

Mate Securing Tactics and the Cost of Fighting in the Japanese Horned Beetle, *Allomyrina dichotoma* L. (Scarabaeidae)

Michael T. SIVA-JOTHY

*Faculty of Agriculture, Nagoya University,
Chikusa-ku, Nagoya, 464 Japan*

Abstract – Males of the horned beetle *Allomyrina dichotoma* L. show a bimodal frequency distribution with respect to horn size. The 2 morphs distinguished by this criteria showed different mate-securing tactics. Major males fought for possession of areas on oak trees that exuded sap. Fights escalated through a series of stereotyped encounters before entering the potentially damaging phase of close-quarter combat when the largest males in particular risked serious damage. Minor males, on the other hand, were never observed to fight with conspecific males, but retreated after making contact with them. Minor males arrived at sap sites earlier in the diurnal cycle than major males and so avoided them temporally as well as behaviourally. Minors appeared to be relatively as successful at gaining copulations as majors, but did so earlier in the diurnal cycle. Since females showed a slight tendency to remate on the same night, minors may lose fertilization opportunities if last male sperm precedence is high. Actual sperm precedence values are not known so the reproductive payoffs for the 2 morphs could not be assessed.

Beetle horns are one of the most spectacular products of sexual selection. They appear to be chiefly employed in male-male combat over restricted resources (e.g., burrows, oviposition sites and/or females), the great variation in horn morphology between taxa probably reflects species specific differences in the way they are brought to bear on opponents. In a few cases apparently bizarre horn architecture has been shown to have a highly specific function in the context of fighting (e.g., Palmer 1978; Eberhard 1979, 1981). Species in which only males have horns often show marked intermale size variation (Palmer 1978; Eberhard 1979; Brown & Bartalon 1986). Eberhard (1980) showed that this variation in a particular horned beetle was bimodal with respect to horn size: “major” males had disproportionately larger horns than “minor” males, who had much reduced horns (horn size has an allometric relationship with body size in most horned species, Otte & Stayman [1979]). The basis of this horn size dimorphism remains obscure, although hypotheses for the maintenance of dimorphisms in insects in general (Gadgil 1972; Maynard-Smith 1976) and in horned beetles in particular (Eberhard 1980, 1982) exist. Moreover, although the tactics of major males are well described and in general appear to be similar in most horned beetle species (i.e., major males fight), the tactics used by minor males are much less well doc-

umented (but see Eberhard 1982).

There are very few reports of serious damage being caused during, or as a result of, horned beetle fights even though these animals often possess powerful and fearsomely armoured weapons. I present descriptive data on the Japanese horned beetle, *Allomyrina dichotoma* L. which suggest that although minor males are not inclined to fight they still manage to secure matings, and that fighting for possession of sap-sites by major males can result in serious (i.e. fitness reducing) injury, especially to the largest.

Study Area and Methods

The study site was a small (800m²) wood consisting mainly of *Quercus serata* Thunb. in the south of Nagoya University campus. Within this wood were 4 wounded oak trees which exuded sap in relatively large quantities. Each wounded tree bore several discrete sap-sites (a sap-site is a lesion in the tree bark that exudes sap) of varying size. The total number of sap-sites on the 4 trees was 14. In mid-spring sap-exuding trees began to produce a pungent odour similar to rotting apples; the phenomenon is probably caused by microbial fermentation of the sap. Sap-exuding trees could be easily located, even in dense woods, by smell alone; presumably the beetles, which

appeared several weeks later, also used olfaction to locate suitable trees.

Observations were carried out on 9 nights between 18th July and 24th August 1986. Observation nights were climatically similar (clear sky and no wind) and, because weather patterns tend to be cyclical in Japanese summers, were about 3–5 days apart. Morphometric data were collected from animals captured in the study area or in woods near the study site. Arrival rates were estimated by counting and then removing all individuals from all sap sites at half-hour intervals on 2 nights. Half-hourly data were pooled for each night. Continuous observations on 5 nights at sap-sites yielded behavioural data.

