

lation carrying the male on her back. After a varied number of intromissions the male gripped the female strongly, inserted his penis deeply, ejaculated, and then left her. He paid no attention to her after ejaculation. Usually he started eating eagerly, being indifferent to her even if she continued to solicit courtship. Yet no further agonistic behavior ensued. Additional copulations were observed sometimes within several hours.

Copulation was highly stereotyped in each sex and was the least variable stage. Nevertheless, individual variation was apparent in the intensity and subtle copulatory activities. The percentage of trials terminating in copulation was significantly higher in homogametic than in heterogametic matings ($\chi^2_{(1)} = 4.66$, $.05 > P > .025$) (Table 1).

Certain aspects of the mating behavior of *Spalax* reflect cricetid affinities, whereas others are common to several unrelated rodents (6). The copulatory behavior of *Spalax* recalls that of *Mesocricetus auratus* in the rear mounting, long duration, repeated mounts, and preejaculatory intromissions. Similar agonistic precopulatory behavior has been reported in *Microtus californicus* and other microtines. A prolonged courtship also occurs in *Microtus californicus* and *Cricetus cricetus*. Finally, remarkable individual variation characterizes also the mating behavior of *Microtus californicus*. Varied vocalizations function in sexual behavior of many unrelated species. Yet, despite cricetid affinities the complex of activities comprising the mating ritual of *Spalax* exhibits specializations presumably linked to its subterranean, highly territorial habits.

Elaborate breeding mounds are built by females in nature during the breeding season of *Spalax* from December to April (7). Encounters between the territorial males and females of *Spalax* elicit aggressive behavior in the laboratory, and presumably also in nature, regardless of sex or season. The sexes are found together in breeding mounds only during the winter reproductive season. Otherwise, males have separate, much simpler mounds than the breeding mounds of females. Copulation in nature is presumably effected within the breeding mounds. It is suggested that the elaborate courtship of *Spalax* may have evolved in order to overcome hostility which characterizes the encounter of the sexes and to induce females to copulate.

Mating behavior is of cardinal importance as an ethologic isolating mechanism (8), and may have played an important role in speciation of *Spalax*, concomitant with cytologic mechanisms (5). First, aggression is much more pronounced in the agonistic stage of heterogametic than homogametic matings, when frequency of bitings is used as an index of aggression. Second, copulations proved significantly more frequent in homogametic than in heterogametic matings (Table 1). If these trends are substantiated on a larger scale by assaying all possible combinations, they may indicate selective matings between chromosome forms. The ethologic barriers to reproduction may prove greater the larger the difference in chromosome numbers. They may complement a cytologic isolating mechanism operating to prevent widespread natural hybridization.

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References and Notes

1. B. Bodnár, *Terre Vie* 4, 323 (1934); E. Nevo, *Mammalia* 25, 127 (1961); I. S. Ognev, *Mammals of the U.S.S.R. and Adjacent Countries*, vol. 5, *Rodents* (Moskva-Leningrad, 1947) [Engl. Transl. Israel Program Sci. Transl., Jerusalem (1963)], pp. 487-556; I. R. Savić, thesis, University Belgrade (1965).
2. S. Schaub, in *Traité de Paléontologie*, P. P. Grassé, Ed. (Masson, Paris, 1958), p. 659; F. Petter, *Mammalia* 25, 485 (1961); C. A. Reed, *J. Mammalogy* 39, 386 (1958); G. B. Corbert, *The Terrestrial Mammals of Western Europe* (Foulis, London, 1966), pp. 210-212.
3. J. R. Ellerman and T. C. S. Morrison-Scott, *Checklist of Palaearctic and Indian Mammals 1758-1946* (British Museum, London, 1951), pp. 553-556.
4. J. Walknowska, *Folia Biol. (Krakow)* 11, 293 (1963); B. Soldatović, S. Živković, I. Savić, M. Milošević, *Z. Säugetierk.* 32, 238 (1967); P. Raicu, S. Bratosin, M. Hamar, *Caryologia* 21, 127 (1968).
5. J. Wahrman, R. Goitein, E. Nevo, in *Comparative Mammalian Cytogenetics*, K. Benirschke, Ed. (Spring-Verlag, New York, 1969); ———, *Science*, in press.
6. C. A. Reed, *J. Comp. Physiol. Psychol.* 39, 185 (1946).
7. E. Nevo, *Mammalia* 25, 127 (1961).
8. N. Tinbergen, in *Sex and Behavior*, F. A. Beach, Ed. (Wiley, New York, 1965), pp. 1-33.
9. I thank Professors S. A. Barnett, F. A. Beach, E. Mayr, C. A. Reed, N. Tinbergen, and D. Zohary, Mrs. S. Blondheim, and Dr. Sarah Nevo for critical reading of the paper.
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Mimicry of Hymenoptera by Beetles with Unconventional Flight

