TERRITORIAL BEHAVIOR OF THE SUBSOCIAL BEETLE *HELISCUS TROPICUS* UNDER LABORATORY CONDITIONS (COLEOPTERA, PASSALIDAE)

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Folia Entomológica Mexicana No. 70: 53-63 (1986)

Recibido para publicación: 20 enero 1986.
Aceptado para publicación: 26 mayo 1986.

RESUMEN

El comportamiento territorial de *H. tropicus,* su variación estacional y la participación de cada uno de los sexos en dicho comportamiento fueron estudiados por medio de la introducción de pasalidos "extraños" en nidos huéspedes instalados en el laboratorio. Se encontró que únicamente los nidos colectados en la época de reproducción presentan este comportamiento. Este se manifiesta por medio de la producción de reacciones agonísticas ostensibles (embestidas, mordidas y huidas) al contacto entre los huéspedes y los intrusos. En todos los casos observados los huéspedes iniciaron la agresión y los intrusos presentaron un comportamiento de huida. La mayor parte de estas interacciones fueron unidireccionales (de los huéspedes a los intrusos); sin embargo, ocasionalmente, se observaron también algunas interacciones agonísticas recíprocas que tuvieron el mismo resultado que las anteriores. Ambos sexos participan en la defensa del nido, pero la agresión es más frecuentemente dirigida hacia los individuos del mismo sexo. También se observó que algunos de los intrusos pueden ser tolerados por las parejas territoriales; con los datos disponibles no es posible explicar el origen de estas variaciones en el comportamiento.

PALABRAS CLAVE: Comportamiento Territorial, Passalidae, Insectos subsociales, México.

ABSTRACT

Territorial behavior, its seasonal variation and the participation of each sex were studied in *H. tropicus* by introducing "foreign" passalids into host nests installed in the laboratory. Only nests collected in the reproductive season exhibited this behaviour, which comprises obvious agonistic reaction (attacks, bites and retreats on contact between the host and intruders. In all observed cases the hosts initiated the aggression and intruders presented the escape response. The majority of these interactions were unidirectional (from host to intruder), but occasionally some reciprocal agonistic interactions were observed that nevertheless had the same end result. Both sexes participated in nest defense but aggression was more frequently directed at individuals of the same-sex. It was also observed that some intruders were tolerated by the host pair; with the data available it is not possible to explain the origin of this variation in behaviour.

KEY WORDS: Territorial behaviour, Passalidae, Subsocial Insects, Mexico.

INTRODUCTION

Passalids are saproxylophagous subsocial beetles (Wilson, 1971). The reproductive unit begins with the formation of a monogamous pair; after fertili-

zation, which occurs in decaying tree trunks, both members of the pair stay together and cooperate in the construction of galleries and care of the young. After their eclosion, the young adults remain for some time in the nest and help their progenitors with the care of the younger members of the brood; later they disperse and form new nests (Ohaus, 1900, 1909; Gray, 1946; Reyes-Castillo, 1975; Schuster 1975a; Reyes-Castillo & Halffter, 1983; Valenzuela-González & Castillo, 1984; Valenzuela-González 1985; Schuster & Schuster 1985) Generally these insects have a seasonal life-cycle (Pearse *et al.,* 1936; Gray, 1946; Schusted 1975a; Valenzuela-González, 1985).

Some observations carried out by Gray (1946) and Mullen & Hunter (1973), suggest the existence of a seasonal territorial behaviour in *Odontotaenius disjunctus* (Illiger). Other studies varried out by Alexander *et al.* (1963) and Schuster (1975a) with the same species and by the latter author with *Passalus affinis* (Percheron), also support the existence of this behaviour in the two species. Nevertheless, in all these cases the observations were scant and occasional. In previous publications we have reported various aspects of the reproductive behaviour (Valenzuela-Rodríguez & Castillo, 1984) and biology (Valenzuela-González, 1985) of *Heliscus tropicus* (Percheron), a passalid belonging to the tribe Proculini and having a wide distribution in Mexico. In the present study we report the results obtained from a series of experiments carried out under laboratory conditions with the object of studying the territorial behaviour of these insects, its seasonal variability and the role of each sex in this same behaviour.

