putative relationship. True mutualism needs to be demonstrated rather than inferred: mutualism is thought to be widespread, but is absent from much of evolutionary theory (Wilson, 1983; May, 1984).

In this paper, we are concerned with the relationship between dung beetles of the genus *Scarabaeus* (Coleoptera: Scarabaeidae) and flies of the genus *Ceroptera* (Diptera: Sphaeroceridae). *Ceroptera* and the sphaerocerid genera *Borborillus* and *Limosina* are known to be associated with dung beetles (Meigen, 1838; Lesne, 1896; Roubaud, 1916; Sivinski, 1983; Marshall, 1983; Marshall & Montagnes, 1988). They are said to be phoretic on the beetles (even in flight in the American species *Borborillus frigipennis* (Sivinski, 1983)) and 'kleptoparasitic' in that they lay their eggs in the dung-balls of the beetles before they are stored underground (Rouboud, 1916; Sivinski, 1983). Papp (1977) even characterizes *Ceroptera* in part by their enlarged tarsal claws and pulvilli, which Marshall & Montagnes (1988) interpret as modifications for grasping the host. Marshall (1983) cites the habit of 'riding on dung beetles' as a synapomorphy for the genus, and therefore connected with the evolution of the genus from a *Limosina*-like ancestor. *Ceroptera* species have also been caught in light traps (J. Deeming, *pers.comm.*): for example, Nigerian *Ceroptera* were collected in a Robinson trap, but probably entered it riding on beetles; in Oman M. D. Gallagher and J. C. Deeming ran a mercury-vapour light suspended against a white sheet, to which were attracted both *Scarabaeus sacer* L. carrying *C. aharonii* Duda and free-flying *C. aharonii*, implying a free-living existence during at least part of their adult lives.

In this paper we report the results of observations and experiments that explore further the relationship between beetle and fly, using an association discovered in Portugal between *C. rufitarsis* (Meigen) and *S. cicatricosa* Lucas.

Materials & methods

Scarabaeus cicatricosa Lucas (identified by A. Kirk-Spriggs, National Museum of Wales, Cardiff: see Baraud, 1977) is known to have a range from Morocco (Tangier,

coll. 4.iv.1986) to southern Spain (Cadiz, Zahara, coll. 31.iii.1984) (adult material collected A. Kirk-Spriggs and deposited in the National Museum of Wales: J. Deeming, *pers.comm.*). Very little is known about its biology. It appears to be reasonably common in dune areas close to the sea between Caparica and Fonte da Telha, near Lisbon, Portugal, where we collected four individual beetles (two of each sex (sexed from Balthasar, 1963)) together with their associated flies (n = 19). The flies were identified from Duda (1938), confirmed subsequently by J. Deeming (National Museum of Wales, Cardiff).

Beetles and flies were kept in a 1 m x 0.3 m glass-sided aquarium tank with sand, and were provided with sheep dung (= 'dung-pats') from which the beetles cut dung-balls for burial in the sand either as food or brood-balls (see Halffter & Matthews, 1966). Three batches of flies subsequently hatched (n = 15, 17 & 15) during the lifetime of the beetles.

Several experiments used a simple 'Y'-tube, where individual flies chose between two arms with different odours wafted down by a fan; extraneous influences were minimized by randomizing in which side the test odours were placed. All mean values are cited as one standard error.

Results

Flies remained on the beetles at all times, even during flight. When beetles were not flying, the flies often congregated around the beetle's anus, apparently feeding on secretions from it. There were no systematic differences in the number of flies associated with different beetle sexes ($\chi^2_1 = 2.2$, $p > 0.05$) or individuals ($\chi^2_3 = 4.4$, $p > 0.05$).

a) Fly behaviour

Flies placed equidistant between a host and a non-host beetle of the same size and colour always chose their natural host ($\chi^2_1 = 12.0$, $p < 0.001$). Given a choice between host and non-host odour in the 'Y'-tube, 17 of 20 flies chose host odour ($\chi^2_1 = 9.8$, $p < 0.01$), and maintained this preference when only offered the odours from faecal material ($\chi^2_1 = 5.0$, $p < 0.05$). Flies did not discriminate in a choice between dung odour and a control ($\chi^2_1 = 3.2$, $p > 0.05$), but chose host visual and olfactory cues over dung odour ($\chi^2_1 = 12.0$, $p < 0.001$).

We tried to determine the recognition distance of beetles by flies, by removing flies and determining the distance at which flies hopped back onto the beetle: This distance was 6.5 ± 0.5 cms.

