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Research article

The first record among Dolichoderinae (Formicidae) of parasitism by Strepsiptera

D. P. Hughes [1], **G. Moya-Raygoza** [2] **and J. Kathirithamby** [1]

[1] *Department of Zoology, University of Oxford, South Parks Road, OX1 3PS, UK, e-mail:david.hughes@zoo.ox.ac.uk*
[2] *Departamento de Botanica y Zoologia, C.U.C.B.A., Universidad de Guadalajara, Km 15.5 carretera Guadalajara-Nogales, Las Agujas, Zapopan, C.P. 45110, Apdo, Postal 139, Jalisco, Mexico*

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Summary. We present the first record of parasitism of *Dolichoderus bispinosus* nests by Strepsiptera belonging to the family Myrmecolacidae. This becomes only the fourteenth species of ant and the fifth subfamily to be identified as a host to Strepsiptera. Of the three colonies examined all were parasitized. Prevalence of parasitism among adult ants was less than 2% in each case. However, among alate males of one colony, nearly 24% were parasitized. In conjunction with a reanalysis of previously published data we discuss the possibility that ant castes are differentially parasitized by Strepsiptera. We review the natural history of strepsipteran parasitism in ants, effects on host behaviour and incidences of parasitism in the hope of enabling detection of this parasite by myrmecologists.

Key words: Strepsiptera, Myrmecolacidae, *Dolichoderus bispinosus*, parasitism, behaviour change.

Introduction

Ants are infected by Strepsiptera belonging to the family Myrmecolacidae which have a unique host-parasite relationship; males parasitize ants and females parasitize Orthoptera (Kathirithamby, 1989). Westwood (1861) was the first to report strepsipteran parasitism of ants. It was Ogloblin (1939) who established that myrmecolacids have this dual host nature and was also the first to conclude that parasitism results in nest desertion and abnormal behaviour, such as positive phototaxis (Table 1). He found many nocturnal or crepuscular ants active in daylight; particularly on the tips of grasses. Observations by Cook (1996: Ch V), on *Solenopsis invicta* Buren, found positive phototaxis under laboratory conditions and indirect evidence of elevational seeking in the field. He further noted that parasitized ants were lethargic and would not sting in the late stages of parasitism.

Host location is conducted by the 1st instar larvae of the parasite, which enter the colony, likely to be via phoretic transport, where they are assumed to infect larval ants. Unlike other endoparasitoids of ants, such as eucharitids (Hymenoptera: Eucharitidae), Strepsiptera remain associated with the host even after host metamorphosis. Following host eclosion the male parasite forms a pupa, the anterior portion, i.e. cephalothecae, of which extrudes through the intersegmental membranes of the gaster. When fully developed the male emerges from the pupae and flies off to find and mate with a female. Unlike eucharitids, it appears that male strepsipteran emergence occurs only after the host has departed from the nest, which follows an apparent behavioural change in the host (Cook, 1996). Such a change mirrors infection by other parasites of ants: *Cordyceps* fungi, mermithid nematodes and trematodes (reviewed in Schmid-Hempel, 1998:35–62). Ogloblin (1939) documented cases of parasitism from 4 ant genera in 3 sub-families (Table 1) and all displayed abnormal behaviour. Since that study, only two additional genera in two subfamilies have been added to the list of ant hosts of Strepsiptera (Table 1, Hofeneder, 1949; Luna de Carvalho, 1972). Here we report a new host record, *Dolichoderus bispinosus* Olivier in the subfamily Dolichoderinae. This host record is the fifth extant subfamily known to be parasitized by Strepsiptera. Notwithstanding host taxonomic revision, it appears there are now 14 ant species known to be hosts of Strepsiptera and this is only the fifth species where parasitized ants were collected from within colonies.

