

increased after any given event, then there are expected to be more multiple events in some samples than the predictions of the Poisson theorem.

The origin of the MEPP is not yet completely understood. The change in the statistical pattern of release brought about by changing the extracellular calcium concentration suggests that a main determinant of the probability is the state of the presynaptic membrane,

which can be modified by calcium ions.

Our experiments illustrate that under normal conditions a spontaneous synaptic event is independent of the preceding one. When the extracellular concentration of calcium is increased this independence no longer occurs. Thus, by changing the concentration of calcium one can transform the spontaneous release from one pattern of statistical behavior to another, from a Poissonian to a non-Poissonian random discharge.

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4. For effect of calcium concentration on the frequency of MEPP's in mammalian neuromuscular junction see: P. W. Gage and D. M. J. Quastel, *J. Physiol.* **185**, 95 (1966); J. I. Hubbard, S. F. Jones, E. M. Landau, *ibid.* **194**, 355 (1968).
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6. P. W. Gage and J. I. Hubbard, *Nature* **208**, 395 (1965).
7. R. I. Birks and M. W. Cohen, in *Muscle*, W. M. Paul, E. E. Daniel, C. M. Kay, G. Monckton, Eds. (Pergamon Press, Oxford, 1965), p. 403.
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9. Supported in part by a Singer fund research grant.

13 July 1970

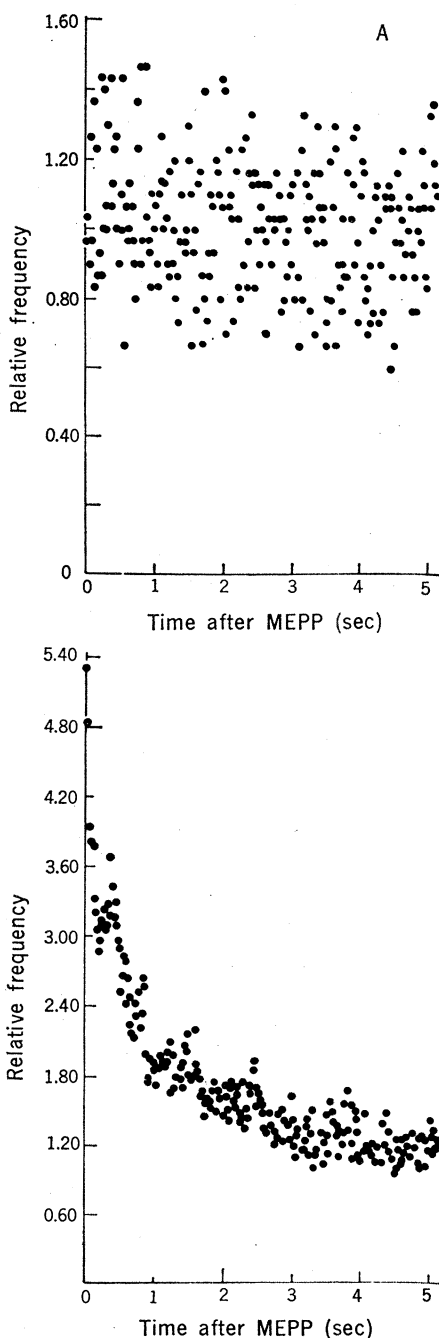


Fig. 1. Relative frequency of MEPP's following any given MEPP. The frequency of the MEPP's was estimated in successive 20-msec periods after each MEPP and divided by the mean frequency (see text). (A) Normal concentration of calcium (1.8 mmole/liter); (B) high concentration of calcium (15.0 mmole/liter).

Interference of HEPES with the Lowry Method

We, too, have experienced a similar difficulty in the determination of protein in the presence of HEPES (*N*-2-hydroxyethylpiperazine-*N'*-2-ethane sulfonic acid) (1). Our resolution of the problem was to measure the protein by a modified version of the microbiuret method (2), scaled down in volume such that the color developed from 0.4 ml of protein solution, when mixed with 0.2 ml of reagent, could be determined in silica microcells (0.5 ml). Any interference due to salt crystallization that might arise with buffers of high ionic strength is easily overcome by clarifying the mixed solutions in a bench centrifuge before measurement.

The method was unaffected by the presence of HEPES, is relatively nonspecific for the type of protein, and moreover produces a linear standard curve, with sensitivity not much less than with the Lowry procedure.

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15 September 1970

Prey Population: A Parsimonious Model for Evolution of Response to Predator Species Diversity

Ricklefs (1) proposes a model to account for "clutch size in birds" which seems hardly applicable to birds as a class. The model can be applied comfortably only to those birds which feed their nestlings on animal food, and more specifically to those which feed altricial young on motile prey. Pigeons (Columbidae) produce animal food from their own crops. Brood parasites do not feed their young at all. Young precocial birds feed themselves, many on vegetable matter. That apparent

cavil aside for the moment, it is worth while to consider the logical structure underlying the hypothesis, and the consequences logically to be expected from it.

One is immediately struck by the erection of an "adaptive system" which adjusts the strategies of foraging behavior among predatory birds to the productivity of their prey. As what seem to be his only examples of analogous "systems of predator-prey adaptation of diverse species" Ricklefs cites

Smith's study (2) showing mutual benefits to host and parasite in a "system" of brood parasitism, rather a different sort of relationship, and one of his own (3) comparing developmental rates of precocial and altricial birds, I am not convinced that one needs a "system" to account for evolution of traits permitting survival at different levels on the trophic heap. Prey do not, after all, really "evolve to minimize the efficiency of their predators"; they evolve to maximize the likelihood of producing progeny themselves. Many influences, predation being only one, might prevent their reproducing successfully (4).

