

MANDIBULAR FORCE OF ADULT AND LARVAL PASSALIDAE IN FAMILY GROUPS*

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RESUMEN

La fuerza de las mandíbulas de larvas y adultos de grupos familiares de diversas especies de coleópteros de la familia Passalidae fue medida mediante un dinamómetro. Los resultados muestran diferencias significativas entre las fuerzas ejercidas por los adultos y las larvas, situándose los adultos tenebrales entre estos dos extremos. En vista de la disparidad de las fuerzas mandibulares entre adultos y larvas, estas últimas dependen para su alimentación de los pedazos de madera que los adultos extraen de las paredes de las galerías donde habitan. Es evidente que el comportamiento subsocial presentado por este grupo de insectos, está reforzado por esta dependencia alimentaria de la larva.

ABSTRACT

The mandibular force of larvae and adults of family groups of various species of Coleoptera of the family Passalidae was measured with a dynamometer. The results show significant differences between the mandibular forces of adults

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and of larvae, while teneral adults showed intermediate strengths. The differences in mandibular force indicate that the feeding of the larvae depends on the pieces of wood that the adults extract from the walls of their galleries. The food dependency of the larvae reinforces the subsocial behavior of this group.

INTRODUCTION

Passalid beetles are known to be subsocial. The only known life cycle within this group is that of the Northamerican species *Odontotaenius disjunctus* (Illiger), described by Gray (1946). Partial data gathered to date on the life cycle of some tropical species show similarity in all major respects with *Odontotaenius*. The extent to which subsociality is obligatory has been the subject of debate in the past. Four recent studies coincide in considering passalid beetles to possess one of the highest levels of subsocial behaviour known for insects (Schuster and Schuster 1985; Reyes-Castillo and Halffter 1983, 1984; Valenzuela-González and Castillo 1983).

One area of discussion has centred on the feeding of the larvae by the adults of a family group. The adults chew wood from the ends of the family's living-galleries into splinters and the larvae in turn chew the splinters. Ohaus (1900) suggests that this behavior occurs because the mandibles of the larvae are too weak to remove splinters directly from the walls of the galleries, while Heymons (1929) and Pearse *et al.* (1936) have denied this. In the present work, larvae and adults have been caused to nip a dynamometer with their mandibles and the maximum forces registered in such nips have been measured with a view to quantifying one of the capabilities which the animals must use if they are to remove splinters from gallery walls.

MATERIALS AND METHODS

The experimental protocol and the apparatus used in these experiments were in the main identical with those described previously (Jarman 1980); the only change made was that a third dynamometer lever, even smaller than the two previously described, was available. This third lever was small enough to be placed between mandibles

only 0.5 mm apart and it had a compliance of 1.1 μm per gram-weight (113 μm per Newton).

Animals were only used for these experiments when adults and larvae were found together in the same tunnel. Such suitable families were found while collecting during August and September 1982 in different localities of the States of Puebla and Chiapas, México (Table 1).

Each individual was caused to squeeze the dynamometer lever ten times while being stimulated by the experimenter in such ways as seemed to result in the most forceful nips on the lever by the mandibles. This was normally a combination of handling and breathing on the insect.

RESULTS

Table 1 shows the results obtained from those family groups where at least two larvae and a mature black adult were collected, appeared in good condition and lived for at least a week after the experiments (normally they survived for much longer). In no case did omitted data contradict the published results.

In every family group studied, the mandibles of the larvae all squeezed the apparatus much less strongly than did those of the weakest adults, as shown in Table 1. Ranking the forces in increasing order within family groups, letting L and A represent forces produced by larva and adult respectively, we have for group 2 LLLAA, for family 5 LLLLA and for group 9 LLAA. The probability of an arrangement as extreme as this occurring by statistical fluctuations if the adults were not consistently stronger than the larvae would be only 0.001. If we disregard the information inherent in the pairing of adults with larvae of the same species, of the same family group, and instead just treat the fourteen insects as a single group of medium-sized passalids, the series is LLLLLLLLLLAAAAA, with a probability of only 4×10^{-6} .