Elytra-length was the only measurement made on individuals observed in the field because it could be easily obtained without disturbing them. All individuals were marked us-

ing enamel paint (Mitsubishi paint-marker PX-21) on the rear portion of their elytra (scratching numbers onto the elytra was more permanent, but involved too much handling and often resulted in the immediate dispersal of a marked individual).

Fighting experiments were carried out in the field by removing all individuals from a particular tree and introducing males caught at other sites. Some males were introduced on a sap-site and left undisturbed for 10 min, these males were termed "owners". Males introduced onto sap-sites which had an owner were termed "intruders". In most cases a pair of beetles was tested twice at the same site with owner/intruder status being swapped between tests. The male remaining at the site was considered to be the winner regardless of the number of levels the conflict escalated through.

All observations were made in low-level red light emanating from a National BF-175 head-mounted lamp. This type of illumination did not appear to affect beetle behaviour.

Statistical tests and levels of significance are given where applicable.

Results

The Beetle

A. dichotoma is found throughout most of Japan; both males and females show size variation (Fig. 1). Males also have horns; a long, stout head-horn and a shorter prothoracic-horn. Adults appear in late June when they can be found on sap-exuding trees at night. Most activity occurs in the dark and it is likely that tactile senses are more important than visual ones, although the beetles have relatively good eyesight and respond rapidly to low levels of white light. During the day the beetles bury themselves in leaf litter. Copulation occurs on or near sap-sites. A single, virgin female contains about 30–40 eggs in her ovaries (personal observation) and they are laid individually, or in small clusters (2–5) in humus or other wood-based detritus near rotting logs. The larvae feed on humus and rotting wood and develop to the final instar before the end of the year. They overwinter in the final instar well below the ground surface and pupate in early spring the following year. Adults begin emerging in mid-June and disappear at the beginning of September.

Population Morphometry

Morphometric analysis of 67 males revealed unimodal frequency distributions for fore-femur length, pronotum width, elytra length and elytra

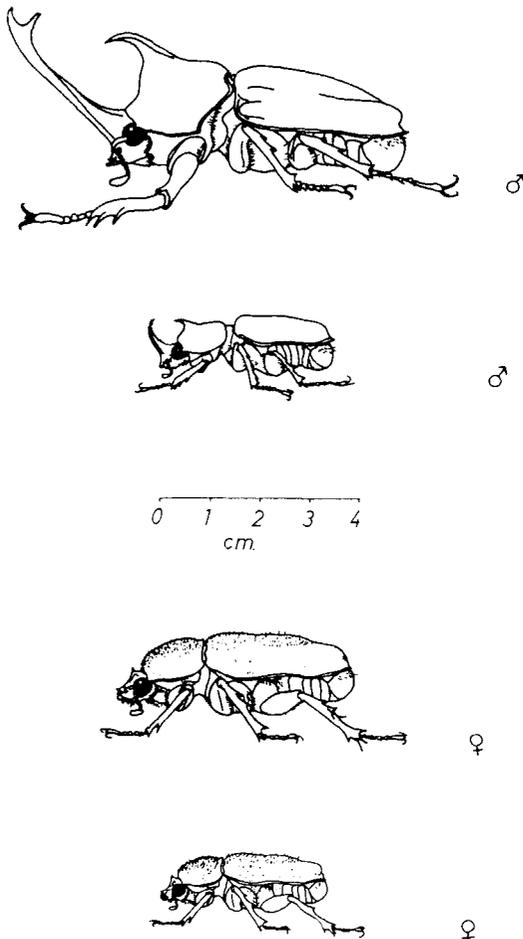


Fig. 1. The general appearance of, and size variation in, male and female *A. dichotoma*. The biggest and smallest individuals are shown for each sex.

width. Horn length showed a distinct bimodal distribution (Fig. 2). Analysis by Taylor's method (1965) indicated the distinct possibility of trimodality, however the status of the intermediate mode (15–23 mm horn length) is unclear as sample sizes were small. Intermediate forms were treated as "majors" in this study; the population was divided at a horn length of 16 mm (Fig. 2). The distinction between minors and majors in the field was made using elytra length, the dividing point being approximately 26 mm (Fig. 3).