When threatened by a looming object (a small box), nearly all flies (24/28) moved into the mesothoracic groove, a gap behind the prothoracic coxae (see Fig. 1). By permitting beetles to climb a pole and take flight, we observed flies moving to this groove about 0.5 s before the elytra were raised for flight: on catching beetles in flight, it was obvious that flies ride in the groove during flight. From observation and subsequent calculation, beetles normally appear to carry a maximum of

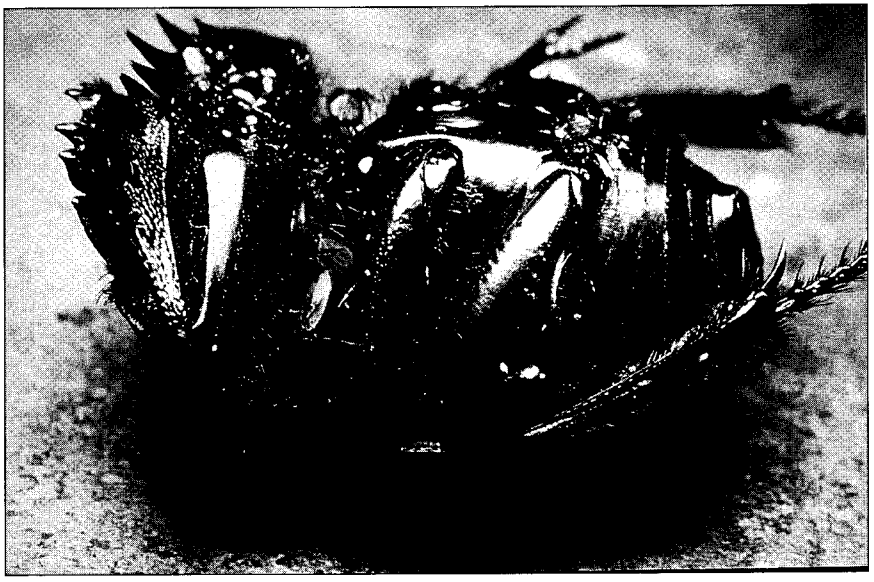

Figure 1. Photograph of the beetle *Scarabaeus cicatricosa* with attendant sphaerocerid flies *Ceroptera rufitarsis* taking refuge in the mesothoracic groove. This situation occurs just before flight, and whenever objects loom in the visual field of the flies. *(Photograph by David Fox, Nottingham University)*

7 flies. Experimentally we loaded beetles with either 7 or 10 flies and allowed them to take flight: Those loaded with 10 flies lost the excess (3), but those loaded with 7 lost none.

Flies only left their host either to feed on a dung-pat, or to move to another beetle and there appeared to be frequent interchange of flies between individual beetles. Flies copulated either on the beetles (n = 7 observations) or on dung-pats (n = 4); females oviposited generally on dung-balls (n = 9) rather than on dung-pats (n = 2). All flies remained on beetles within the mesothoracic groove while the beetles were burying their dung-balls underground. Flies emerged from both food- and brood-balls, between 37 and 60 days after burial; each generation of adults dying before the subsequent one emerged.

Mouthparts of the larval flies were of the 'rasping' rather than the 'piercing' type (see Duda, 1938).

b) Beetle morphology

Unlike the rest of the underside, the cuticle of the mesothoracic groove has small circular pits, each with a single bristle curving over it (Fig. 2). Pits are about 1000 um by 650 µm and 350 µm deep. The bristle is the correct size for flies to use them for holding on while in the groove, since their tarsal claws are about 80-100 µm

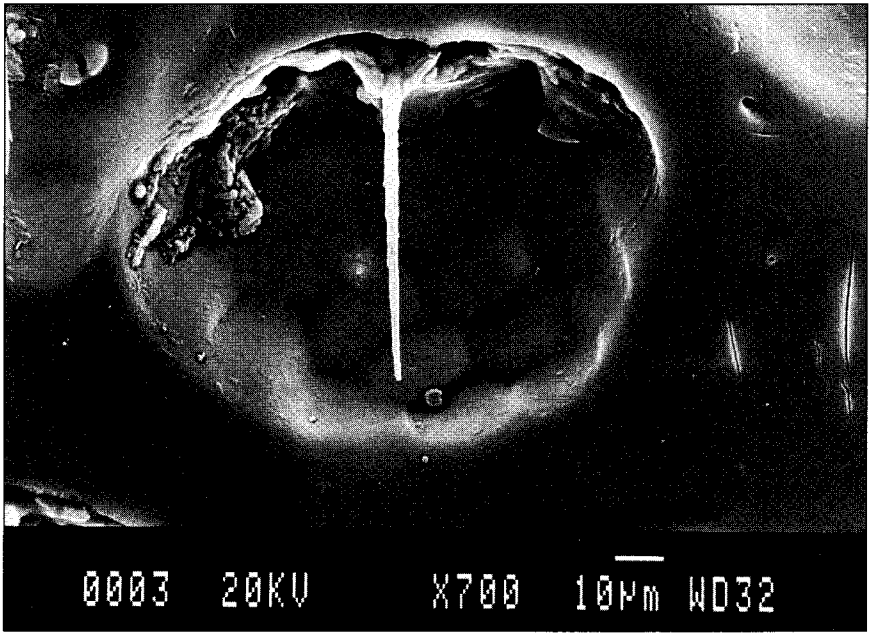

Figure 2. SEM photograph of one of the many cuticular pits situated in the mesothoracic groove of the beetle *Scarabaeus cicatricosa.*