METHODS

The insects were collected in "El Suspiro", a locality in the municaplity of Berriozabal, Chiapas, Mexico. The location, techniques of collection and type of nests utilized for the observations of the insects have been previously described (Valenzuela-González & Castillo, 1984; Valenzuela-González 1985). With the object of studying the existence of territorial behaviour in these insects, a series of experiments was carried out where "instrusive" individuals were introduced into host nests previously installed in the laboratory. These nests were occupied by passalids all collected from the same nest in the field so that there was no modification of the host group. The original nest wood was also utilised for the experiments.

After their installation in the laboratory, the insects remained for five days in complete darkness to allow them to become accustomed to their new surroundings. Following this period, the homospecific introduction experiments were started using individuals collected at the same time and place as those

from the host nest. Thus insects of unknown age were used, although to reduce the influence of this factor only individuals that had aquired adult colour were utilized. Typically, with this species the adults attain their characteristic black colour at approximately four months.

During the agonistic interactions between passalids, obvious acts physical aggression such as attacks and bites were seen, although usually accompanied by other acts including exploratory movements, antennal tapping and stridulations (Gray, 1946; Alexander *et at.*, 1963; Mullen & Hunter, 1973; Schuster, 1975a; Valenzuela-González & Castillo, 1984). However, these latter acts also manifest themselves in other situations (Alexander *et al.*, 1963; Schuster, 1975a, b; Buchler *et al.*, 1981; Valenzuela-González & Castillo, 1984). For this reason, to study territorial behaviour, the criteria used for the existence of aggressive behaviour were the presence of attacks, bites and escapes (the rapid withdrawal of the attacked individual). When this type of interaction between host and intruder was not seen during an observation period of 30 minutes after initial contact between the two, the intrusions were considered to be tolerated by the host nest. In such cases of tolerance, three other similar intraductions with different individuals were carried out, each with an intervening periodo of 24 hours. If after these four trials no territorial behaviour was observed, it was considered to be absent from the nest in question. With the object of studying the possible seasonal variation in the behaviour, two groups of insects were studied. One group consisting of pairs of passalids collected from July to October (n=28), during the hegiht of the breeding season, the other group being passalids collected from February to May (n=23), when the reproduction of *H. tropicus* had ceased in the area (Valenzuela-González, 1985).

As these insects display no external sexual dimorphism and in order to differentiate the reactions of each member of the pair and the influence of the sex of the intruder, a series of tests were carried out with marked passalids. The technique for marking is described in Fresneau & Charpin (1977). Four intruder introduction tests were carried out in each nest, two with males and two with females. Intruders were sexed by anesthetizing (with CO_2) opening the pygidial plate and observing the presence of abscence of an edeaguous with a microscope. During sexing, they were handled very carefully to avoid any possible injury. Hosts were sexed in the same way, but after theend of the experiments. These experiments were varried out withan interval of 24 hours between each trial, alternating between males and females. With respect to the eight nests utilised as hosts for these tests, only those containing individuals that had previously demostrated agonistic behaviour were used.