To put the large difference between larvae and adults into perspective, a larger database than that presented here is needed. This is made up by accreting to the data that are presented above the previously-published data of Reyes-Castillo and Jarman (1981) as well as some unpublished data that have accumulated since then. The augmen-

Table 1.

List of passalid specimens used in this work. Each individual nipped the dynamometer ten times. The figure in the last column is the force in grams-weight exerted in the greatest nip, while that in previous column is the mean of the forces of the ten nips.

SPECIES	SEX/ STADIUM	MASS (g)	Force (g-wt)	
			MEAN	GREATEST
Family 2 <i>Heliscus</i> <i>tropicus</i> (Percheron) ^a	Larva III	0.35	4.70	8.64
	Larva III	0.35	4.55	11.2
	Larva III	0.40	5.92	9.63
	♀ Adult	0.53	114.9	146.1
	♂ Adult	0.49	106.2	120.8
Family 5 <i>Passalus (Pertinax)</i> <i>punctatostriatus</i> (Percheron) ^a	Larva III	0.31	28.1	38.9
	Larva III	0.33	26.8	46.4
	Larva III	0.37	35.4	48.7
	Larva II	0.26	16.2	32.6
	Adult teneral	0.32	16.6	27.2
	♂ Adult	0.41	135.0	170.9
Family 9 <i>Odontotaenius</i> <i>striatopunctatus</i> (Percheron) ^a	Larva III	0.69	7.26	18.2
	Larva III	0.76	6.59	10.6
	♀ Adult	0.83	183.2	221.2
	♂ Adult	0.74	164.2	180.5
Family 8 <i>Heliscus</i> <i>vazquezae</i> Reyes-Castillo y Castillo ^a	♀ Adult	0.47	136.1	158.3
	♂ Adult	0.61	169.1	230.6
	♀ Adult	1.21	252.5	342.5
	♂ Adult teneral	0.74	89.1	119.5
	♀ Adult teneral	0.69	76.3	90.2
Family <i>H. vazquezae</i> ^c	♀ Adult	1.02	200.4	288.4
	♂ Adult	0.89	134.1	169.9
Family 10 <i>Proculejus</i> <i>brevis</i> (Truqui) ^b	♀ Adult	1.40	138.7	208.5
	♂ Adult	1.32	79.2	139.0

SPECIES	SEX / STADIUM	MASS(g)	Force (g-wt)	
			MEAN	GREATEST
Family <i>P. brevis</i> b	♀ Adult	2.08	151.5	262.3
	♀ Adult	1.36	141.4	205.1
	♂ Adult	1.47	271.4	352.5
	♂ Adult	1.67	176.8	288.4
Family 1 <i>Heliscus tropicus</i> (Percheron) a	♀ Adult	0.68	134.4	196.5
	♀ Adult	0.71	170.0	208.1
	♂ Adult	0.68	127.1	219.0
	Larva III	0.43	8.72	13.9
Family <i>Proculus beckeri</i> (Zang) d	♀ Adult	6.48	750.3	897.4
	♂ Adult	7.26	759.9	1015.0
	♂ Adult	7.26	457.8	668.7
	♂ Adult	6.70	571.0	715.8
Family Unidentified	Adult	0.24	86.9	99.5
	Larva	0.20	5.79	7.69
	Larva	0.20	6.24	13.2
Miscellaneous specimens <i>Oileus heros</i> (Truqui) c <i>Petrejoides orizabae</i> Kuw. c <i>H. vazquezae</i> c	Adult	4.10	282.1	355.1
	Adult	0.28	58.1	88.3
	♀ Adult	1.09	241.0	262.8
	♂ Adult	0.88	211.2	237.6
Unidentified	Adult	0.28	167.7	209.7
	Adult	0.28	188.8	218.6

g - grams, g-wt grams/weight.

Números romanos: second (II) and third (III) larval instars.

a - Barranca de Patla, Puebla.

b - Camotepec, Piedras Encimadas, Puebla.

c - Xicotepec de Juárez, Puebla.

d - El Bosque, La Trinidad, Chiapas.