long. We found smaller pits with less prominent bristles in *S. laticollis* L., a species from which no *Ceroptera* flies have been recorded (A. Kirk-Spriggs, *pers.comm.*).

c) A possible advantage of hosting flies to the beetles?

Beetles might benefit from the association with flies, since the flies may eliminate mites; this was suggested by a chance observation. When not carrying flies (before a new fly generation had emerged), the beetles were particularly susceptible to mite infestation, probably brought in accidently with sheep dung. The mites were probably a species of *Rhizoglyphus*. Mites attached themselves to the soft cuticle in between sclerites and especially around the mouthparts, where they clearly caused the beetles some trouble by hindering movements and feeding. Mites cleared quickly once the flies returned. However, the beetles died before experiments could be done to test this hypothesis.

Table 1 summarizes our conclusions and speculations about the benefits of this interaction.

Discussion

Ceroptera flies probably use olfactory cues to find dung or beetles, but once on the

Table 1. Summary of the supposed benefits of the interaction between *Scarabaeus cicatricosa* and *Ceroptera rufitarsis*.

Benefits to the flies	***Benefits to the beetles***
Transport between food sources	Possible reduction or elimination of mites
Transport to other flies for mating	
Reduced inter-specific larval competition	
Increased protection for larvae	
Emergency food supply (anal secretions)	

dung or beetle, they probably use visual cues to discriminate the two. The mean distance from which flies flew onto beetles was only 6.5 cm, and throughout our experiments the flies never strayed voluntarily further than this from their host. The mesothoracic groove clearly facilitates fly retention during flight in some way, probably by the small pits (Plate 2) with their single bristles. The function of these pits is unknown, but Balthasar (1963) thought they had some excretory role. However, there were no obvious openings in the cuticle within the pit even at high magnification, whilst such openings were obvious outside the pits. The foot-size of the fly corresponds reasonably well with pit dimensions, but we never actually saw flies using the pits to hang on. The pits are also present in another sympatric species of scarab, *S. laticollis*, but this species has never been recorded with attendant flies (A Kirk-Spriggs, *pers.comm.*). *S. sacer* plays host to *Ceroptera* flies (*C. aharonii* in Oman), but there appear to be no pits in the mesothoracic groove of this species (J.C. Deeming, *pers.comm.*).

The number of flies per beetle appears to be limited to seven by the groove size, and this may constrain the reproductive strategy. Fly larvae are protected in a relatively constant environment (the dung-ball), away from predators and inter-specific competition (except possibly with the scarab larva): larval mortality is low at low population levels (Sivinski, 1983). The strikingly low fecundity that we recorded over three generations in captivity (approximately 1:1) suggests that flies have a low fecundity in the field, possibly because of few opportunities for reproduction, a limit to the ability of a dung-ball to provide nutrients, and the limited number of phoretic opportunities once both beetles and flies have emerged.

It is interesting that flies remained on the beetles while the beetles buried the dung. Female Scarabaeinae are said to chew the dung thoroughly when underground and rebuild their dung-balls (Halffter & Edmonds, 1982), possibly in order to kill predatory-fly eggs. Thus it would be important for female *Ceroptera* to oviposit after this process was complete.

Adult flies fed upon dung when they could. When no dung was provided, flies congregated around the anus of the beetle host. Since beetles produce excretions high in bacteria, it is probable that flies can feed on beetle excretions during periods of food shortage. It is possible that flies feed on the secretions of the sternite glands (Pluot-Sigwalt, 1982), but these occur further away from the anus than where the flies were apparently feeding. Fly larvae clearly feed on dung or decay

bacteria, since they have 'rasping' mouthparts rather than the 'piercing' mouthparts of predators.