Morphometric analysis of 66 females revealed unimodal frequency distributions for all body parameters. Females do not possess horns. Females were, on average, smaller than males and showed less variation in each morphometric category.

Non Reproductive Behaviour of Females at Sap Sites

Females began appearing at sap sites at 20:00 and had usually departed by 6:00 the following morning. Peak numbers at the study site occurred between 24:00 and 4:30, whilst peak arrival rates occurred between 22:00 and 24:00 (Figs. 4 & 5).

Females flew to sap-exuding trees and began feeding at sap sites shortly thereafter. If the site was crowded with conspecific females "head-butting" between females was sometimes observed. These scuffles were usually brief. Occasionally (n=3) females were attacked by major males in what may have been cases of mistaken identity. In 1 such case the attacked female was thrown from the tree. When a mobile female collided with a stationary conspecific it showed

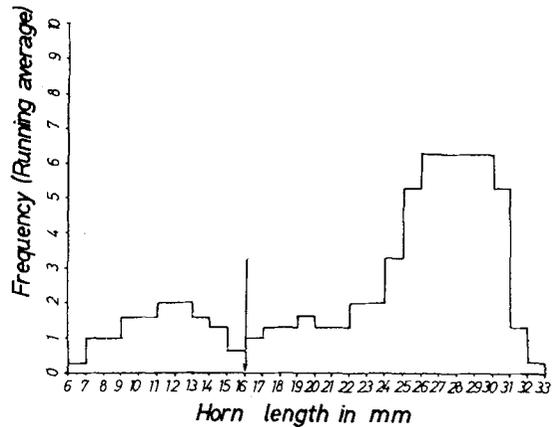


Fig. 2. A running average frequency histogram of horn-length in male *A. dichotoma*. The downward pointing arrow registers the division separating minor and major males.

no overt behavioural change, but carried on its way (n=16). If a conspecific collided with a stationary female the latter did not change its attitude in any detectable way (n=20). Females usually stayed at a particular sap site throughout the night (140/182 observations) but would occasionally move on to another site on the same tree (30/182 observations) or leave the tree altogether (12/182 observations).

Behaviour of Major Males at Sap Sites

Major males flew to sap sites at 20:00 and remained until about 6:00. The peak in the number of majors present at sap sites occurred around 1:00–3:00 (Figs. 4 & 5). It appears

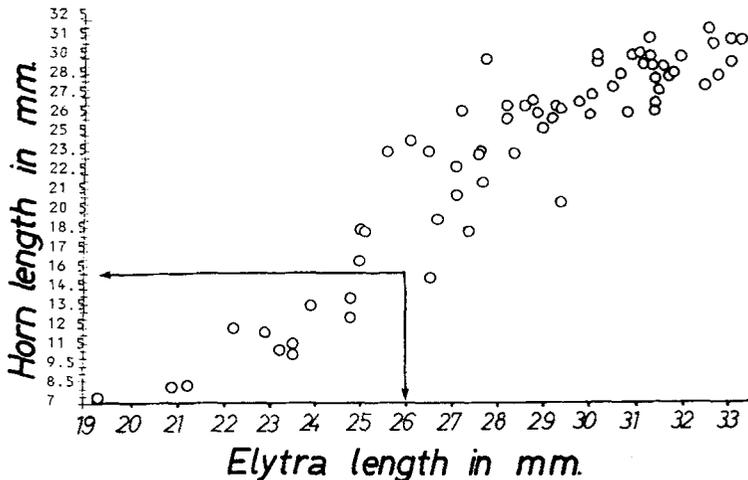


Fig. 3. A graph showing the relationship between horn-length and elytra-length in male *A. dichotoma*. A horn-length of 16 mm (the division between minors and majors from Fig. 2) corresponds approximately to an elytral-length of 26 mm, as indicated by the arrows.