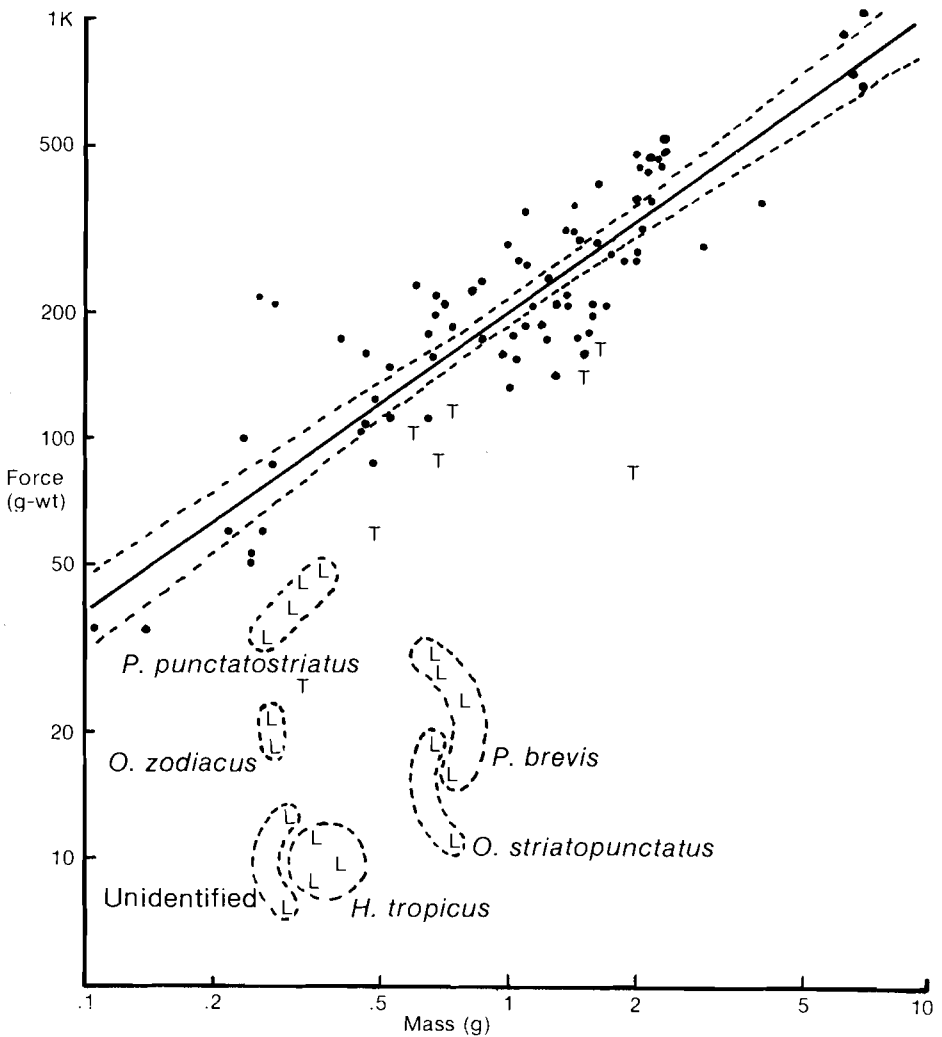


Figure 1.

Graph connecting maximum force exerted by the mandibles of passalids with their mass. The broken lines indicate 95% probability limits for predictions of the force that might be exerted by the typical adult of a given mass. Also shown are points plotted for larvae (L) and teneral adults (T) that have been measured. Both scales are logarithmic.