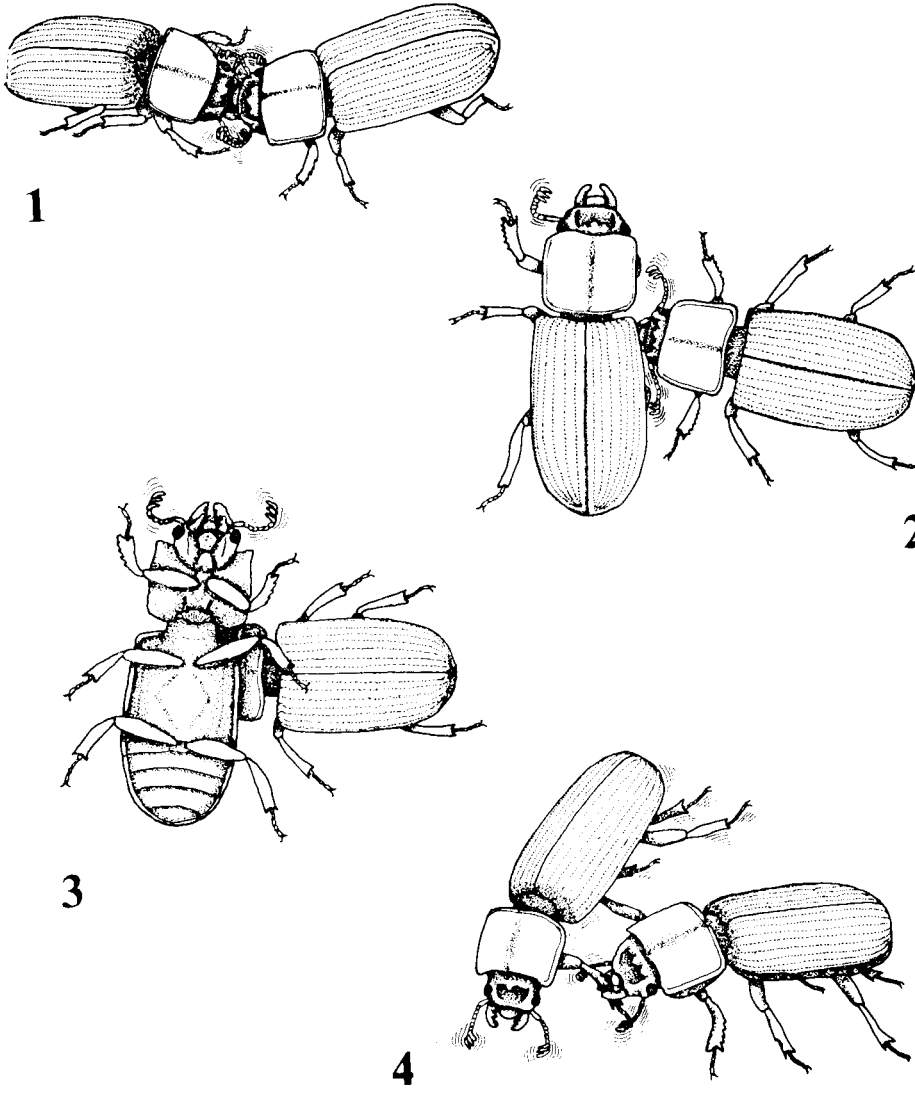
RESULTS

1) Description of behaviour. Of the 51 experiments performed, in 11 cases (21.6%) aggressive interactions were recorded. In each case the host insects initiated the aggression and were victorious, with the intruders presenting an escape response to the aggression. The agonistic interactions observed during these encounters were markedly "violent". Because of the intensity and persistence of the aggression, it is probably that if the introdus had been left indefinity in the host nest the final result would have been the death of the intruder, principally due to the bites inflicted by the powerful mandibles that these insects possess (Reyes-Castillo & Jarman 1981).

The behaviour observed was similar to that described by Gray (1946), Alexander *et al.* (1963) and Schuster (1975a) in *Odontotaenius disjunctus* (Figure 1). The stimulus that seems to trigger of the aggression is the establishment of contact with the intruder. The insects may aproach very close to one another but without contact no reaction is apparent. Before directly aggressive behaviour manifests itself (attacks and bites), antennal exploration and tapping is performed over the body of the other individual. These acts were observed in every encounter (n=45). Usually stridulations were also heard but coul not be verified in all cases and possibly in some cases they were not audible. On one occassion before aggression, a rotation behaviour was also noted which was similar to that present during courtship behaviour (Valenzuela-González and Castillo 1984).

