12. ——— and P. H. Tuft, *J. Exp. Biol.* **27**, 59 (1950); H. Mohri, *ibid.* **33**, 73 (1956); T. Fujii, S. Utida, T. Mizuno, S. Nanao, *J. Fac. Sci. Univ. Tokyo Sect. 4* **7**, 335 (1955).
13. D. Nishioka and N. Cross, in *Cell Reproduction*, E. Dirksen, D. Prescott, C. F. Fox, Eds. (Academic Press, New York, 1978), p. 403.
14. In our observations in the goldfish, no sperm motility occurred by reduction in sperm density after addition of sufficient isotonic solution to increase volume by as much as 800-fold, or by introduction of air or oxygen for 1 hour in isotonic medium, or by incubation in isotonic solution at *p*H 7.7, which is the optimum for continued sperm motility.
15. We thank H. A. Bern, University of California, Berkeley, and H. Mohri, University of Tokyo, for reading this manuscript and the director and staff of the Misaki Marine Biological Station of the University of Tokyo and of the Otsuchi Marine Research Center, Ocean Research Institute, University of Tokyo, for providing the materials. Supported in part by grants-in-aid from the Japanese Ministry of Education.

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Antbutterflies: Butterflies That Follow Army Ants to Feed on Antbird Droppings

Abstract. *Females of three species of tropical rain forest ithomiine butterflies orient to swarms of army ants (*Eciton burchelli*) and feed on bird droppings found there. The antbirds associated with swarm raids of these ants provide a predictable source of droppings, an otherwise sparsely distributed resource.*

Females of three butterfly species of the Ithomiinae (Lepidoptera: Nymphalidae) are associated with raiding swarms of the army ant *Eciton burchelli* (Hymenoptera: Formicidae) and feed on bird droppings in the swarm vicinity. Many species of birds, primarily in the antbird family, Formicariidae, deposit droppings as they follow swarms of *E. burchelli* to feed on insects flushed from the leaf litter by the ants (*1*). Thus army ant swarms provide a predictable source of nutrients as bird droppings, and the odors associated with the swarms may allow the butterflies to orient to the location of fresh droppings to feed.

As a result of an initial observation that, at Finca La Selva in Costa Rica (*2*), females of three species of ithomiines (*Mechanitis polymnia isthmia*, *Mechanitis lysimnia doryssus*, and *Melinaea lilis imitata*) assembled in high densities at *E. burchelli* swarms and fed on bird droppings there, we undertook a 1-year study of the behavior, sex ratios, and turnover within such assemblages. From these data we sought clues as to the nature of associations between the ants, birds, and butterflies.

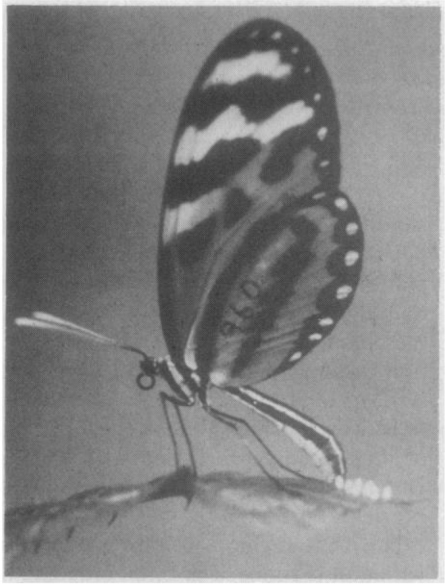

Fig. 1. Adult of *Mechanitis lysimnia doryssus* laying eggs on its *Solanum* host plant at Finca La Selva, Costa Rica. Larvae feed in groups and sequester poisonous compounds from the leaves, which provide protection from predation by antbirds, as adults.

Nonfloral feeding by adult Lepidoptera is a poorly explored phenomenon (*3*) although it can have significant effects on reproductive biology. Reproduction in most kinds of butterflies is thought to be restricted by the amount of nitrogenous reserves accumulated during larval feeding (*4*, *5*). Many butterflies, particularly temperate butterflies, feed primarily from flowers and thereby obtain sugar to provide metabolic energy. For these butterflies, larval reserves are the major, if not only, source of nitrogenous materials available for egg production. When the butterfly emerges from the pupal case, the number of eggs to be laid is thought to be a finite number determined by the quantity of nutrients accumulated during larval feeding (*4*, *6*, *7*). This general life pattern does not hold for several groups of butterflies. Adult *Heliconius* (Nymphalidae: Heliconiinae) butterflies use free amino acids in pollen to augment egg production, thereby extending their reproductive life (*8*). Other Neotropical butterflies, including the subfamily Ithomiinae, feed on bird droppings, and it is believed that they are using uric acid or partly digested proteins as a source of nutrients essential for egg production (*6*, *8*, *9*). Some ithomiine species are able to live at least 4 months (*8*), and probably produce egg clusters (Fig. 1) throughout their lives (*10*). If ithomiines depend on bird droppings as a nutritional resource necessary for prolonged egg production, then selection should favor efficient exploitation of predictable sources of fresh bird droppings. Raiding swarms of the army ant *E. burchelli* are such a predictable source.

