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BEETLE HORN DIMORPHISM: MAKING THE BEST OF A BAD LOT

There has been interest recently in the occurrence in a single species of more than one adaptive behavior or morphology. One kind of explanation for dimorphisms of this type is that they constitute frequency-dependent evolutionary stable strategies (Gadgil 1972; Maynard Smith 1976), with the reproductive payoffs for one type equal to those for the other because of the balances of costs and benefits for the two forms, and that they are thus maintained in a sort of balanced genetic polymorphism. A second possibility is that payoffs for the two forms are not equal but that the alternative forms represent facultative alternatives designed to function in different circumstances (different body size, season, etc.; see Warner et al. 1975; West-Eberhard 1979; Dawkins 1980 discusses both types of explanation).

A classic example of such a dimorphism occurs in some species of horned beetles in which there are two more or less distinct forms: large individuals with well-developed horns ("majors"), and smaller ones which lack or have only poorly developed horns ("minors") (Arrow 1951). Evidence is accumulating (Eberhard 1977*a*; Palmer 1978; Eberhard 1979 and references; Eberhard 1980; M. Peinador, in prep.) that beetle horns commonly function as weapons in intraspecific battles. The fact that the horns of many species represent substantial proportions of the beetles' body weights argues that natural selection in these species has strongly favored increased fighting ability. Since beetles do not grow after their last moult (and minors are thus comdemned to remain minors for their entire adult lives), the continued existence of hornless or nearly hornless forms seems paradoxical since one might think that selection should eliminate those individuals poorly equipped to fight.

This study of the dimorphic horned dynastine beetle *Podischnus agenor* Oliver shows that the behavior and ecology of minor males differs from that of major males in ways which suggest that the minor form is a facultative adaptation designed to reduce direct competition with major males, and thus to compensate partially for the competitive disadvantage resulting from the minors' smaller size.

THE BEETLE

Larval *Podischnus agenor* live underground and feed on humus in the soil, while adults emerge aboveground in the rainy season (September to December in Cali, Colombia, where this study was conducted) to burrow in thick-stemmed grasses such as sugar cane and corn where they feed and mate (Guagliumi 1962; Eberhard 1977*b*). Laboratory rearing data (Guagliumi 1962) indicate that the life cycle lasts about a year, and field observations (Eberhard 1977*b*) show that females become common in sugar cane stalks about 1–3 wk after males have begun to appear aboveground in large numbers.

Only adult males have horns, and they use them as clamps and levers in

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complex fights for possession of burrows in cane stalks (Eberhard 1977*b*, 1979). Larger males consistently defeat smaller ones. Large males have well-developed horns on both head and prothorax, but small ones have relatively short head horns and only vestiges of thoracic horns. These differences in horn development are not simply extremes of a smooth gradient, but rather represent two distinct morphs, as shown by the bimodal distribution of head horn lengths in the population and the sigmoid relation between head horn length and elytral width (a convenient measure of body size; fig. 1).

Behavioral Differences between the Morphs

Podischnus agenor obviously evolved in an environment different from that of today in which the beetles find huge plantations of food plants available. It is thus not appropriate to measure the present day reproductive successes of the two forms and then make subtle interpretations of their evolutionary origins. It is, however, valid to look for behavioral differences between the forms, assume that these differences must have been adaptive when they evolved, and then draw inferences about how and why the different forms may have arisen.

By marking males with numbers scratched on their elytra and then following their activities in selected portions of cane fields throughout the approximately 3-mo season of maximum adult activity for two successive years, I found that the behavior of minors differed in two important ways from that of majors. First, minors were active earlier in the season than majors (fig. 2); they constituted a substantial part of the male population when females were still uncommon, then later virtually disappeared. In 1976 but not 1977 they reappeared in reduced numbers toward the end of the season. It is not known whether the smaller males' earlier emergences were simply the result of their having shorter developmental times or whether other mechanisms are involved; the latter seems more likely since smaller females did not appear earlier than larger ones. The important point is that earlier emergence could reduce the probability of direct conflict with majors.