Once initiated, the aggressive interactions were mainly attacks and bites. During the attacks, the aggressor passalid continually pushed and its rival with its mandibles, apparently trying to locate them under the body of its opponent so that it might then, on suddenly lifting its read, overturn its opponent. During these attacks the insects would keep the mandibles open and try to bite on contact with one another. However, because of the hardness of the cuticle and because the majority of the attacks took place over the thorax or abdomen of the rival, the bites were rarely serious. Nevertheless, applied to a leg or antenna, the strength and duration of a bite (of the order of several seconds) could be sufficient to sever the appendage. On several occasions we observed that during the bites the aggressor "carried" the other passalid by the bitten appendage, generally a leg, and pushed it violently against the walls of the gallery where the latter managed to escape (Figs. 1-4).

During these interactions the recipients of aggression frequently adopted a position similar to that described by Mullen and Hunter (1973) for *O. disjunctus* as "submission". In these cases the attacked passalid placed itself laterally with respect to the other, hiding its ipsilateral legs and antenna under



Figs. 1-4. Aggresive interactions in *Heliscus tropicus*. 1) frontal assault; 2) lateral assault, with "submission" position of the attacked beetle; 3) lateral assault with the aggresor overturn its opponent; 4) aggressor carring the opponent by the bitten leg.

its body, sucho that it lowered this side to the level of the ground. At the same the contralateral legs remained firmly attached to the ground or walls of the gallery. Thanks to this adopted stance, the aggressor could not easily bite the rival's appendages nor easily overturn it. All these interactions terminated with the rapid retreat of the intruder; if the latter restablished contact with the host insect, the aggressive behaviour would immediately begin again.

In the majority of the cases only one of the insects (the host) showed aggression. However, on two occasions the intruders responded to attacks and established an aggresive interaction. The longest duration of such an interaction was 4 minutes and 25 secons. The passalid hosts were always the victors with the intruders retreating at the end of combat. In the natural state it is probable that this type of encounter finishes with the exit of the intruder from the nest as in the cases reported by Schuster (1975a). However in the present experiment interactions were carried out in a closed nest from which the insects could not flee; this fact might explain in part the "violence" of the observed interactions.

2) A study of territoriality in nests collected during and after the breeding season. In none of the 23 nests collected outside the reproductive period could we confirm the presence of territorial behaviour towards the intruders used. On the contrary, of the 28 nests in a reproductive phase, 11 cases (39.3%) of agonistic reactions to intruders were observed. These results suggest that territorial behaviour is closely linked to reproduction. In this respect it is worth mentioning that of the 11 nests in which this behaviour was confirmed, in four of these we observed courtship and in one case copulation between the host pair. In addition we carried out similar experiments with pairs of *Proculejus* sp. and *Spurius bicornis* (Truqui) which were observed to copulate under laboratory conditions. The introduction of homospecific intruders provoked immediate agonistic interactions similar to trose bescribed above.

3) A study of territoriality as a function of the sex of the host and intruders. Table 1 shows the results obtained and indicates that individuals of both sexes can participate in the defence of the nest. Nevertheless the males showed more frequent aggression to male intruders than to females ($X^2=6.8$; $p < 0.001$); similarity, female hosts showed more frequent aggression to female intruders than to males ($X^2=4.5$; $p < 0.05$). It is interesting to note that only two intrudes (females in both cases) were observed that provoked no agonistic reaction on the part of either of the hosts, in all eight tests.

TABLE 1

The number of times that males and females of territorial pairs of *H. tropicus* reacted (+) or did not react (—) agonistically to homospecific intruders of both sexes in their nests and percentage of positive reactions

Hosts	Intruders	(+)	(—)	%
♂	♀	14	2	87.5
♀	♀	12	4	75
♂	♂	7	9	43.7
♀	♂	5	11	31.1
			11	31.3