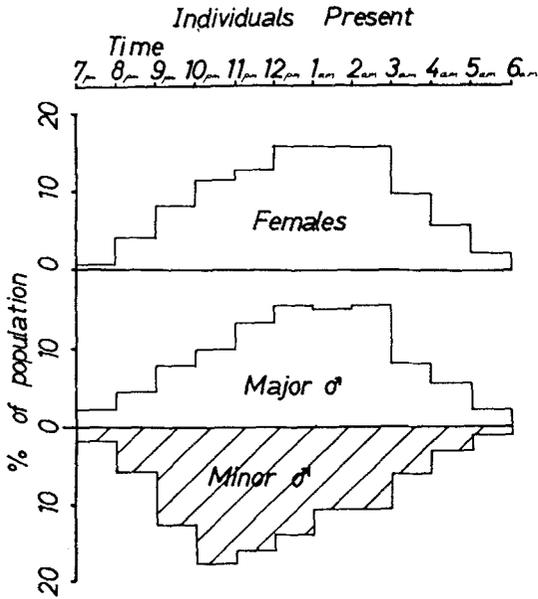


Fig. 4. The % of the total numbers of individuals in each category present at the study site over a period of 2 nights observations.

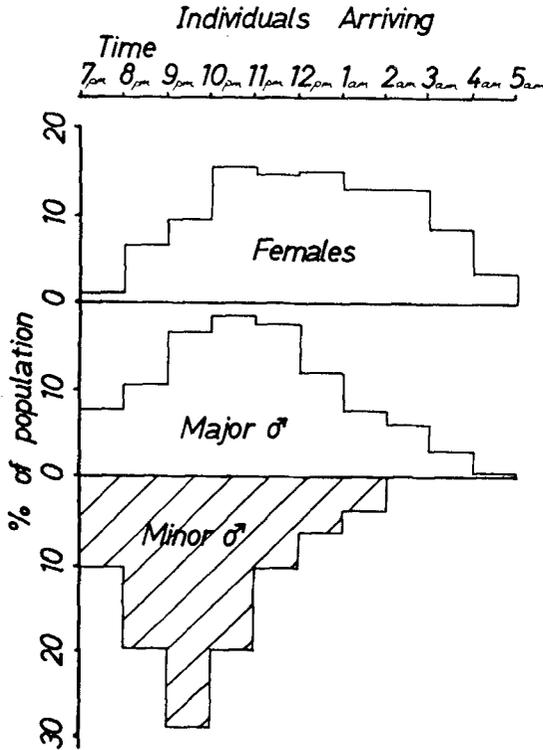


Fig. 5. The % of the total numbers of individuals in each category arriving at the study site each hour. Data from half-hourly observations pooled over 2 nights.

that major males have a similar arrival schedule and peak in numbers at the same time as females.

Once a male had arrived at a sap site he began feeding. Feeding was interspersed with bouts of inactivity or movement around the feeding site. If at any time a major male encountered another male in his vicinity a series of stereotyped behaviours usually followed. Upon first contact both males turned to face the source of the disturbance and thereby presented the heavily armoured front of their bodies to the opponent. Some males departed without any developments beyond this level of contact. Those pairs that remained in contact began a series of brief tussles during which the large head-horns touched and pushed against each other. If the encounter extended further it entered a potentially protracted phase of close-quarter combat where each male tried to insert his head-horn under the prothorax of his opponent and prise the rival off the vertical tree surface (Fig. 6). One of the fighting males eventually left or was thrown off the tree onto the ground a meter or so below. A thrown individual was never observed to climb the tree to reengage in combat ($n=20$) but, if able, usually flew away shortly after the fall. The outcome of encounters between major males at all levels of escalation appears to be depend-