Abstract. *Flower-visiting beetles of the genus Acmaeodera (Buprestidae) bear a striking resemblance to Hymenoptera in flight. Unlike most other beetles, they fly with their membranous hindwings only, and their forewings, which are inseparably coupled and permanently held over the abdomen, bear color markings commonly found on the abdomens of bees and wasps.*

In Arizona and in Florida, we have noticed certain flying insects that appeared to be bees or wasps, but which on close inspection turned out to be harmless beetles of the genus *Acmaeodera* (Buprestidae) (1).

Ordinarily, when beetles fly, they spread apart their hard front wings (elytra) and hold them out to the sides, relying for propulsion on the rapid beat of their hindwings (2). Buprestids, as a group, conform to the rule (Fig. 1A). But in *Acmaeodera*, the front wings are inseparably coupled along their middorsal junction (through a tight-fitting tongue and groove joint), and they are permanently restricted to their resting position over the back of the abdomen. *Acmaeodera* fly with their membranous hindwings only, without the usual pair of spread elytra projecting conspicuously from the sides (Fig. 1B). Bees, wasps, and other Hymenoptera, also fly with what ap-

pears to be a single pair of membranous wings (actually, they use all four wings, but the two of each side are hooked together and beat as a unit). Thus, through the simple expedient of retaining the elytra over the back, *Acmaeodera* achieve the image of hymenopterans in flight. For aerodynamic and other reasons, the expedient may not have been so simple to evolve. It called for special modifications, of which one—emarginate elytra (Fig. 1C) that permit the hindwings free motion at their bases during flight—is readily apparent.

An obvious diagnostic character of many bees and wasps, and one of the few reliable ones for when they are flying, is the conspicuous pattern of transverse colored bands (usually yellow, red, or white) that adorns their abdomen. *Acmaeodera* appear to imitate this pattern, although in their case the markings are on the elytra which

permanently cover the abdomen. Most *Acmaeodera* observed by us (*A. amabilis*, *A. amplicollis*, *A. decipiens*, *A. disjuncta*, *A. gibbula*, and *A. pulchella*) possess aposematic (warningly colored) markings, and in some cases the resemblance to abdomens of Hymenoptera living in the same area is striking (Fig. 1F).

What little evidence we have suggests that the species of *Acmaeodera* are not intrinsically offensive to predators and may therefore be considered to be Batesian rather than Müllerian mimics. They appear to lack defensive glands or mechanical weapons of any sort, and the few specimens that were given to a bird—a long-captive jay (*Apelocoma ultramarina*)—were eat-

en without hesitation (3). Birds, as aerial and visually oriented predators, are likely to have been instrumental in forcing the evolution of the mimicry.

Acmaeodera is not unique among insects in imitating Hymenoptera in flight. Many flies of various families (for example, Syrphidae, Asilidae, and Bombyliidae) have abdomens that are brightly striped (Fig. 1E), and it may require an expert to distinguish them from Hymenoptera in flight. In flies the resemblance has involved no structural modification of the wings, which are membranous and consist of a single pair.

