"mutual" (Ghiselin's word, not mine) adaptation, orthogenesis, or interspecific group selection (5).

For my model to work it is not necessary, as Ghiselin implies, that predators limit the size of the populations of their prey. All that is required is that predators exert a strong selective force on their prey. The ability of a predator to exploit a prey population differs from the performance of regulatory function. Similarly, Ghiselin seems to confuse absolute abundance of prey and availability of prey to a particular predator. As he himself points out, predators are only one of the factors that affect prey population parameters.

Although Ghiselin's questioning of the relationship between predator diversity and prey exploitation only touches on a peripheral part of my model (an alternative explanation for latitudinal gradients in clutch size based on seasonality of food resources is offered), his corresponding model deserves comment. Ghiselin's point about lineal food chains seems irrelevant; what is important is the diversity of predator strategies that affect the prey. Ghiselin fully misses the mark here in assuming that the evolution of one predator-avoidance pattern by the prey does not affect its ability to evolve effective avoidance of another predation strategy. It would seem that the more numerous and varied the predation techniques, the more difficult adaptive solutions must become for the prey. An elaboration of Ghiselin's model should make the point. A grasshopper's flight response may help it to avoid being eaten by meadowlarks and dickcissels, but it poses other problems if flycatchers or other aerial predators are present. Thus, evolution to avoid meadowlarks, which search for prey on the ground, would be compromised by the presence of kingbirds and sparrow hawks, which search from elevated vantage points. As Janzen (6) points out about the defensive traits of leguminous plants against pea-weevils (Bruchidae), "all seem effective against at least one species of bruchid but only rarely against all bruchids . . . most can be countered by evolution of the bruchid."

Diverse predators do, in fact, employ a variety of searching and prey-capture techniques. For example, tropical forest insects are beset by foilage-gleaning birds, lizards and snakes, primates, tree frogs, mantids, predacious hemiptera, parasitic diptera and hymenoptera, fungi, and other microorganisms. It remains to determine whether the diversity

of predation strategies varies inversely with geographical gradients in avian clutch size.

Overall, Ghiselin appears to have missed the significance of the question posed by my report, namely: What determines the availability of food resources to predators? The point of the discussion was that the level of availability (7) reflects evolution of predator populations to exploit their prey, and of prey populations to avoid their predators. The level itself is not an evolved or adaptive character per se but is established by adaptations of predator and prey to important aspects of their environment, namely, prey and predators, respectively. Because of the "principle of compromise" increased diversity of predation strategies must reduce ability of mutual prey species to evolve effective antipredator adaptations and consequently the "availability" of the prey to predators must increase (8).

In two other "systems" that have been examined—Smith's comprehensive observations on oropendula-cowbird relationships in Panama (9) and my examination of mortality-development rate relationships among seven species of birds (10)—outcomes of the predator-prey counteradaptation system have appeared remarkably uniform. We may view this as follows. Given prey species as a constant, the rate at which predators can exploit their prey is confined within an upper limit by the ability of the predators to adapt to relevant prey characteristics, and within a lower limit by competition with other predators (11). As the intensity of competition (competitive overlap) increases, the lower limit approaches the upper limit. In a sense this is trivial. In all populations, individuals are replaced approximately once, on the average, each generation. We might expect that among similar species corresponding segments of the life history cycle might contribute in a similar magnitude to the maintenance of the population. The value of the model which I have proposed lies in providing a conceptual

basis for interpreting specific schedules of fecundity and mortality as ecological and evolutionary phenomena.

This conceptual approach should apply equally well to any exploitative interaction, including those that involve plants (12), in which predator or parasite productivity is ultimately limited by prey characteristics, that is, in which competition exists among predators or parasites whose food resources overlap.

