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MATING HABITS IN THE GENUS *ACRAEA*, WITH A POSSIBLE EXPLANATION FOR MONOSEXUAL POPULATIONS (LEPIDOPTERA: NYMPHALIDAE: ACRAEINAE)

ANDREI SOURAKOV and THOMAS C. EMMEL

Dept. of Entomology and Nematology, University of Florida, Gainesville, Florida 32611; and
Dept. of Zoology, University of Florida, Gainesville, Florida 32611, USA

ABSTRACT.– Mating *Acraea* butterflies have been observed with rough "take-down" behavior by males and opposite dorso-ventral orientation of male and female abdomens, supporting theories of authors that males dominate copulation behavior without any pre-copulatory ritual, followed by use of a sphragis to protect their sperm investment in each female. The observations support the view that harassment of mated females may be a selective force which has led to genetic factors causing female-dominant populations in some *Acraea* species

KEY WORDS: Africa, *Acraea*, behavior, Coleoptera, Ethiopian, Ghana, Kenya, Lycaenidae, mating behavior, *Meleageria*, population ecology, Russia.

The speciose genus *Acraea* (Nymphalidae: Acraeinae) consists of many species similar in appearance and found in widely varied habitats across the Afrotropical region.

A peculiar feature of this genus is that it has evolved a physical contraceptive mechanism to prevent repeated mating of the same female. This mechanism is represented by the sphragis — a mating plug secreted by a male during copulation and attached to the outside of the female's abdomen. The sphragis blocks the entrance into the mating tube for the spermatophores of subsequent males, should they attempt later copulation. It is found in several other groups of Lepidoptera, such as, for example, *Parnassius* (Papilionidae) (see review in Drummond, 1984).

On two trips to Africa, in October 1994 and August 1996, we observed courtship behavior in two species of *Acraea*. In the first case, we observed how the male of *Acraea quirinalis* Grose-Smith in Kakamega Forest, western Kenya, landed on a resting female and knocked her onto the ground. Grasping the female's dorsum with its legs, the male bent his abdomen ventrally from its position on top of the female and successfully mated with her. The above "takedown" behavior has been observed previously (Eltringham, 1912). On the 1996 trip to Ghana, we observed a pair of *Acraea epaea* Cramer *in copula* in the Kissi Forest near Cape Coast. There, the male had already attached himself to the female and was hanging down passively, as it is the case in many butterflies. However, unlike most butterflies, his position assumed the same orientation in copulation as in the first case: the dorso-ventral position of the abdomen of the male was inverted 180° from that of the abdomen of the female, an orientation which could result only from a copulation event similar to the one observed in Kakamega. This manner of copulation, in which a male mounts on top of a female's back, though common in insects (e.g., beetles), is unusual in butterflies. Most male butterflies alight next to a female, standing parallel and facing in the same direction, and curve their abdomens around to copulate, resulting in a successfull pairing of male and female facing in opposite directions but with the same dorso-ventral orientation of their abdomens.

In the case of *A. epaea*, a second male was present as well (Fig. 1). He was grasping the female with his feet from the top as if preparing to mate with her, despite the fact that his potential place had already been occupied.

The behavioral pattern observed in the above two cases supports the common opinion that the genus *Acraea* has not evolved the usual complex mating ritual found in butterflies, in which a female has a choice of mating partner and usually rejects attempts of repeated mating by signaling with a characteristic spread wing position. It is thought instead that an *Acraea* female does not have any choice in mating, so a male protects his sperm from competition with sperm of the subsequent males by plugging the mating tube (e.g., Eltringham, 1912).

Drummond (1984) suggests that a double fertilization might occur if a just-mated female was immediately captured by a second male who copulated with her while the sphragis from the first mating was still soft, or when the sphragis, subjected to humid conditions, dissolves or falls off. Apparently the first case may explain the bizarre behavior shown by the second male of *A. epaea* (top of Fig. 1), who waits for the female to "become available". If he can mate immediately after the first mating is over, his spermatophore would be the one utilized for fertilization and the sphragis secreted by the first male would not yet be hardened to prevent that. This hypothesis is supported by the

observations of Marshall (in Eltringham, 1912), who observed females of *Acraea* with several sphraga attached to their abdomen. All of these sphraga were deformed, which most likely resulted from the above scenario of rapidly following each others' consequent matings.

Apparently in some species of *Acraea*, the harassment of mated females by the males has led to an entirely different preventive mechanism. As we discussed above, the survival of a species with a 1:1 sex ratio, in which males are constantly testing females for being mated by a physical attempt to copulate, is hardly feasible, as the females would have no time left for feeding, searching for host plants, or egg-laying. Probably in response to such situation, at least one species of *Acraea* has evolved a highly uneven sex ratio in some of its populations. In certain East African populations of *A. encedon* (Linnaeus), more than 90% of the individuals were found to be females (Owen, 1971). This character was proved to be genetically determined by interbreeding experiments, and has been explained as an adoption of a mutation that successfully has spread through the population and is referred to as the presence of a driving Y chromosome. How did such a feature appear and became established, when it should be disadvantageous to a population and should lead to its extinction? Owen suggests that this event is relatively young and unique and has appeared as a response to human habitat disturbance. This explanation is substantiated by other known cases of unusual populations resulting from mutagenic factors (as, for example, an unusual population of *Meleageria daphnis* (Lycaenidae), in southern Russia, in which 60% of females are gynandromorphs, which appeared recently, probably as a result of the Chernobyl atomic disaster (Dantchenko *et al.*, 1996)).

However, there is a possibility that female-dominant populations are a natural occurrence in response to wet habitats. In such habitats, according to Drummond (1984), the sphragis does not harden and cannot protect females from multiple matings. In these populations, the reduction of number of males in relation to each female would increase the chances of females to successfully mate and reproduce. Owen states that "these predominantly female populations occur only in habitats disturbed by man in the more humid parts of tropical Africa; normal populations occur in drier undisturbed savanna." Thus, the presence of a greatly skewed sex ratio in favor of females may reduce mating pressure to a level balanced by the number of multiple matings that can be succesfully carried out by individual males.

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Fig. 1 *Acraea epaea* Cramer, *in copula* in the Ghana rain forest; the first male to mate with the large female in the center of the photograph mounted from above, curving his abdomen downward, and ended hanging with his abdomen twisted at almost 180° from the dorso-ventral orientation of the female's abdomen. A second male grasps the female from above, as if waiting for his turn to mate. (© 1997 Andrei Sourakov)

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