In addition, as shown in table 1, minors were less often recaptured in tunnels other than those in which they were marked (the beetles' burrowing activities usually caused the stalk to die, and burrows were inhabited for an average of only 4.3 days, $N = 322$). This was true despite the fact that proportionally more minors were marked early in the season each year and thus were more available for recapture. This difference in recapture rates could conceivably result from minor males having either lower survivorship or greater tendency to disperse. Direct data on longevity in the field are not available, and of course are extremely difficult to obtain in mobile species such as this one, but there are indications that the differences in recapture rates probably resulted at least partly from differences in dispersal tendencies. Most recaptures of both major and minor males were of individuals which had been found only a short time before. In 1976, for example, 56% of the 57 beetles which were recaptured had first been seen and marked less than 8 days previously. Minor males kept under very unfavorable conditions (captured late in the season and kept without food in moistened frass

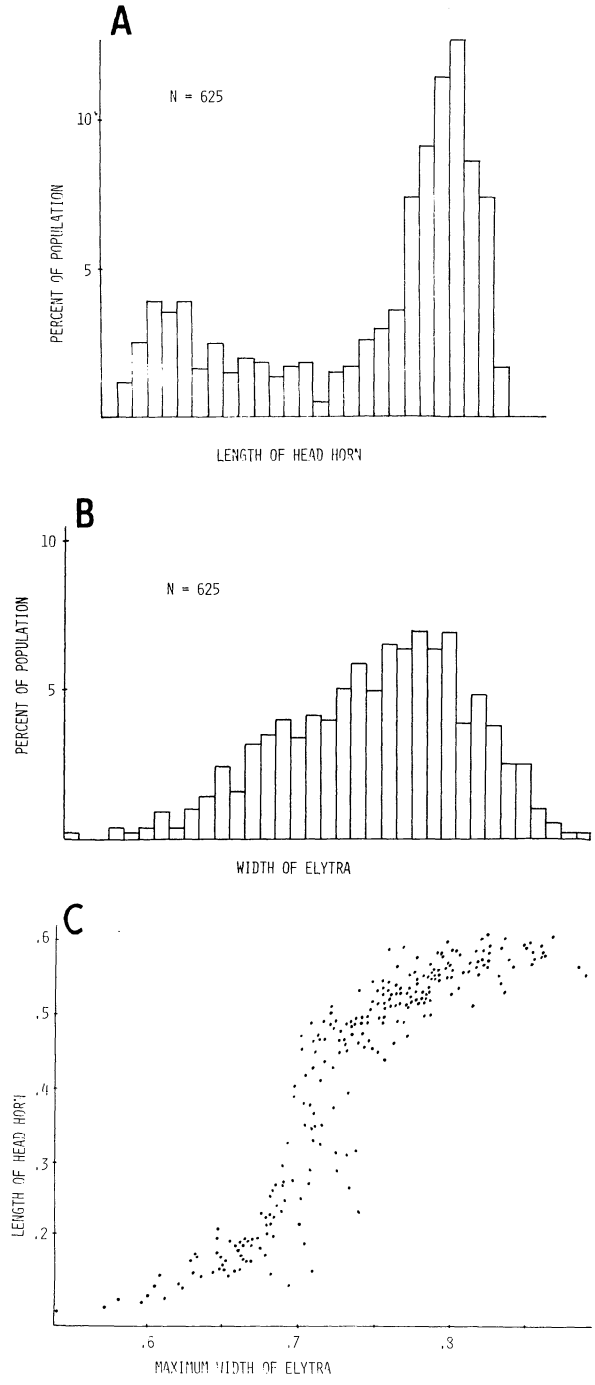

FIG. 1.—*A*, Distribution of head horn lengths; *B*, distribution of elytra widths (an indicator of body size); and *C*, relationship between elytra width and head horn length in *Podischnus agenor*.