Materials and methods

We collected 3 nests of the ant *D. bispinosus* between 20–24th June 2002 from Los Tuxtlas Biological Station, Veracruz State, Mexico (18º 35′ N 95º5′ W). The station lies within 700ha of primary and secondary rain forest and all nests were collected at the edge of the forest in bright, sunlit conditions, within 400 m of one another. 2 of the 3 nests were within abandoned *Nasutitermes* (Termitidae: Nasutitermitinae) carton nests, approximately 1m from the ground and in these cases the whole colony was collected. The remaining nest was recovered from an old tree stump (approximately 1.5m long) and represents a partial collection of a colony. For nests B and C, all adults were dissected whilst for nest A the adults were visually checked for signs of parasitism (Table 2). Immatures were not dissected.

Dissection and visual examination was done using a dissecting microscope. The pupa of the male strepsipteran, which is largely endoparasitic, is very difficult to see and requires scrutiny of the dorsal surface of the gaster using a microscope. The protruded region (cephalothecae) is the same colour as the host's tergites and detection is facilitated by examining the ant in profile under a strong light source. Voucher specimens of *D. bispinosus* parasitized by male Myrmecolacidae, within pupae, have been deposited at Coleccion Nacional de Insectos, at the Instituto de Biologia, Universidad Nacional Autónoma de México.

Results and discussion

The identity of the strepsipteran is currently under consideration and a major revision of this family is needed (Kathirithamby et al., in prep.). All 3 nests contained parasitized individuals with prevalence of infection among adults (number of infected/total number) being lower than 2% for each nest (Table 2). However, in nest A, almost 24% of alate male ants were infected. This difference between prevalence might indicate that, at the time of infection, all host larvae within this nest were males, or alternatively, that male larvae are preferentially parasitized. At the same location, in 2001, Kathirithamby and Hughes (2002) found parasitism only among alate males of *Camponotus planatus* Roger (but very low levels, 2/98). Data collected on 237 *S. invicta* individuals from 7 colonies from Texas in 1987 (Kathirithamby and Johnston, 1992), whilst not accounting for colony of origin, did seem to suggest that no difference existed between the number of individuals parasitized within 3 examined castes (worker, alate female, alate male). A statistical analysis of this data, by us, showed no significant difference in prevalence among the 3 castes; Logistic Regression, Wald = 1.08, 2 d.f. $P = 0.58$ (overall mean ± SE = 0.48 ± 0.03). The origi-

Table 1. A list of original published records of Strepsiptera (Myrmecolacidae) within extant ant genera

Sub-family	Genus and species	Location and notes	Reference
Myrmicinae	*Solenopsis saevissima pylades* Forel *S. saevissima quinquecuspis* Forel *S. saevissima richteri* Forel	Salta, Misiones and Puerto Aguirre, Argentina: (S), AB: a 'few' found on top of grass stems (elevation seeking). Sampled many thousands from nests but none parasitized.	Ogloblin, 1939
	S. invicta Buren *	Texas, USA: (N), abundant	Kathirithamby and Johnston, 1992
	S. invicta Buren*	Texas, USA: (N&S), very rare, < 3%, but only workers sampled.	Cook et al., 1997
	S. invicta Buren*	Texas, USA: (N&S), AB: positive phototropism in lab and elevation seeking in lab and field	Cook, 1996
	Pheidole radoszkowskii Mayr *reflexans* Santschi *P. fallax emiliae* Forel	Misiones, Argentina: (S), soldier parasitized, AB: daytime activity and elevation seeking for a normally crepuscular species	Ogloblin, 1939
	Pheidole sp.	Misiones, Argentina: (N), soldiers and workers parasitized AB: as *P. radoszkowskii*	Ogloblin, 1939
	Pheidole sp.	Natal, South Africa: (N), many parasitized minor workers	Kathirithamby, 1991
	Crematogaster sp.	Angola: (S), 20 parasitized males attracted to black light	Luna de Carvalho, 1972
Formicinae	*Camponotus* sp. (maybe *maculatus* F)	Rombola, Sri Lanka: (S) single worker	Westwood, 1861
	Camponotus punctulatus Mayr *cruentus* Forel	Misiones, Argentina: (S) AB: daytime activity and elevation seeking for normally crepuscular species	Ogloblin, 1939
	Camponotus crassus Mayr	Misiones, Argentina: (S) AB: as *C. punctulatus cruentus*	
	Camponotus planatus Roger *	Veracruz, Mexico: (N), parasitized males and pupae	Kathirithamby and Hughes, 2002
Pseudomyrmecinae	*Pseudomyrmex gracilis atrinodus* Santschi	Misiones, Argentina: (S), AB: elevation seeking	Ogloblin, 1939
Ecitoninae	*Eciton dulcius* Forel*	Cordoba, Argentina: (S), one individual	Hofeneder, 1949
Dolichoderinae	*Dolichoderus bispinosus* Oliver *	Veracruz, Mexico: (N), abundant in alate males	Present study