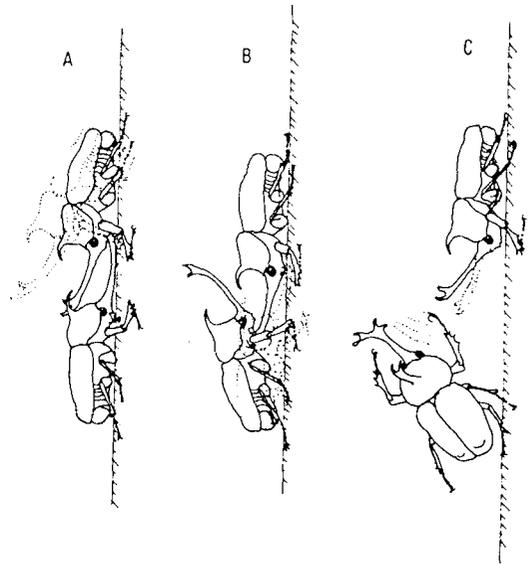


Fig. 6. Major males fighting on a tree surface. A) The lower male manages to insert his head-horn under the upper male, however the later makes a quick movement away from the tree as indicated by the dotted lines. B) This causes the lower male's attempted throw to fail, and simultaneously exposes his underside. The upper male moves in closer, inserts his head-horn and C) throws the lower male. Position on the tree has no effect on outcome.

ant mainly on male size, "but ownership" status also has an effect (Table 1). Escalated fights occurred more frequently between males of similar size (5/15 fights) than between males of dissimilar size (1/20 fights that occurred between males who differed by more than 2 mm horn length).

A second form of combat not directly observed in the field but seen in the laboratory on several occasions was the side attack. The attacking male would approach an opponent from the side and trap it between the head- and prothoracic-horn (Fig. 7). In this circumstance the trapped beetle always let go of the substrate and was dropped to the ground. During attacks of this kind 2 neat punctures were made in the loser's exoskeleton by the very sharp prothoracic horns. Similar puncture marks were often found on wild-caught *A. dichotoma* and on one occasion constituted serious damage (e.g., Fig. 8d). Such punctures can form the source of rips in the elytra and underlying wing; damage that would probably severely impair a male's ability to fly.

As well as punctures from prothoracic horns, major males are prone to damage caused by falls after being thrown from a tree. Such damage can be as serious as the loss of the head-horn (Fig. 8). In all observed cases of head-horn loss (n=4) the damage was borne by very large males. A fall of 1 m or more onto a head-horn is sufficient to snap it off at the base. This kind of loss has obvious effects on fighting ability and probably individual fitness as a result thereof. Fig. 9 shows the size distribution of damaged males compared to the sample population from which they were taken. Fig. 10 is shown for comparison with Fig. 9. The size distribution of female shows no abrupt upper limit. Damage of any kind is chiefly restricted to major males, whilst serious damage (i.e., any damage that overtly affects fighting or fleeing ability) is restricted to only the very largest of these majors.

Behaviour of Minor Males at Sap Sites

Minor males began arriving at sap sites at 20:00 and peaked in numbers at about 22:00. They

tended to arrive and peak before major males and females (Figs. 4 & 5). However, even though they preempted the peak in female numbers they still gained access to early arriving females.

Minor males were never observed to fight with other males, either in the laboratory or in the field. On 1 occasion, however, a minor was observed to bring his reduced head-horn to bear on a female which he managed to dis-

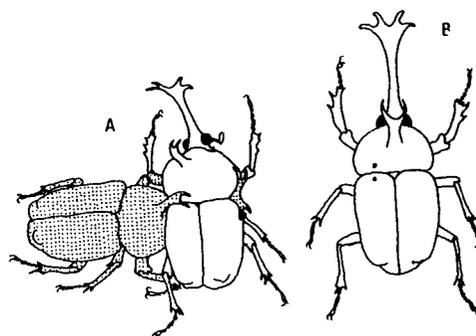


Fig. 7. The side attack. A) The shaded male has successfully grasped the 'white' male in a side attack. 'White' has released his hold on the substrate. B) An example of the damage caused in a typical side-attack. Two neat punctures in the exoskeleton (which ooze haemolymph for some hours).