One wonders about the sequence in which the two processes that led to the mimetic resemblance in *Acmaeo-*

dera—the immobilization, and the coloration of the elytra—have evolved. It would be erroneous to presuppose that elytral immobility has by necessity evolved first. An elytral color scheme imitative of a hymenopteran abdomen can be adaptively justified even in a conventional flier, since the resemblance may benefit the beetle at rest rather than in flight. In this connection it is interesting that aposematic elytral markings, including transverse “hymenopteran bands,” occur in a diversity of conventional fliers among the Buprestidae (for example, some species of *Buprestis*). Because the beetles of this family share the general habitats, and often even the flower-visiting habits of Hymenoptera (Fig. 1D),

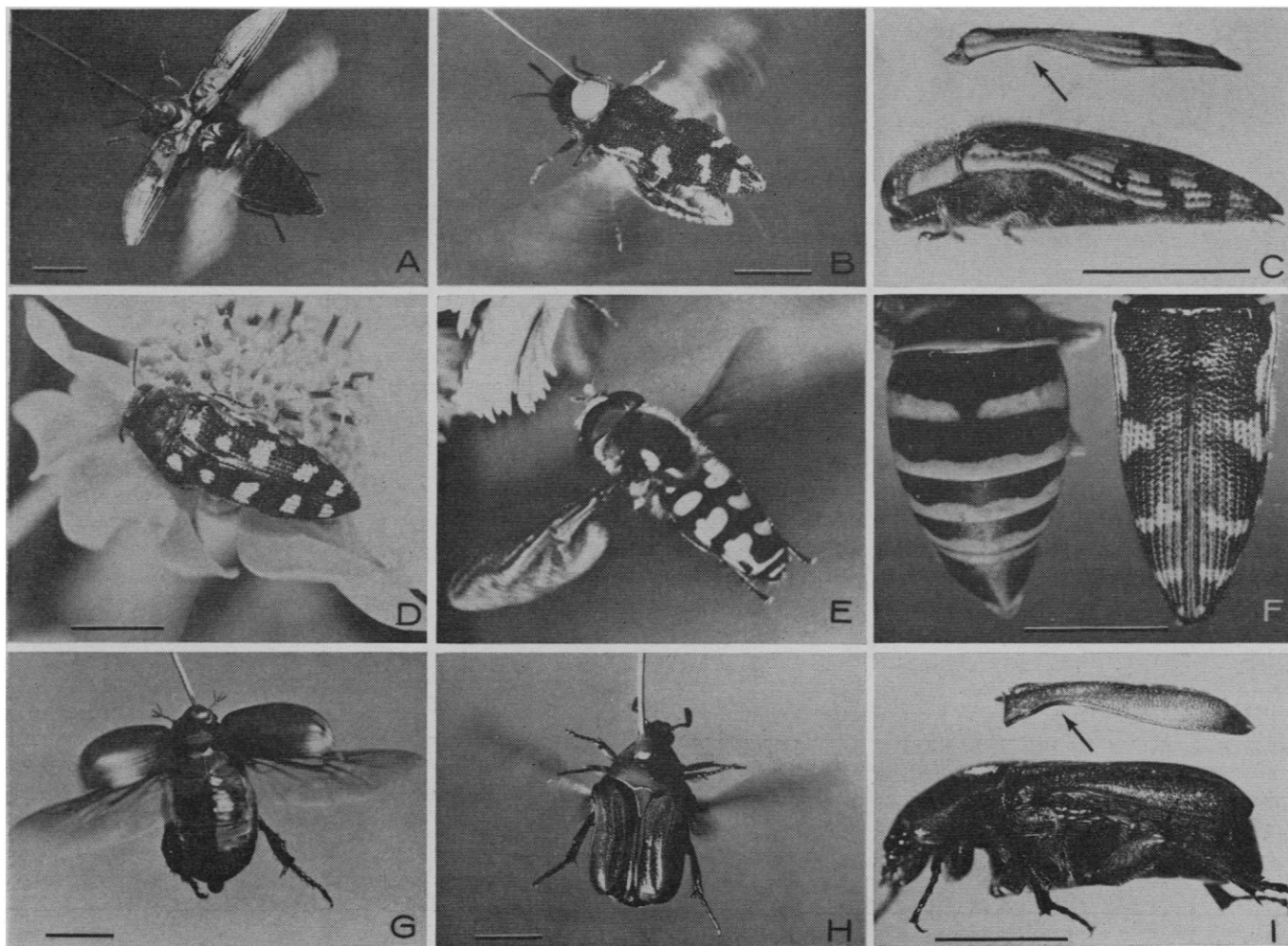


Fig. 1. (A) *Buprestis maculipennis*, a conventional flier; note spread elytra. This beetle, as those in B, G, and H, has been fastened to a wire tether glued to its pronotum. (B) *Acmaeodera pulchella*, in tethered flight; note unsprea elytra. (C) *Acmaeodera amplicollis*, in profile view; note emargination (arrow) in isolated elytron; during flight the shield formed by the locked elytra is slightly raised above the abdomen, as is evident in B, and the beating hindwings project outward beneath the elytral emarginations. (D) *Acmaeodera gibbula*, at rest on a composite flower. (E) Unidentified syrphid fly, of a type bearing “hymenopteran markings” on its abdomen. (F) Abdomen of yellow-jacket wasp (*Vespula squamosa*) (left), whose pattern of yellow bands on black is closely similar to the elytral markings of the sympatric buprestid *A. pulchella* (right). (G) Typical scarabaeid beetle (*Anomala marginata*) in tethered flight; elytra are spread. (H) A cetoniine scarabaeid (*Euphoria limbalis*) in tethered flight; elytra are unsprea. (I) *Euphoria limbalis* in profile view; note emargination (arrow) in isolated elytron. Reference lines, equivalent to 5mm, are shown in all figures, except in E, for which precise scale is unknown. (Photo E by Harald Döring, courtesy of Frank W. Lane.)

their apparent frequent imitation of the latter, even if only in the sedentary context, makes sense. *Acmaeodera* might thus simply have carried matters one step further, by locking its elytra and taking its hymenopteran rump to the air.