At Finca La Selva, two other types of adult ithomiine groupings are known to occur. Male butterflies may be found in high densities at certain species of plants which provide precursors for the sex pheromone [ithomiine males bear scent scales which emit the sex pheromone (*3*, *11*, *12*)]. In addition, there are courtship aggregations composed mainly of males. Both males and females are attracted to the courtship area (*12*); however, the sex ratio is strongly shifted toward males (Table 1). At ant swarms we find the only ithomiine aggregations with female-biased sex ratios (Table 1).

At dense ant swarms, a large contingent of female butterflies, approximately 8 to 12 at one time, may be observed flying low over the front of the swarm. As many as 30 individuals have been captured over a period of a few hours. It is possible that many more individuals may be present at the swarm, since it is difficult to see and capture butterflies in a dense forest habitat. The butterflies exhibit searching behavior, dipping down momentarily in the midst of the dense swarm, and occasionally stop to feed at fresh bird droppings.

It appears that the butterflies are attracted from a large area to the swarms, possibly by some odor produced by the

Table 1. Sex ratios (male:female).

Species	Pheromone plants	Courtship groups	Ant swarms	At emergence from pupae
M. polymnia	36:1	28:13	10:99	60:64
M. lysimnia	1:0	22:4	2:40	
M. lilis	1:0	3:2	5:31	1:5

Table 2. Abundances.

Species and sex	Individuals (number per hour)		Probability‡
	Ant* swarms	Without ants†	
M. polymnia ♀	2.65	.256	.001
M. polymnia ♂	.267	.341	.4
M. lysimnia ♀	1.07	.085	.01
M. lysimnia ♂	.054	.085	.3
M. lilis ♀	.829	0	8×10^{-5}
M. lilis ♂	.134	.085	.3

*Thirteen swarms, for a total of 37.4 hours. †Five sessions, for a total of 11.7 hours. ‡Computed by means of a *t*-test. Each swarm or session is treated as one datum; these are used to compute the mean, weighted by the length of the session.

ants. While it was not possible to test this directly, data were gathered as to the absolute abundance of *Melinaea* and *Mechanitis* in the presence and in the absence of ant swarms (*13*). Table 2 shows that capture of new female individuals per hour is significantly higher at swarms, roughly ten times the capture rate in the absence of a swarm, suggesting that the butterflies are strongly attracted to the swarm area or remain in the area once encountered, or both. Since females lack scent scales, the predominantly female concentrations probably are not self-aggregating as are the courtship groups. The butterflies may be using the strong odors produced by *E. burchelli* swarms for orientation to the swarm area, although once in the swarm vicinity, other factors, such as visual cues, are important in locating bird droppings.

We observed the behavior of the butterflies briefly before capturing them. At ant swarms, 49 percent of the butterflies captured were involved in feeding behavior; 26 percent were actually feeding on bird droppings, while the other 23 percent were flying low over the ground and stopping to examine white spots, such as lichens or fungal mycelium, which resemble bird droppings. Of the remaining 51 percent, 37 percent were flying, 7 percent were sitting on leaves, and 7 percent were alternating between flying and sitting. Some of these 51 percent may also have been involved in feeding behavior at the swarm, although this was not observed in the brief interval before capture.

Ithomiine butterflies are well-known aposematic models for mimicry complexes (*14*) and are not attacked by the insectivorous birds present at the swarms. Bird droppings at ant swarms could be a resource available only (i) to those butterflies and other large insects that are protected from bird predation by distasteful compounds or (ii) to palatable Batesian mimics of such species.

Drummond (*15*) first reported the association between butterflies and army ants. He observed females of *Mechanitis lysimnia doryssus* and *M. polymnia isthmia* (*16*) following a swarm of *E. burchelli* in Honduras. Drummond hypothesized that the *Mechanitis* were attracted to the swarm by an odor that mimicked the courtship scent of the male butterflies, thus explaining why only females were attracted to the swarm. Since Drummond made this hypothesis, it has been shown that *Mechanitis* males as well as females are attracted to the courtship scent (*12*); thus his hypothesis does not explain why predominantly females are found at the ant swarms. While Drummond observed the same dipping flight pattern that we observed, he did not see them alighting to feed on bird droppings.

Young (*9*), who did not observe the phenomena, responded to Drummond by suggesting the alternative hypothesis that "butterflies were being 'fooled' by the swarm raid odors. The odors of decay associated with the swarm raid triggered food searching behavior by these butterflies, causing them to follow the army ants." Our observations suggest that the butterflies are not being fooled at all, but rather take advantage of the swarm as a predictable source of an important nutrient.