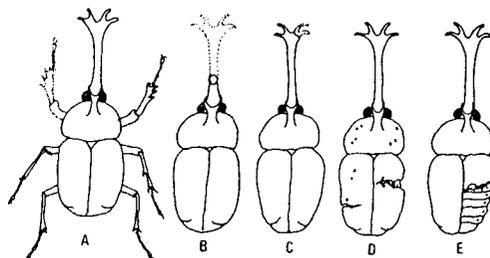


Fig. 8. Examples of damage caused as a result of fighting. A) Loss of fore-limb caused by a fall. B) Loss of head-horn caused by a fall. C) Loss of part of head-horn. D) The damage resulting from several side-attacks: Punctures and rips. E) A side-attack can result in both the elytra and underlying wing being ripped off the attacked individual.

Table 1. A table to show the % of males in each category who won fights regardless of the level of escalation. Numbers in parenthesis indicate sample size.

	% WINNERS		
	Bigger Male	Simmilar Sized Male	Smaller Male.
Owner	100 % (10)	90% (10)	33.3% (15)
Intruder	66.6% (15)	10% (10)	0 % (10)

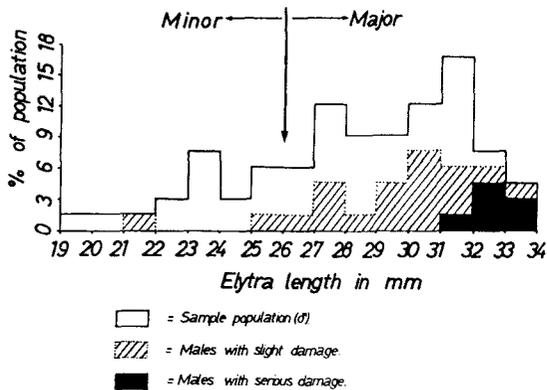


Fig. 9. A frequency histogram of the eltra-length of 67 males, showing the incidence of males with slight and serious damage.

place from a feeding site.

Minor male behaviour at sap sites was stereotyped. They fed relatively infrequently and between feeding bouts moved around the sap-site. This led to frequent collisions with conspecifics. The initial response of a minor to a collision was to back-off and assume a head-forward attitude. If the minor had made contact with a major the latter began the sequence of behaviours that in other circumstances led to fighting. Upon the second contact the minor always fled about 30–50 cm away from the sap site and then remained stationary ($n=17$). After several minutes (range: 2–10 min) the minor returned to the sap site and resumed feeding or perambulating. The short head-horn on minors appeared to serve a useful function during these encounters by maintaining a “safety zone” in front of any potentially hazardous objects. Occasionally a minor would be caught off-guard by the lunge of a nearby major and would be thrown off the tree. Several such incidents were observed ($n=15$) and in each case the minor climbed back up the tree to the sap-site from which he was thrown, or one nearby (c.f. major behaviour). In 1 case a persistent minor was thrown from, and returned to, the same sap-site 7 times. Minors were never observed to suffer damage as the result of a fall, however they occasionally (2/16) showed damage caused by side-attacks.

If a minor collided with a female he assumed the usual head-forward attitude, however, because females did not usually respond to collisions there was no subsequent contact. In this circumstance minors slowly moved forward, made contact and withdrew again. This sequence could be repeated several times before the minor actually maintained contact with the female and began to antennate her elytra; the first be-

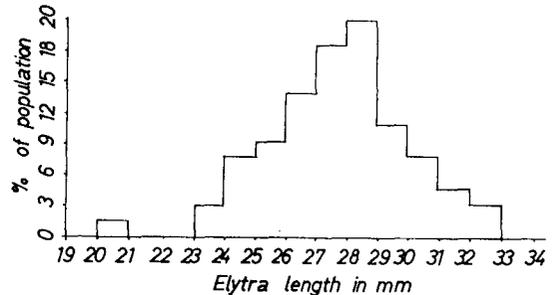


Fig. 10. A frequency histogram of female elytra-length ($n=66$).

aviour in a series that sometimes terminated with copulation.

Copulation and Mating Frequency

Obata & Hidaka (1983) have suggested that female *A. dichotoma* secrete a contact pheromone that elicits copulatory behaviour in males. Field observations suggest that males may distinguish receptive and non-receptive females soon after contact and antennation. Copulation follows a complex sequence of courtship behaviours and short intromissions (Siva-Jothy in preparation).