The only other beetles with fully developed elytra known to fly with elytra unspread are the cetoniine scarabs (family Scarabaeidae, tribe Cetoniini) (2) (compare Fig. 1, G and H). Although the significance of flight modification in this group remains to be explained, mimicry may again be involved, perhaps only as a contributing factor, and then only in some species. *Euphoria limbalis*, which we have observed on Lignumvitae Key, Florida, has the same darting and hovering flight and lives in precisely the same habitat as a large carpenter bee (*Xylocopa micans*). The bright greenish elytra of the beetle, which impart upon its body the metallic sheen of the bee, heighten the resemblance. Both beetle and bee were seen to feed in numbers on blooming palms. As evidenced by its acceptability to our captive jay, the beetle is apparently edible. *Euphoria limbalis*, like other cetoniines, has the elytra notched where the hindwings project in flight (Fig. 1, part I) in striking similarity to what *Acmaeodera* has evolved in parallel (see 4).

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References and Notes

1. The observations were made in the Chiricahua Mountains, Arizona, and in Monroe and Highlands counties, Florida. We thank R. Archbold for the use of the facilities of the Archbold Biological Station; Mr. and Mrs. R. Niedhauk for permission to conduct studies on Lignumvitae Key, Florida; and G. H. Nelson, G. C. Eickwort, and R. D. Gordon for identification of the buprestids, Hymenoptera, and scarabaeids, respectively. Report No. 24 of our series, *Defense Mechanisms of Arthropods*.
2. J. W. S. Pringle, *Advan. Insect Physiol.* **5**, 163 (1968) and references therein. In some beetles the elytra have an intrinsic beat, but they contribute negligibly to thrust.
3. During its 6 years of captivity, the jay was offered no Hymenoptera (except wingless, cryptically colored formicine ants), and was therefore not expected to discriminate against a mimic of Hymenoptera, such as *Acmaeodera*, on sight alone.
4. A cerambycid beetle (*Tragocerus forniosus*), mimicking Hymenoptera and supposedly flying with elytra unspread, is figured in R. A. Fisher, *Genetical Theory of Natural Selection* (Dover, New York, 1959).