ROBERT E. RICKLEFS

Department of Biology, University of Pennsylvania, Philadelphia 19104

References and Notes

1. J. Ghiselin, Science, this issue.
2. R. E. Ricklefs, ibid. 168, 599 (1970).
3. See Webster's New International Dictionary, 2nd edition (1953).
4. It should be pointed out that "adaptation by prey to minimize the efficiency of their predators" is not incompatible with adaptation to "maximize the likelihood of producing progeny themselves." In most senses, strategies that minimize particular functions take into account contingency costs that affect overall production.
5. In a parallel instance involving accepted usage, the term "ecosystem" does not connote adaptation or any other kind of purposeful interaction in a superpopulation, but merely encompasses the outcome of interrelationships which conform to a Darwinian view of nature.
6. D. H. Janzen, Evolution 23, 1 (1969).
7. An operational definition of availability would be based upon the rate of food gathering per unit of time-effort. Absolute abundance would be one of several components of availability. T. Schoener [Amer. Natur. 103, 277 (1969)] and M. Rosenzweig and P. Sterner [Ecology 51, 217 (1970)] among others have given useful operational definitions of availability.
8. In my first paper, I neglected to point out one a basic assumption of this model, namely, that prey availability does not increase as fast as predation diversity. If this were not the case, increased predator diversity would not increase the level of interspecific competition. This does not seem reasonable if the total prey production available to all predators on a given trophic level is independent of, or does not increase with, increasing predator diversity. The abundance component of availability must be relatively important in this regard, especially over wide ranges of predator diversity.
9. N. G. Smith, Nature 219, 690 (1968).
10. R. E. Ricklefs, ibid. 223, 992 (1969).
11. R. H. MacArthur and R. Levins, Amer. Natur. 101, 377 (1967).
12. Plants are capable of more sophisticated antipredator adaptations than Ghiselin would have us believe. Janzen (6) lists 31 traits which the Leguminosae may employ to reduce bruchid beetle attack. Further discussion of plant defensive mechanisms may be found in S. D. Beck, Annu. Rev. Entomol. 10, 207 (1965); P. P. Feeny, J. Insect Physiol. 14, 805 (1968); S. W. Applebaum, ibid. 10, 783 (1964); N. Smythe, Amer. Natur. 104, 25 (1970); and others.

28 September 1970   ∎

Brood Care in Halictid Bees

Batra and Bohart (1) have recently shown that Knerer's (2) conclusions about progressive feeding in halictids cannot be drawn from the data he obtained on weight gain during larval development. The 60 percent weight gain found in growing halictid larvae

(1, 2) is probably characteristic for the family. It is doubtful, however, that either progressive feeding or the "hygroscopic nature" of the provisions is responsible for most of this increase.

In my studies (3) of weight gain of Augochlora pura, a solitary halictine

(4), I found that the mature larvae weighed 62 percent more than the provisions bearing eggs. The increase could be accounted for as water uptake by the larvae, not the provisions. The relative water content of the provisions remained constant (43 ± 2 percent) throughout larval development, while the growing larvae contain about 70 percent water. Pollen balls by themselves did not gain weight. The greatest increase in amount of water in the larva takes place when the provisions are almost consumed. Many insects are known to take up water as vapor through the cuticle (5), and halictids are probably no exception.

Malyshev's (6) statements on the hygroscopic nature of provisions were apparently without experimental support. If the provisions were as hygroscopic as Batra and Bohart (1) believe, there would be no need to postulate progressive feeding, and no need for Batra (7) to have added a honey supplement to provisions in the laboratory.

The nature of cell construction of halictids, particularly the waterproof nature of the cell lining (3), preserves high humidity inside the cells. If the cells are opened, however, as is apparently the case for *Evylaeus malachurus* (2), it may be necessary for the adults to moisten the provisions to compensate for water loss.

DOROTHY G. K. MAY
Department of Entomology,
The University of Kansas,
Lawrence 66044

References

1. S. W. T. Batra and G. E. Bohart, *Science* **168**, 875 (1970).
2. G. Knerer, *ibid.* **164**, 429 (1969).
3. D. G. K. May, thesis, University of Kansas (1970).
4. K. A. Stockhammer, *J. Kans. Entomol. Soc.* **39**, 157 (1966).
5. J. W. L. Beament, *Advan. Insect Physiol.* **2**, 67 (1964).
6. S. I. Malyshev, *EOS* **11**, 249 (1935).
7. S. W. T. Batra, *Insectes Soc.* **11**, 159 (1964).

25 May 1970

May (1) has supported our conclusion (2) that the excess weight gain of halictid cell contents cannot be used, as it was by Knerer (3), as evidence of progressive provisioning by these bees.