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References and Notes

1. E. O. Willis and Y. Oniki, *Annu. Rev. Ecol. Syst.* **9**, 243 (1978); R. A. Johnson, *Proc. Linn. Soc. N.Y. Nos. 63-65* (1954), p. 41; T. Belt, *The Naturalist in Nicaragua* (London, 1874).
2. An Organization for Tropical Studies field station located in the lowland Caribbean rain forests of Heredia Province, Costa Rica.
3. L. E. Gilbert and M. C. Singer, *Annu. Rev. Ecol. Syst.* **6**, 365 (1975).
4. F. Engelmann, *The Physiology of Insect Reproduction* (Pergamon, New York, 1970).
5. V. B. Wigglesworth, *The Principles of Insect Physiology* (Chapman & Hall, London, 1972).
6. H. Dunlap-Pianka, C. L. Boggs, L. E. Gilbert, *Science* **197**, 487 (1977).
7. P. A. Labine, *Evolution* **22**, 799 (1968).
8. L. E. Gilbert, *Proc. Natl. Acad. Sci. U.S.A.* **69**, 1403 (1972).
9. A. M. Young, *J. Lepid. Soc.* **31**, 190 (1977).
10. Female butterflies of all ages collected from the field and dissected were found to contain either mature eggs or nearly mature eggs. Relative age was determined by wing wear.
11. T. E. Pliske, *Ann. Entomol. Soc. Am.* **68** (No. 6), 935 (1975); *Environ. Entomol.* **4**, 474 (1975); L. E. Gilbert, "Organization for Tropical Studies, Advanced Population Biology Course Reports" (Organization for Tropical Studies, San Jose, Costa Rica, 1969), p. 69.
12. W. A. Haber, thesis, University of Minnesota (1978).
13. The data for abundance in the absence of ant swarms were gathered at the same sites where the ant swarms are sampled, at the same time of day, and, if the weather permitted, on the following day. When weather conditions changed, the swarm sites were again sampled as soon as the weather returned to the original condition. Individuals were netted, marked with a number on the wing, sexed, identified, and released. Butterflies were released by being placed on vegetation. With this method of release, they do not exhibit escape behavior, but sit on the vegetation for from a few seconds to a few minutes, then resume flight as if they had not been disturbed. In Table 2, individuals captured more than once in a day are counted as one capture.
14. L. P. Brower, J. V. Z. Brower, C. T. Collins, *Zoologica* **48**, 65 (1963); H. W. Bates, *Trans. Linn. Soc. London* **23**, 495 (1862).
15. B. A. Drummond, *J. Lepid. Soc.* **30**, 237 (1976).
16. *Mechanitis lysimnia doryssus* and *M. polymnia isthmia* were formerly known as *M. polymnia doryssus* and *M. isthmia isthmia*, respectively [K. S. Brown, *Syst. Entomol.* **2**, 161 (1977)].
17. We thank F. M. Carpenter, B. A. Drummond, L. E. Gilbert, K. Karrer, A. Klein, R. E. Silberglied, and E. O. Wilson for comments and encouragement. Supported by a RIAS grant from the Organization for Tropical Studies, a grant from the Anderson fund of Harvard University, a grant from the Barbour fund of the Harvard Museum of Comparitive Zoology, and a grant-in-aid of research from Sigma Xi.

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Evolution of Clutch Size in Birds: Adaptive Variation in Relation to Territory Quality

Abstract. *Reproductive output from enlarged or reduced magpie broods showed that each female generally lays a clutch of optimal size. This size varies considerably between females. Approximately 85 percent of the within-years variation in clutch size was associated with differences between territories. Colonial bird species, lacking individual foraging territories, have a smaller clutch size variation than territorial species.*

Lack (*1*) postulated that clutch size in birds is adjusted to the maximum number of nestlings for which the parents can find food. Provided that clutch size is largely inherited (*2*), the most productive clutch size will, by the force of natural selection, be the commonest one (*1*). Here I further develop this hypothesis, and propose that in a bird population there is not only one optimal clutch size but many. The optimal strategy for the birds is to be highly flexible in their choice of clutch size, in order to adapt clutch size to available resources. Territory quality is the most important factor in determining the optimum clutch size in territorial birds.

To support this hypothesis I present experimental field data from a breeding population of magpie *Pica pica*, showing that the optimal clutch size is *n* for birds that choose to lay *n* eggs, regardless of the actual value of *n*. Clutch size variation between different birds in the same territory and the same birds in different territories indicates that 81 to 86 percent of the within-years variation in magpie clutch size is linked to differences in territories. Furthermore, the influence of exclusive foraging areas on clutch size variation is reduced in birds breeding in colonies, and this leads to a smaller clutch size variation in colonial than in territorial species.

To analyze optimal clutch sizes in a population of individually marked mag-

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