Females usually only copulated once (24/27) during the course of an observation period, if at all. On 3 occasions however, a particular female was observed to recopulate with another male on the same night. Minor males copulated significantly earlier in the diurnal activity period compared with majors (2-tailed Mann-Whitney U-test, $P < 0.05$, $U=29$). Measurements of males and females found in copula showed that the proportion of minors/majors was similar to the population in general (7/27, and 14/67 respectively) and that there was no significant difference between the size of females that copulated with minor males and females that copulated with major males (Mann-Whitney U-test, $P=0.24$, $U=12$). These data suggest that minor males gain a similar relative proportion of copulations to majors, and that assortative mating is probably not occurring.

Discussion

Insect species which show male dimorphisms usually also show behavioural differences between morphs (e.g., Alcock 1979; Hamilton 1979). *A. dichotoma* is no exception. Major males fight for possession of sap sites and the females these sites attract, whereas minors were never observed to fight, but used “stealth” as a means of encountering potential mates and avoiding potential opponents. In the latter re-

spect, the minor habit of arriving and peaking earlier in the diurnal cycle will enable them to avoid majors. Because minors tended to gain copulations earlier in the night than majors it follows that the mates of minors will be more likely to remate on the same night, especially if there is no assortative mating. Consequently, even though minors appear to be relatively as successful as majors in gaining copulations they may suffer as a result of sperm competition later in the evening. The degree of last male sperm precedence (P_2) in scarabaeid beetles is not documented, but P_2 values can be as high as 0.99 in the Tenebrionidae (Schlager 1960) or as low as 0.52 in the Dermestidae (Vick et al. 1972). (A P_2 value of 0.5 means that eggs are fertilized in equal proportions by both males after a double mating; a P_2 of 1.0 means the last male fertilizes all eggs under the same conditions, whilst a P_2 of 0.0 means the first male has precedence [see Gwynne (1984) for a complete explanation and review]). Consequently it was not possible to assess the degree of the disadvantage suffered by minor males as a result of early copulation.

Fighting amongst major males in *A. dichotoma* has potentially serious effects (Fig. 8). Males can lose head-horns, or can have whole portions of their elytra and wings ripped off. Undoubtedly these injuries will have severe effects on a male's subsequent ability to defend a sap site and thereby his ability to gain access to females. Not surprisingly therefore, full-contact fighting is preceded by a series of escalating pre-fight assessment phases during which males can disengage contact. Such phases have been reported for other species where fighting has large metabolic costs or can result in injury (Parker 1974). Interestingly, however, there are only a few reports of assessment-like phases before fights in other horned beetle species (e.g., Beebe 1944; Mathieu 1969; Hamilton 1979), and there are almost no reports of serious injury occurring as a result of fights (but see Eberhard 1979). It is possible that damage does not occur in other species as frequently as it does in *A. dichotoma*, however, many horned beetle species have fearfully armoured weapons that seem designed specifically to cause injury (Otte & Stayman 1979). A possible reason why damaged individuals may not be detected more often is that most scarabaeid (as well as lamellicorn) beetles are nocturnal so usually conceal themselves during the day: it may therefore be difficult to find damaged or mortally wounded individuals that are likely to die in, or be unable to move from, their place of concealment. The results from this study suggest that it is the very largest males who are most susceptible to serious injury in *A. dichotoma*. The frequency distributions of

horn length and elytra length for males show an abrupt tail-off at their upper limits when compared to females. Restriction of horn loss to the very largest males may be due to an allometric relationship between body weight and head-horn base-circumference. The cost of serious damage may therefore act as a normalizing selection pressure and counterbalance the benefits of larger body-size during conflicts. A development from this line of argument is that big beetles may be "bluffers" (Hamilton personal communication). If there is an upper limit to body size because of the high cost of fighting, but there is also a high probability of winning low-level encounters just by *seeming* to be big, then the best size to be is the biggest that would be credible to an opponent. Males may therefore allocate developmental resources to produce large exoskeletal structures at the expense of musculature. The result would be similar skewed and truncated distributions to those in Figs. 2 & 9.