The peripheral question as to how the cell contents gain weight (water) remains unresolved. Some water absorption through the spiracles or the cuticle of the larva is possible. Healthy larvae should be maintained in a humid atmosphere without provisions in order to test this hypothesis ade-

quately. Halictid provisions, consisting of a mixture of honey and pollen, are probably hygroscopic. Extracted honey, when kept at high humidity, gains up to 33 percent in weight because of hygroscopicity (4).

The provisions are stored in cells having a porous cap or no cap. Cells typically are in soil that is moist enough to support vegetation. Air spaces in such soil remain at 100 percent relative humidity (5), thus the nest (except perhaps near the entrance) and the cells would be at or near 100 percent relative humidity.

Young halictid larvae initially feed at one area on the surface of the spheroidal provisions, creating a small, moist-appearing indentation beneath the mouthparts. This concavity evidently lowers the vapor pressure at that point, so that water from the saturated cell atmosphere condenses there. It is thus continually ingested by the young larva. Unlike *Augochlora* (1), an exceptional halictid that nests in wood, the greatest increase in water content of *Nomia* occurs during the early larval instars (2). The provisions with brood of the solitary soil-nesting andrenid bee *Calliopsis* dried out at 93 percent relative humidity but appeared normal when kept at 100 percent relative humidity (6). The high humidity requirement of halictine provisions, among other factors, may account for my need to add diluted honey to provisions kept at high, but evidently not 100 percent, relative humidity (1, 7).

General condensation in the cell may also be an important source of water. It regularly forms on the cell lining,

provisions, and brood of halictid bees when the soil temperature decreases. Condensation forming on the larvae and provisions of *Pseudopanurgus* is swallowed (8), and the larvae of this solitary, soil-dwelling panurgine bee, like halictid larvae (2), grow rapidly before much provision is consumed.

Progressive provisioning in halictine bees was tentatively postulated (7) because females of *Dialictus zephyrus* were seen opening sealed cells and touching, with their glossae, provisions bearing brood. Radioactive tracers and dyes (7) should be used to determine if this behavior represents progressive provisioning, the addition of secretions, or the removal of substances from the provisions. It remains significant to the study of the evolution of insect social behavior that halictine bees *may* progressively provision when contacting the developing brood, whether in sealed (7, 9) or in open (3, 9) cells.

S. W. T. BATRA

2-Q Plateau Place,
Greenbelt, Maryland 20770

References

1. D. G. K. May, *Science*, this issue.
2. S. W. T. Batra and G. E. Bohart, *ibid.* **168**, 875 (1970).
3. G. Knerer, *ibid.* **164**, 429 (1969).
4. F. W. Fabian and R. I. Quinet, *Mich. State Coll. Agr. Exp. Sta. Tech. Bull.* No. 92 (1928), pp. 1–41.
5. H. O. Buckmann and N. C. Brady, *The Nature and Properties of Soils* (Macmillan, New York, 1963).
6. A. F. Shinn, *Univ. Kans. Sci. Bull.* **46**, 753 (1967).
7. S. W. T. Batra, *Insectes Soc.* **11**, 159 (1964); *Univ. Kansas Sci. Bull.* **46**, 359 (1966).
8. J. G. Rozen, Jr., *Amer. Mus. Novitates* No. 2297 (1967), pp. 1–43.
9. S. W. T. Batra, *J. Kans. Entomol. Soc.* **41**, 120 (1968).

5 August 1970   ∎

Density of Low Temperature Ice

Delsemme and Wenger (1) present results showing a very large density, 2.32 g cm^{-3}, for water ice formed below 100°K at pressures of 6 to 8 × 10^{-3} mm-Hg. We have measured both the density and refractive index of ice formed under similar temperature and pressure conditions without observing abnormally high densities or a high refractive index.

We determined the density of low temperature ice by uniformly condensing water vapor over a very well-defined, cryogenically cooled, flat surface at a known constant mass deposition rate, $\dot{m}$. As the ice formed, its constant thickness deposition rate, $\dot{\tau}$, was mea-

sured, which allowed the ice density, ρ, to be calculated from

$$\rho = \frac{\dot{m}}{A\dot{\tau}} \qquad (1)$$

where A is the deposition area. In order to measure the thickness deposition rate as accurately as possible, we used optical thin-film interference techniques (2) with monochromatic light. By using these techniques we obtained both the thickness deposition rate and the refractive index of the ice as it was deposited.

In our experiments water vapor was condensed under vacuum on the outside of a hollow copper cryosurface