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Size Discrimination on the Skin

Abstract. Reasons are given for rejecting the two-point threshold as the standard measure of spatiotactile resolution. As alternative techniques, thresholds were obtained for disc-size and disc-annulus discriminations. Disc-annulus thresholds are comparable to two-point values, but disc-size thresholds are smaller by a factor of 10. Thus, at least part of the cutaneous system is better organized for localization and sizing of a stimulus than for detection of discontinuities in it.

The two-point threshold is considered the standard measure of spatiotactile resolution. As a result, the major portion of man's integument is thought to be insensitive spatially; thresholds run as high as 48 mm (1). This test appears to have emerged from thinking relevant to vision, where it is important to separate objects which must be manipulated. This logic may be appropriate for the fingers or tongue, which are manipulative structures with small two-point thresholds (1). However, it makes less sense for the remainder of the skin surface, which serves as a warning system, eliciting reflexive action and visual attention. For these body parts, it would not be as important tactually to separate stimuli as to determine their locus, size, quality, and intensity.

Two-point thresholds are considerably larger than point localization thresholds, and the two procedures differ only in simultaneous versus successive presentation of points. Thus, lateral inhibitory interaction between points would occur only in the two-point determination. Though lateral inhibition appears to sharpen contours (2), it may interfere with detection of gaps. In addition, the extensive overlapping of tactile receptive fields should hamper gap detection and facilitate size discrimination.

Our study tested the hypothesis that size discrimination would demonstrate a sensitivity that is not generally recognized for the skin senses. The intent is to develop tests that will reflect underlying physiological processes and anatomical organizations, such as size of field, amount of overlap, extent of lateral inhibition or facilitation, and so forth (3).

Four individuals served as subjects. The stimuli consisted of solid plastic cylinders, integral sixteenths of an inch (1/16th inch = 1.59 mm) in diameter, and approximately 4 inches (10 cm) long. Two series of threshold determinations were made. In one series standard and test stimuli were impressed on the same patch of skin on

the belly of the forearm (same arm). In the other series, the standard was impressed on the right and the test stimulus on the left forearm or vice versa (other arm).

In both series, threshold determinations were made up and down from four standard stimuli, 4, 8, 16, and 24 sixteenths of an inch. At each standard the up- and down-thresholds were averaged to obtain the difference limen (DL). To obtain an up-threshold a test stimulus was chosen which seemed too big. Then 50 trials were run in which test and standard stimuli were impressed on the skin 0.5 to 1.5 seconds apart. The subjects reported which of the two stimuli, the first or the second, was larger. Order of presentation and, in the other-arm series, association with the right or left arm, were randomized. Threshold was defined as the distance from the standard at which the subject correctly identified the test stimulus as larger 75 percent of the time. If the first test stimulus yielded better than 75 percent correct, a series of 50 trials were run with a smaller stimulus. Threshold was calculated by linear interpolation from the two bracketing test stimuli. The down-thresholds were determined in the same way except that the test was smaller than the standard stimulus.

Care was taken to apply the two stimuli as evenly as possible and without systematic bias (4). Stimulus pressure was always firm and sufficient to leave a complete, visible ring on the skin. As a check on the influence of pressure, up and down disc-thresholds were obtained from two subjects under four conditions of stimulus pressure, with a standard of 16 sixteenths. In these series, the stimuli were just sufficient to produce a visible ring (LL), very firm and bordering on noxious (HH), or a combination of these (LH or HL). In the latter two conditions, heavy and light pressures were randomized over presentations of test and comparison stimuli.

Two-point and disc-annulus thresholds were also determined for each