Acknowledgements—I thank Prof. W. D. Hamilton for many valuable comments and suggestions, Prof. Y. Itô for discussions, Dr. Y. Tsubaki for discussing (and solving) problems as well as providing invaluable help, and D. Siva-Jothy, Dr. T. Hidaka, and Dr. N. Yamamura for commenting on drafts of the manuscript. This work was conducted whilst the author was in receipt of a JSPS/Royal Society post-doctoral fellowship.

References

- Alcock, J. 1979 The evolution of intraspecific diversity in male reproductive strategies in some bees and wasps. In: M. S. & N. A. Blum (eds.) *Sexual selection and reproductive competition in insects*. pp. 381–402. Academic press, New York.
- Beebe, W. 1944 The function of the secondary sexual characters in two species of dynastine (Coleoptera). *Zoologica* 29: 53–57.
- Brown, L. & J. Bartalon 1986 Behavioural correlates of male morphology in a horned beetle. *Am. Nat.* 127: 565–570.
- Dawkins, R. 1980 Good strategy or evolutionary strategy? In: G. W. Barlow & J. Silverberg (eds.) *Sociology: Beyond nature/nurture?* Westview, Boulder.
- Eberhard, W. G. 1979 The function of horns. In: M. S. & N. A. Blum (eds.) *Sexual selection and reproductive competition in insects*. pp. 231–258. Academic press, New York.
- Eberhard, W. G. 1980 Horned beetles. *Sci. Am.* 242: 166–182.
- Eberhard, W. G. 1981 The natural history of *Doryphora* sp. (Coleoptera, Chrysomelidae)

- and the function of its sternal horn. *Ann. Entomol. Soc. Am.* 74: 445–448.
- Eberhard, W. G. 1982 Beetle horn dimorphism: Making the best of a bad lot. *Am. Nat.* 119: 420–426.
- Gadgil, M. 1972 Male dimorphism as a consequence of sexual selection. *Am. Nat.* 106: 574–580.
- Gwynne, D. T. 1984 Male mating effort, confidence of paternity, and insect sperm competition. In: R. L. Smith (ed.) *Sperm competition and the evolution of animal mating systems*. pp. 117–150. Academic press, New York.
- Hamilton, W. D. 1979 Wingless and fighting males in fig wasps and other insects. In: M. S. & N. A. Blum (eds.) *Sexual selection and reproductive competition in insects*. pp. 167–220. Academic press, New York.
- Mathieu, J. M. 1969 Mating behaviour of five species of Lucanidae (Coleoptera, Insecta). *Can. Ent.* 101: 1054–1062.
- Maynard-Smith, J. 1976 Evolution and the theory of games. *Am. Sci.* 64: 41–45.
- Obata, S. & T. Hidaka 1983 Recognition of opponent and mate in Japanese horned beetle, *Allomyrina dichotoma* L. (Coleoptera, Scarabaeidae). *Kontyû Tokyo* 51: 534–538.
- Otte, S. & K. Staymann 1979 Beetle horns: Some patterns in functional morphology. In: M. S. & N. A. Blum (eds.) *Sexual selection and reproductive competition in insects*. pp. 259–292. Academic press, New York.
- Palmer, T. J. 1978 A horned beetle which fights. *Nature* 274: 583–584.
- Parker, G. A. 1974 Assessment strategy and the evolution of fighting behaviour. *J. Theor. Biol.* 47: 223–243.
- Schlager, G. 1960 Sperm precedence in the fertilization of eggs in *Tribolium castaneum*. *Ann. Entomol. Soc. Am.* 53: 557–560.
- Taylor, B. J. R. 1965 The analysis of polymodal frequency distributions. *J. Anim. Ecol.* 34: 445–452.
- Vick, K. W., W. E. Burkholder & B. J. Smittle 1972 Duration of mating refractory period and frequency of second matings in female *Trogoderma inclusum* (Coleoptera, Dermestidae). *Ann. Entomol. Soc. Am.* 65: 790–793.

(Received 19 August 1987: Accepted 15 October 1987)