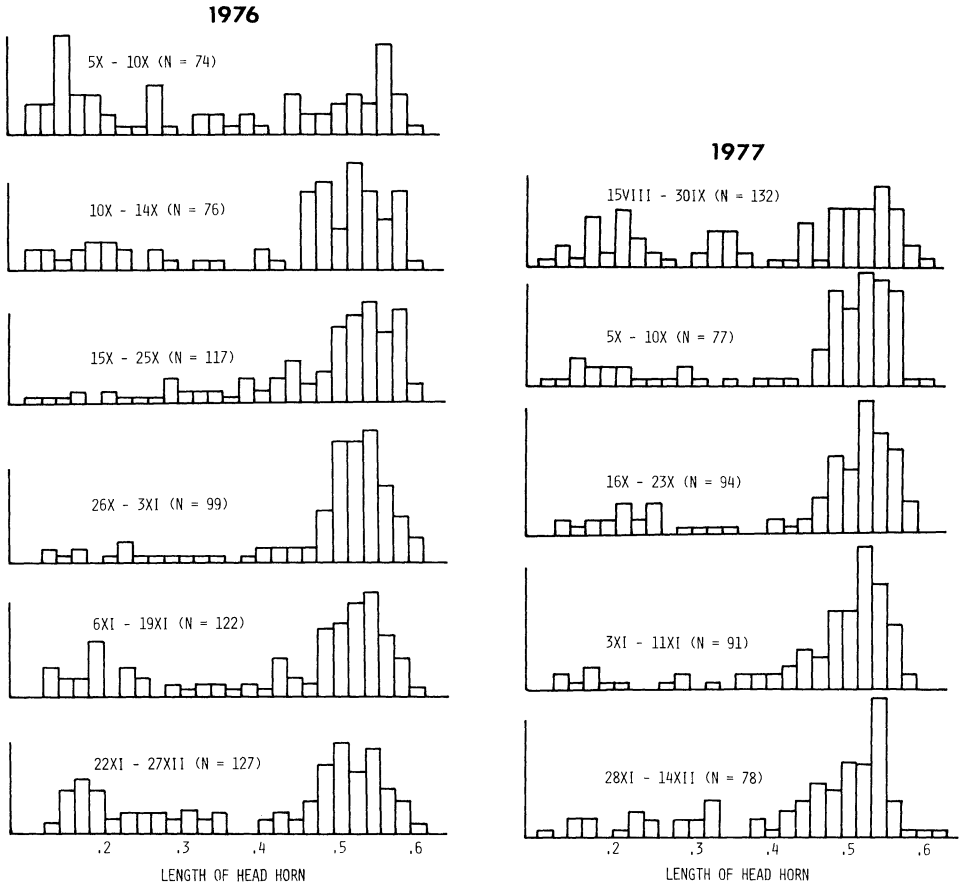

FIG. 2.—Changes in relative numbers of males with different head horn lengths during the rainy seasons of 1976 and 1977. Small-horned males were more common early in the season in both years.

from burrow entrances) lived on the average more than a week (8.5 days, $N = 22$). Under better conditions (captured early in the season and kept with abundant food) they lived for an average of nearly 2 mo and their longevity did not differ significantly from that of majors ($P > .4$, Mann-Whitney U test). Thus the more than eightfold difference in recapture rates was probably not due exclusively to senescence differences; even under extraordinarily difficult nutritional circumstances in captivity, old minors lived on the average longer than the median lapse of time between first sighting and recapture.

It is still possible that the differences in recapture rates could be due to differences in predation rates on the two forms, although there is no reason to expect this. I saw only scattered, occasional evidence of predation in the field (small accumulations of elytra and hard body parts) during several hundred hours of observation both at night and during the day. There was no sign of predation on beetles in their burrows in the cane.

TABLE 1

RECAPTURES OF MALES OF DIFFERENT SIZES (larger males recaptured more often)

	Major (Head Horn > 1.17 cm)	Intermediate (1.17 ≥ Head Horn ≥ .56 cm)	Minor (Head Horn < .56 cm)
1976	24%(N = 289)	8%(N = 95)	4%(N = 75)
1977	10%(N = 296)	9%(N = 114)	0%(N = 47)
Mean	17%(N = 585)	9%(N = 209)	2%(N = 122)

NOTE.—N = total numbers of individuals marked.

