set theory. But, unlike the axiom of choice and the continuum hypothesis, the three are all of a form such that, if they are not disprovable in ZF set theory, then they are true. To show that this is the case, one can consider the statement

For all $x_1, \ldots, x_m$, $P(x_1, \ldots, x_m)$ holds (1)

where the x_j are positive integer variables and for each fixed $x_1, \ldots, x_m$, the statement $P(x_1, \ldots, x_m)$ is decidable in ZF set theory. To say that statement (1) is false is equivalent to saying "There exist $x_1, \ldots, x_m$ such that $P(x_1, \ldots, x_m)$ fails" and so to "For some $x_1, \ldots, x_m$, $P(x_1, \ldots, x_m)$ is disprovable in ZF set theory" (the latter equivalence is "metamathematical," that is, expressed and proved outside of ZF set theory). Thus, to prove (outside of ZF set theory) that such conjectures are not disprovable in ZF set theory would be to prove them (*1*).

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References and Notes

1. I learned this point from B. Dreben at Harvard University in 1957; it is presumably common knowledge among mathematical logicians.

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Altruism in Mountain Bluebirds?

Harry W. Power (Report, 11 July 1975, p. 142) claims to provide evidence against the existence of altruistic behavior in mountain bluebirds because new males that formed consort relations with widowed parents did not provide either defense or food for the adopted offspring.

I am in full agreement with Power's general views on the evolution of social behavior. Cases of apparent altruism are rare in animal societies and, when examined in detail, usually prove more explainable in terms of kin selection or reciprocal altruism with a time lag than in terms of true altruism. But I feel that ultimate and proximate controlling factors are confused in Power's study, and the results do not actually represent a "test" for the existence of altruistic behavior.

Studies in which breeding birds have been removed from their territories and the occurrence of replacements recorded have been common in ornithology for 25 years (*1*). Such studies frequently have shown that a nonbreeding surplus of individuals, especially males, exists and that these birds are capable of moving into vacated territories. The new slant added by Power is an examination of the degree of parental investment provided by these new consort birds to the offspring of their new mates. In his words, "One way to measure the frequency of true altruism is to give animals the choice of behaving altruistically or selfishly." This logic is sound *provided* that one basic assumption is met: the animal in question must really have a "choice"—it must be equally able to provide parental care or to withhold it.

Intensive studies of the endocrine basis of reproductive behavior in birds have shown a tight interrelationship between parental behavior and hormonal state (*2*). As an individual bird progresses through a breeding cycle, from initial courting through nest-building activities and egg laying to incubation and feeding young, its hormonal state changes sequentially. Visual, auditory, and tactile information available during any one particular phase of the breeding cycle helps produce changes in the underlying hormonal condition of the bird; these hormonal changes, in turn, alter the bird's responsiveness and receptivity to various cues in the nest environment. Thus a bird feeding nestlings has attained a certain physiological state, and passage through the earlier stages of the breeding cycle has played a significant role in leading to the attainment of this state. Individual birds that are not in a comparable hormonal condition would not be expected to provide parental care for nestlings, regardless of genetic relationships. The plasticity of parental behavior has definite limits. In the few studies where nest contents have been experimentally altered [by presenting young prematurely or by exchanging young of various ages for eggs or vice versa (*3*)], results have generally shown: (i) young are often, but by no means always, accepted when presented to mated pairs that have progressed to the incubation phase, and especially the late incubation phase, of the normal breeding cycle; but (ii) young are ignored or attacked if presented either to unmated adults or to pairs that have not advanced through the nest-building or egg-laying stages of breeding.

In interpreting Power's results, we must ask the following. If a parent mountain blubird is collected and a surplus, nonbreeding, bird moves into the vacant territory, would this new bird be expected to be in the appropriate physiological condition to assume a parental role? Since the new consort has not been a territory holder, has not mated, nor has it engaged in any of the previous phases of the nesting cycle, I would say no. Thus the "test" for altruism in this study does not represent a real choice. The maximum "altruistic" response that could be expected would be for the new consort bird to experience an accelerated physiological adjustment so that it

attained the appropriate hormonal condition and became responsive to the young nestlings in a foreshortened period. The lack of an immediate acceptance and feeding of the new young by most consort bluebirds thus need not imply anything about the presence or absence of altruistic behavior.

One can legitimately inquire about the ultimate adaptiveness of the particular hormonal regulation system that mediates breeding behavior in songbirds. Why should there have evolved a system of checks and balances wherein stimuli from one phase of the breeding cycle help to physiologically prepare the birds for the next phase? One possible explanation relates directly to the question of the evolution of altruism versus selfishness. The system would serve to maximize individual reproductive fitness by minimizing any chance that a bird would accept any nest or provide parental care to offspring at a stage of development different from that of its own. This would minimize "wasted" parental investment on young that are not genetically its own. This is a fascinating question, but *not* the one raised or tested by Power's study.

Whatever the ultimate selective forces shaping the hormonal regulation system, we are left with interpreting the short-term parental behavior, behavior that is influenced by many proximate factors including the hormonal regulation system itself. Since there is little reason to expect new consorts to be in the appropriate physiological condition to maximally respond to or feed nestlings, Power's results are not convincing evidence either for or against the existence of altruistic behavior in mountain bluebirds.