ted database, which is presented graphically in Fig. 1, rests on species of widely divergent sizes, and so the sizes of the individual specimens have to be taken into account; it is no longer reasonable to classify the entire experimental group as "medium-sized passalids". The line plotted is the regression line of log (mandibular force) on log (mass). The force of the strongest of ten measured nips was used for this. Also plotted as broken lines are the 95% confidence limits for the regression. The residual deviations of the points from the regression line show approximate normality on the moments test (e.g. Fisher, 1946). The regression line was found to be represented by the relation:

$$\text{long (force)} = 2.286 + 0.702 \text{ long (mass)}$$

or equivalently:

$$\text{force} = 193 (\text{mass})^{0.702}$$

where force is measured in grams-weight, mass in grams and logarithms are to base 10. The standard error of the slope is $\pm .043$

While the deduced relationship between mandibular force and mass for adults is reasonable and free from anomalies, the same cannot be said for the corresponding relationship among the larvae tested, and the best that can be done is to treat the family groups of larvae individually. After averaging logarithms of mass and force within each family group, the third stage larvae of *Odontotaenius striatopunctatus* turn out to exert 11.1 times less mandibular force than does a hypothetical passalid adult of the same mass as the larvae. Third stage *Heliscus tropicus* larvae are 9.8 times less strong than adults of the same mass and those of an (as yet) unidentified species 6.2 times less strong. Data from Reyes-Castillo and Jarman (1981) show third stage *Proculejus brevis* larvae nipping 6.6 times less strongly and second stage *Odontotaenius zodiacus* 3.8 times. Out of line with these results is a family of four second and third stage larvae of *Passalus (Pertinax) punctatostratus*, which nipped only 2.1 times less strongly than did adults of like mass. For purposes of comparison, a convenient rule-of-thumb for these species is that an adult has about 1½ times the mass of the third-stage larva of the same species.

Three adventitious results of this research have been the findings that (i) no significant difference was found between the mandibular strengths of male and female adults of the same family group,

(ii) the strengths of teneral adults usually fell between those of larvae and those of mature black adults and (iii) the strengths of the Passalid larvae fell far short of those of a 2-gram Scarabaeid larva (326 g-wt) and two larvae of the Dynastinae *Strategus aloeus*(Lin.) of masses 12 and 17 grams and mandibular forces 516 and 686 g-wt respectively that were also tested. This Scarabaeid larvae are solitary and live in galleries dug in rotting wood, under very similar conditions to passalid beetles.

CONCLUSIONS

Given such a great disparity between the measured mandibular forces of larva and adult, we are forced to conclude that either the adult mandibles are far too strong for gnawing wood (in which case we must postulate an additional function for such strong appendages) or else that the larval mandibles are much too weak for gnawing wood. The more reasonable of these possible conclusions is that the larvae are mechanically incapable of breaking off splinters of wood from the concave interior surfaces of their living-tunnels and that this is linked with the subsocial habit of Passalidae. Many authors have commented on the fact that larvae feed on wood particles that been off by the adults and Gray (1946) notes the fineness of these particles in comparison with the coarseness of chips that are formed when adults first start a tunnel and no larvae are present.

It must be remembered, too, that strong (and properly shaped) mandibles are not the only requirement for efficiently breaking off chips of wood from the concave interior surface of the tunnel. The gnawing may be described as a three-stage process: (1) the open mandibles must be pushed into the surface of the wood, (2) the mandibles must grip wood between them by their closing force and (3) the gripped chip must be either scissored off by the same closing force or else pulled out by a pulling force exerted partly by the legs and aided, perhaps, by head-wagging, etc. The present work concerns itself only with the force involved in the second of these three stages; its conclusions are reinforced by the notion that larvae are not equipped to provide the pushing force for the first stage. Even if they were, the larvae would find it hard to engineer a point d'appui that prevented their bodies slipping while they were attempting to drive their open mandibles into the wood surface.

Thus the balance of evidence is that larval Passalidae of the species studied could not feed themselves by chewing wood splinters directly from the walls of the tunnels in which they live because their mandibles do not grip with enough force to do this, as well as for other reasons. Subsocial behaviour therefore seems to be obligatory, not facultative, for the larvae at their present stage of evolution. We know little of the evolutionary events that led to either subsocial behaviour or the weakness of the larval mandibles and cannot therefore say that either 'caused' the other nor whether both were independently caused by a third evolutionary pressure.

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