In view of the importance of maintaining contact with a host beetle, new flies should emerge from the dung-ball at the same time as the beetle. Nothing is known about *S. cicatricosa*, but Halfter & Matthews (1966) and Matthews & Matthews (1991) both cite a development time of 5-6 weeks as usual in scarabs. Three emergence times of flies agreed with this prediction: although emergence times were between 5 and 8 weeks after oviposition, the peak emergence was at the beginning of the 6th week. These data should be interpreted cautiously, since beetles were absent from our study site during summer. It is probable that *S. cicatricosa* only flies during spring, and this in turn implies some sort of diapause during development. Since no beetle eggs were laid in the laboratory (only food-balls were buried), it is possible that fly eggs and/or larvae respond to cues in brood balls (e.g. burial depth) and enter diapause themselves.

After the beetles received their second portion of sheep dung, they developed a heavy mite infection, at a time when they had no associated flies. The infection lasted four days, but disappeared overnight after the flies returned. Mites are known to be commonly associated with scarab beetles (Halffter & Matthews, 1966) and are thought to be phoretic (Krantz, 1991), but we think they are likely to affect beetle movement and feeding, and hence decrease fitness. The hypothesis that *Ceroptera* flies benefit scarab beetles by reducing or eliminating mite infestations deserves an experimental test.

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Summary

The relationship between a scarab beetle (*Scarabaeus cicatricosa* Lucas) and a fly (*Ceroptera rufitarsis* (Meigen)) is described. Flies ride at all times on the body of the beetle: during flight of the beetle, up to seven flies congregate in a mesothoracic groove which is endowed with pits to which the flies' feet can cling. Various aspects of fly behaviour and ecology were studied; these appear to be adapted to their phoretic lifestyle. We discuss possible advantages and disadvantages to the beetles of carrying flies.

References

Balthasar, V. (1964) *Monographie der Scarabaeidae und Aphodiidae der palaearktischen und orientalischen Region*. Czechoslovakian Academy of Sciences, Prague.

Baraud, P. (1977) Coléoptères Scarabaeoidea. Faune de l'Europe occidentale Belgique, France, Grande-Bretagne, Italie, Péninsule Ibérique. *Nouvelle Revue d'Entomologie*, **7(3) supplement:** 1-352.

Duda, O. (1938) Sphaeroceridae. *in* E Lindner (ed) *Der Fliegen der palaearktischen Region*, **6(57):** 1-182.

Halffter, G. & Matthews, E. G. (1966) The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera, Scarabaeidae). *Folia entomologica mexicana*, **12-14:** 1-312.

Krantz, G.W. (1991) The nature of the association between *pisentii*-group mites (Acari: Macrocheliidae: Macrocheles) and dung beetles of the genus *Scarabaeus* (Coleoptera: Scarabaeidae) in southern France. *Acarologia*, **32:** 3-12.

Lesne, P. (1896) Moeurs du *Limosina sacra* Meig. (famille Muscidae, tribu Borborinae). Phenomènes de transport mutuel chez les animaux articulés; origine du parasitisme chez les insectes diptères. *Bulletin de la Société entomologique de France*, **1896:** 162-165.

Marshall, S, A. (1983) *Ceroptera sivinskii*, a new species of Sphaeroceridae (Diptera) in a genus new to North America, associated with scarab beetles in southwestern United States. *Proceedings of the entomological Society of Washington* **85:** 139-143.

Marshall, S. A. & Montagnes DJS (1988) *Ceroptera longicauda*, a second North American species in the kleptoparasitic genus *Ceroptera* Macquart (Diptera: Sphaeroceridae). *Proceedings of the entomological Society of Washington*, **90:** 189-192.

Matthews, E. G. & Matthews, T. (1991) Ecology of dung beetles. *in* I. Hanski & Y. Camberfort (eds) *Dung beetle ecology*. Princeton University Press.

May, R. M. (1984) A test of ideas about mutualism. *Nature,London*, 307: 410-412.

Meigen, J. W. (1838) *Systematische Beschreibung der bekannten europäischen zweiflügelischen Insekten*, **Vol.** 7: 409.

Papp, L. (1977) A contribution to the knowledge of species of the subfamily Ceropterinae (Diptera: Sphaeroceridae). *Acta zoologica hungarica*, **23:** 371-385.

Pluot-Sigwalt, D. (1982) Diversité et dimorphisme sexuel de glandes tégumentaires abdominales chez les Coléoptères Scarabaeidae. *Compte Rendus de l'Academie des Sciences, Paris*, **294:** 945-948.

Roubaud, E. (1916) Novelles observations de phorésie chez les Diptères du groupe des Borboridae. *Bulletin de la Société zoologique de Paris*, **41:** 43-45.

Sivinski, J. (1983) The natural history of a phoretic sphaerocerid Diptera fauna. *Ecological Entomology*, **8:** 419-426.

Wilson. D. .S (1983) The effect of population structure on the evolution of mutualism: a field test involving burying beetles and their phoretic mites. *American Naturalist*, **121:** 851-870.