The probable differences in emergence times and dispersal may represent ways in which minor males reduce direct competition with majors, by avoiding them both in time and in space. Both behaviors would minimize the minors' disadvantages as poor fighters which result from their small size.

Maintaining the Dimorphism

For the complex behavioral and morphological dimorphism of this species to be maintained by genetic differences between morphs there would have to be (1) linkage among genes for horn morphology, body size, emergence time, and dispersal tendency, and (2) absence of environmental effects, especially larval nutrition, on adult size. This combination of conditions seems very unlikely. A large number of genes must be involved in determining these characters, and larval nutrition is known to influence adult size in many insects (Wigglesworth 1965). Beetle horn development is rigidly associated with extremes of adult size; there are no small "majors" nor large "minors" known. Furthermore, size-related facultative polymorphisms are well known in insects. Numerous well-studied examples occur in the social Hymenoptera in which the extensive behavioral and morphological differences between workers and queens are determined by differences in quantity and quality of larval food (Brian 1979). Similar size-related behavioral polymorphisms are also known in solitary aculeate Hymenoptera (Alcock 1979). Finally, experimental manipulation of the nutrition of nymphs of the dimorphic earwig *Forficula auricularia* showed that the amount of food consumed determined the adult morph adopted (Kuhl 1928).

There is an additional, theoretical reason for expecting dimorphisms like that of *P. agenor* to be facultative. If a character depends on or is strongly influenced by body size for its effective functioning (e.g., horns serve for fighting, and larger males are stronger and thus better fighters), then even if the dimorphism originally arises as a genetic polymorphism there will be selection for the ability to switch forms on the basis of body size. This argument applies equally well to the possibility that individuals can choose either morph but make the choice in some probabilistic way without regard to their own particular circumstances ("mixed ESS" strategy; see Dawkins 1980). In effect, males which can choose the alternative behavior and morphology most appropriate for their body sizes will be superior to those condemned to either of the alternatives irrespective of body size (similar arguments are given in West-Eberhard 1979; Cade 1979*a*; Dawkins 1980).

DISCUSSION

The following sequence of events could lead to the evolution of behavioral and structural dimorphisms linked functionally to body size (or other parameters such as age, season, etc.). (1) Under conditions of intense intraspecific competition, natural selection could favor "alternative behavior" (e.g., early emergence). Alleles for this behavior might spread either by the kind of ESS envisioned by Gadgil (1972) or, if their expression was conditioned on appropriate cues (e.g., body size), by the selection described above. In the first case selection would then favor any allele which repressed the alternative behavior in appropriate circumstances. (2) As such a "switch" became established, individuals not carrying both the switch and alternative behavior alleles would be selected against. At this point alternative forms (e.g., small males) would have a fitness less than that of the others, but the difference would be less than it was originally. (3) Selection would favor alleles which further refined the effects of both the switch and alternative behavior alleles. (Phenotypic manifestations would become more pronounced and more consistently associated with appropriate cues, e.g., body size; both characters would often become multi-allelic.) It would also favor morphological modifications appropriate to the alternative behavior (e.g., reduction of horns in small individuals). These changes would further reduce the differences between the fitnesses of the two alternative forms but still not necessarily make them equal.

This scheme contrasts with several discussions of polymorphisms in insects (Gadgil 1972; Alcock 1979; Cade 1979*a*, 1979*b*, Brockman 1979; Brockman et al. 1979) in that alternative morphs could be maintained indefinitely even though their reproductive successes were not equal to those of the original forms.

Although *P. agenor* shows structural as well as behavioral components of its dimorphism, it can clearly be added to the growing list of species with alternative behavioral strategies such as satellite males, etc. (e.g., Warner et al. 1975; Emlen 1976 and references; Hamilton 1979; Cade 1979*b*; Alcock 1979; Thornhill 1979). The acquisition of satellite morphology as well as satellite behavior such as has happened in *P. agenor* is probably particularly likely in holometabolous insects since their adult size is fixed once they mature and is determined largely by larval size prior to adulthood. A switch mechanism sensitive to larval size could thus be positively selected under a long history of intense male-male reproductive competition.

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