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3. J. T. Emlen, Jr., *Condor* **43**, 209 (1941); R. Weidmann, thesis, Oxford University (1956); C. G. Beer, *Behaviour* **26**, 189 (1966); J. T. Emlen, Jr., *ibid.* **33**, 237 (1969).

Emlen correctly states that altruism cannot be tested for in an animal unless it is capable of both altruistic and selfish responses at the time of testing. He questions whether the male consort mountain blue-

birds I studied were capable of behaving altruistically because they had not progressed through all the stages of breeding prior to hatching of young and thus were not in appropriate hormonal condition to foster nestlings.

Emlen bases his critique solely on feeding of nestlings while ignoring the critical category of defense of young, mentioning it only in passing (his first sentence). For my experiment to have been a genuine test for altruism, it was only necessary that the birds be capable of an altruistic response in one category of behavior, not in all categories considered.

Defense behavior was critical in my test for altruism because all studied bird species are capable of giving alarm notes at any time of the year (references 2–4 and 10 in my report), and male consorts gave them during my experiments. Consorts were thus capable of both altruistic (defending) and selfish (not defending) responses. That male consorts only sometimes gave alarm notes, and did so in apparent response to the excitement of the female parents they courted rather than to the distress of the females' young, whereas male parents vigorously defended their young (*1*), implies male consorts were not altruistic when they clearly had the capacity to be altruistic.

Emlen cites studies (his reference 3) showing that adults of several species which have not advanced through nest-building or egg-laying stages attack or ignore young experimentally presented to them. He interprets this to mean that such adults are incapable of fostering young and thus cannot be expected to feed them. His interpretation may be correct. But this result is also consistent with the interpretation that such adults simply refuse to care for young which they are capable of fostering. So far as I know, no experiment has separated incapacity-to-foster from refusal-to-foster, nor is it easy to separate them (*2*).

It is possible that male consorts were capable of feeding young. Feeding of adult females by adult males is a normal component of breeding behavior in mountain bluebirds from early courtship through incubation, and it may also occur while females brood small nestlings (*3*). Is it possible that courting males, capable of feeding adult females, are also capable of feeding nestlings? If so, then the nonfeeding of other birds' nestlings by male consorts is a refusal rather than an incapacity to feed.

Because I did not know whether male consorts were physiologically capable of feeding nestlings, I did not attach as much significance to consorts' nonfeeding of nestlings as to their general nondefense of young. Feeding of nestlings was considered because it is relevant to the overall altruism debate (references 1–4 in my report) in that all aspects of a bird's behavior can be expected to reflect altruistic tendencies if birds are generally altruistic, and its consideration allowed me to propose the hypothesis Emlen paraphrases in his sixth paragraph. I now amend my original hypothesis (paragraph 15 of my report) to state "the stepwise hormonal preparation motivating the carrying out of successive stages of nesting in birds is a proximate expression of ultimate selection for reproductive selfishness, making altruistic errors infrequent." In its new form, the hypothesis does not assume hormonal preparation is a necessary factor, only a motivating one.

In summary, Emlen's assertion that my experiment was not a genuine test for altruism is without merit, even if we consider his own criterion of sound logic, because (i) in the category of defense of young, males were selfish when they clearly had the capacity to be altruistic; and (ii) it has never been demonstrated that courting males of any species are incapable of feeding young, mate feeding suggests courting males are capable of feeding young, and incapacity to feed young—whether present or not—is irrelevant to the significance of observations concerning the defense of young, on which my report primarily relied.

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References and Notes

1. Defense of young by male and female parent mountain bluebirds includes giving alarm notes, forcing fledged young to remain hidden when predators are near, swooping at large mammals (for example, me), and chasing avian predators and small mammals (for example, American kestrels, *Falco sparverius*; least chipmunks, *Eutamias minimus*; and deer mice, *Peromyscus maniculatus*).
2. I telephoned three avian physiologists (James R. King, Robert A. Lewis, and Robert B. Payne) to find out whether they knew of any experiments separating incapacity from refusal. They did not, and agreed it is impossible to separate the alternatives with present evidence.

   I believe incapacity would be experimentally separated from refusal by placing birds in a context where feeding young would promote individual fitness but hormonal motivation was absent. This could be done by allowing birds to pass normally through the stages prior to hatching, and then eliminating their hormonal motivation by gonadectomy or some other treatment. Experimental birds would be compared with sham-operated controls. If both groups fed young, hormonal motivation would be shown to be unnecessary. Although simple in principle, this experiment would be practically difficult because hormone titer would not drop immediately, and hormone preparation would have occurred in previous stages even if it were wholly absent during the nestling stage. But it is even more difficult to draw conclusions from the experiments used as support by Emlen because the birds were provided with neither a hormonal motivation nor a context in which feeding of young would have promoted individual fitness.

   Whether and how much hormonal preparation is required for birds to feed nestlings is further obscured by observations of juveniles feeding nestlings in many bird species, including mountain bluebirds [A. F. Skutch, *Condor* **63**, 198 (1961)].
3. I believe I witnessed a male consort feeding a widowed female with three nestlings during the course of my experiment. The male landed next to the perched female, each bird turned its head toward the other as though the female were accepting food, then both flew off. I was too far away to see if the male carried food or transferred it to the female.