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

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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 temporarily 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 documented (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 using 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