(S) = single individuals taken away from the nest, (N) = individuals taken from within nests. AB = abnormal behaviour. Elevation seeking is moving up to grass tips or bushes, which apparently precedes emergence of the adult male. In some cases the original author had not established host identity beyond genus. * = confirmed host identity. *radoszkowskii* was spelt as *radosckowskii* and *atrinodus* was spelt as *atrinoda* Ogloblin (1939), and neither are legitimate spellings

Table 2. Number of *D. bispinosus* individuals examined, numbers parasitized and relative percentage according to colony. W = workers, M = alate males, F = alate females

Colony		Whole colony	W	M	F
A	total	4633	4460	163	10
	parasitized	82	43	39	0
	%	*0.018*	*0.096*	*0.239*	*0*
B	total	414	318	89	7
	parasitized	5	0	5	0
	%	*0.012%*	*0*	*0.056*	*0*
C	total	1283	1283	–	–
	parasitized	5	5	–	–
	%	*0.004*	*0.004*	–	–

nal study did collect queens but they were never parasitized. At the same location, in 1988, 326 workers from 13 colonies were collected (again not partitioned according to colony). An examination of this data shows that workers were less often parasitized (11.5% or 14/122) than either alate females (43.1% or 66/153) or alate males (47.1% or 24/51) (Wald = 32.70, 2 d.f., $P < 0.001$). It must be stressed that collection methods differed from the present study (ants were shovelled into buckets and water added until rafts of ants formed). Identical methods were used by Cook (Cook, 1996; Cook et al., 1997), who sampled only workers of *S. invicta,* and consistently found prevalence of infection to be lower than 3%. Such collection methods may be biased. At this stage it is purely conjectural to state that the castes are differentially parasitized by Strepsiptera and host choice tests by 1st instar larvae at the time of infections would be useful in clearing this up. However, considering the disproportionally high numbers of workers usually found in colonies, it might be profitable to initially establish parasite presence by first examining alates.

There are very strong justifications for detailing parasite abundance among the social insects (Schmid-Hempel, 1998). Why Strepsiptera have not been more often noticed by myrmecologists is troubling. The parasite-induced change in host behaviour has been posited to reduce casual detection (Kathirithamby, 1991; Ogloblin, 1939). Clearly, detection of Strepsiptera among the social Hymenoptera is difficult, without dissection of nest occupants, due to their largely endoparasitic nature (Hughes et al., 2003). Normally Strepsiptera are encountered as male pupae (and less commonly as neotenic adult females which extrude through the abdomen of the hosts, though not for those infecting ants). In ants, detection is hampered because of the very cryptic nature of the male pupae and the habit of parasitized ants to remain in the nest, among large numbers of siblings, until parasite emergence. Extra-nidal ant collecting methods, such as fogging or Winkler sampling, are unlikely to find parasitized ants as they die quickly after male emergence. Awareness of the behavioural changes accompanying parasitism such as elevational seeking or diurnal activity by normally crepuscular species (Table 1) may promote detection. It is intended that our documentation of a new host sub-family, collation of the literature and incidences of behavioural changes and examination of relative prevalence among ant castes might promote an increased awareness of Strepsiptera among myrmecologists.

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