An interesting conjecture is whether or not populations of birds and of their prey are controlled interdependently. Despite recent debate (5), it seems fairly well established that although many invertebrate populations are limited by density-independent factors, those of vertebrates more commonly respond to density-dependent influences. If we accept both propositions, since they are not mutually exclusive (6), we are confronted by the philosophic difficulties of evolution of a balanced mortality (or productivity, the two being much the same) of animals whose populations are controlled by unconnected factors (7). The problem is whether or not such a balance—such a "system"—really exists at all.

A second, independent question, assuming the predators actually limit the prey, regards Ricklefs' theoretical argument of the greater difficulty experienced by a prey species in "adapting to" a larger rather than a smaller number of kinds of predators. Lineal food chains are less common than food webs, occurring most commonly in inhospitable environments such as the Arctic or the laboratory where species diversity is low (8). It follows that such mutual adaptations as are proposed would be most readily developed where lineal food chains were common, but also that in considering the workability of the model in the real world one must evaluate how it might work where food webs, rather than food chains, were the rule.

This consideration may perhaps best be illustrated by my own didactic model. Assume the existence of two communities having different predator diversity. For simplicity, assume that a single producer—say a grass—is fed upon by one primary consumer—say a grasshopper—in both cases, and the grasshopper by secondary consumers. In the first community, there is only

one secondary consumer, a meadowlark; in the second, a bobolink is added.

If in neither case does the supply of grasshoppers greatly exceed the needs of the birds (9), the fate of all but a very few of the grasshoppers will be to be eaten. (Density-independent mortality may be neglected for the present purpose.) Those few which are not eaten will transmit to their offspring the innate behavioral traits comprising the strategy of survival in contest with a particular strategy of predation. If a particular innate action permitting survival under attack by one particular predator (my first case) be controlled by a single dominant gene, any individual grasshopper carrying that gene will be more apt to escape, while the others will perish. In the second case, two genes are required to confer an equivalent comparative safety on an individual grasshopper. In this situation, grasshoppers carrying both traits should survive, while most others are eaten. That this hypothesis oversimplifies the inheritance of behavior in at least two ways is not germane to the conclusion to be drawn from the argument: provided appropriate mutations occur (which of course they may not), a single species' simultaneous evolution of multiple strategies of escape is likely under selection pressure for development of a compound defense to a compound attack (10).

In my model it is of no moment whether one species of bird or two attack the single species of prey. Because no alternative prey is provided, the likelihood of attack by the strategy of one bird rather than the other will be proportional to the comparative abundance of the predators. The greater the diversity of the predators, the greater will be the diversity of tactics of attack an individual insect will suffer, but their total incidence will be the same. If the fate of all but a very few grasshoppers is to become prey, regardless of how many predators may prey upon them, then the defensive strategy of an enlightened grasshopper must be to avoid at all times falling prey to whichever unpredictable predator may next attack. Unless the predators feed very differently—as in my model they do not—any single tactic, such as crypticity or flight, must suffice for protection against many predators. The tactics of survival must represent the resultant of the most successful responses to the predatory strategies of however many predators may exist. This characteristic of life affects not merely insects,

but rather all except the bear and the tiger, animals too strong to be prey to anything. That tropical insects survive as species at all, despite the amply documented diversity of their predators, suggests that some such mechanism as I propose is at least plausible (11).

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2. N. G. Smith, *Nature* **219**, 690 (1968).
3. R. E. Ricklefs, *ibid.* **223**, 922 (1969).
4. Although to consider the hints of orthogenesis and group-selection (expanded to a new, interspecific scope) in Ricklefs' report might be profitable, it seems inappropriate here.
5. H. G. Andrewartha and L. C. Birch, *The Distribution and Abundance of Animals* (Univ. of Chicago Press, Chicago, 1954); D. Lack, *Population Studies of Birds* (Clarendon, Oxford, 1966).
6. D. Chitty, *Ecology* **48**, 698 (1967).
7. H. S. Horn [*ibid.* **49**, 776 (1968)] suggests that the distinction between density-dependent and density-independent population controls may be more apparent than real. To sustain my argument it is necessary merely that predator and prey populations be controlled by different factors, such as food supply as contrasted with extremes of weather.
8. R. T. Paine [*Amer. Natur.* **100**, 65 (1966)] addresses this topic at length.
9. It is not necessary that the predators interact at all.
10. A further unrealistic aspect of my model, also not affecting the inferences it suggests, is that predators rarely concentrate on a single sort of prey, instead they seem to require variety; see J. A. Gibb, *Ibis* **104**, 106 (1962). Although bobolinks and meadowlarks in nature both do eat grasshoppers, they would prey exclusively upon them only in such a situation as that premised, in which no other prey existed.
11. The problem of how populations of herbivores and of the plants on which they feed can develop by such an "adaptive system" as Ricklefs posits, although not considered in his report, is one which surely should be encompassed in his model. The survival of spiny shrubs on overgrazed range might provide instructive instances of successful all-purpose defenses used by organisms with vanishingly small behavioral repertoires.

28 May 1970; revised 28 August 1970

Ghiselin (1) has apparently misunderstood my conceptual model of clutch size in birds (2), perhaps because of its brief presentation in this journal. I certainly hope so. Ghiselin's own model offered in response seems naïve next to the subtly complex reality of natural communities.

Ghiselin interprets my use of the word "system," which means "an assemblage of objects united by some form of regular interaction or interdependence" (3), as an adaptive structure purposefully oriented toward the evolution of clutch size. Rather, I used the word as a convenient descriptive handle for a set of interactions which do occur; both trophic and antipredator adaptations are readily recognized in nature (4). The model that I presented does not require or even hint at

"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 foliage-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.

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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 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