DISCUSSION

The existence of aggressive behaviour towards intruders, plus the fact that in all observed cases it is the host that initiates this aggression and the intruders who retreats, together indicate the presence of territorial behaviour in these insects. Mereover, our results confirm the observations of Gray (1946) and Mullen & Hunder (1973) in that there exist seasonal variations in the territorial behaviour of these insects which is closely linked to the reproductive period. The biology of the passalids suggests the existence of a strong selection pressure at the level of pair and nest defence. In effect these insects form monogramous pairs with both partners exhibiting parental care (Schuster, 1975a; Reyes-Castillo & Halffter, 1983; Valenzuela-González, 1984); they have a sex ratio of 1:1 (Gray, 1946; Valenzuela-González, 1985), a life cycle that is seasonal (at least in some species such as *H. tropicus*) and invest considerable of time and energy in nest construction prior to mating (Gray, 1946; Schuster, 1975a; Reyes-Castillo & Halffter, 1983; Valenzuela-González & Castillo, 1984; Valenzuela-González 1985).

The abundance of food once located, together with the characteristics of the biology of those insects previously mentioned, might explain the seasonal variations in territorial behaviour. Nevertheless it is important to consider the fact that it was only possible to confirm this behaviour in a proportion of reproductive pairs. We can not exclude the possibility that this type of variation is also seen in the natural state; however it is also possible that it is due to stress produced by their collection and location in the laboratory. Observa-

tions carried out by Gray (1946) on *O. disjunctus,* suggest that important modifications in reproductive behaviour can occur following their collection; our own observations indicate a similar phenomenon in *H. tropicus* (Valenzuela-González, 1984).

The experimental data show that both sexes display this behaviour. Nevertheless the aggression shown by each sex is more frequently directed towards an intruder of the same sex. Territorial defence by both sexes is not very common in insects (see reviews by Price, 1975; Baker, 1983; Fitzpatrick and Wellington, 1983). Cases are known in silphids of the genus *Necrophorus* (Pukowski, 1933; Milne & Milne, 1976) and in cockroaches of the genus *Cryptocercus* (Seelinger and Seelinger, 1983). Both cases presented a similar situation to the passalids, with the insects displaying aggression principally to individuals of the same sex.

Nevertheless, in the case of *H. tropicus,* we also observed that individuals of both sexes sometimes displayed aggression to members of the opposite sex. In fact there can be great variability between one nest and another: in some cases both male and female are very aggressive, while in others only one partner is thus disposed (Valenzuela-González & Castillo, 1940). With data from only eight nests it is difficult to explain the origin of these variations in behaviour of the male and female hosts. The influence of various factors that we could not study, such as age of intruders, strength of pair bond, their physiological state (as well as that of the hosts), the presence or absence of a brood in the nest, the "cohesion" of the host pair, etc., might be a source of some of this variation.

Moreover, during these experiments we observed some cases of intruders that did not trigger off agonistic reactions from the hosts. In the field during the collection of nests of reproducing pairs, in the mejority of cases a single pair of occupants was encountered; however, occasionally more than two adults were found. Similar cases, of tolerance towards certain individuals, has been reported in other territorial insects. For example, Ewing (1972) observed that territorial males of the cockroach *Nauphotea cinerea* tolerate " submissive" males within their territory, whereas other territorials males are immediately repulsed. Possibly this tolerance towards other individuals (probably insects that do not represent sexual competitors to the hosts) by the nest pair, could facilitate construction of galleries and food production for the brood, since the larvae depend on the adults for their food (Reyes-Castillo & Jarman 1981, Reyes-Castillo & Halffter 1983). Nevertheless it would be necessary to carry out complementary studies about these interactions in order to understand the factors that regulate them.

ACKNOWLEDGEMENTS

I am very greateful to M. en C. Pedro Reyes-Castillo from the Instituto de Ecología for his continual helpful discussions during this work and to Dr. Guillermo Ibarra from CIES for critical review of the manuscript. I also thank Dr. Peter Baker from CIES for his comments and help with the translation of the papel and Mrs. Alvaro García-Ballinas, Antonio López-Méndez and Miguel Pérez Bautista for their assistence during the collection of the insects.

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