Mountain Bluebirds: Experimental Evidence Against Altruism

Abstract. *The frequency of true altruism in nature requires assessment because, if true altruism is common, Darwin's theory of natural selection is inadequate to account for all of evolution. An experiment provided birds with the opportunity to behave truly altruistically. One member of each of 25 wild pairs was collected. Ten of these were replaced naturally by courting birds, or consorts. Only one consort fostered the young of her prospective mate, and her behavior was interpretable as a reproductive error. Other consorts behaved reproductively selfishly.*

True altruism can be defined as the promotion of other's reproductive success while reducing one's own inclusive fitness. The reality of true altruism has been debated; Wright and Wynne-Edwards (*1*) have argued for it, while Williams, Simpson, Lack, Wiens, and Brown (*2*), among others, have convincingly presented arguments and evidence denying it. The case for true altruism has been further weakened by Hamilton's (*3*) and Triver's (*4*) distinguishing kin altruism and reciprocal altruism, respectively, from true altruism.

The altruism debate is of consequence because (i) true altruism is frequently assumed in basic presentations of biology (*5*); (ii) if true altruism commonly occurs, Darwin's (*6*) theory of natural selection would be inadequate to account for all of evolution since it assumes reproductive selfishness; and (iii) resolution of the debate may affect social policy insofar as officials assume that humans, like other animals, are basically either altruistic or selfish. Thus it is important to assess the frequency of true altruism in nature.

One way to measure the frequency of true altruism is to give animals the choice of behaving altruistically or selfishly. I performed an experiment to alter the foraging behavior of wild mountain bluebirds (*Sialia currucoides*) which also gave some bluebirds the opportunity to behave altruistically toward the offspring of others (*7*).

Work was conducted in Montana during the first nestling period of 1972. To alter foraging behavior, I manipulated brood size and number of attendant adults per nest (Table 1) because foraging behavior changes with individual work load, and these variables affect work load. One attendant adult was collected at each of 25 nests on day 12 of the nestling stage. This day, a little more than midway through the nestling stage, was chosen to make sure surviving males and females were capable of providing equivalent parental care; earlier in the nestling period there is a qualitative division of labor between the sexes. Collecting adults created an opportunity for others to replace them and help care for their young. Each nest was observed for about 30 minutes on each of the 2 days after collection; each nest was visited approximately once every 2 days thereafter until young had fledged.

All young fledged in the normal period of 20 days even though surviving adults were unaided in 24 of 25 cases. The exceptional case is considered below.

Prospective replacement mates were called "consorts" after Stein and Urdang's (*8*) fifth definition of a consort as a companion but with the suggestion of a lover. Consorts courted mateless birds but were not properly mates because no copulations between consorts and courted birds were observed until after fledging and courted birds initially seemed only to tolerate the presence of consorts.

Ten consorts occurred out of a potential 25, eight males and two females; one additional male and female were briefly seen, but I did not determine whether they were consorts or merely passersby. If adult sex ratio is biased toward males or first year males are reluctant to breed (or both), or if females seldom breed later in the season, then it is not surprising that not all 25 collected birds were replaced (*9*).

All male consorts were first observed within 4 days of collecting the original birds: four on the first day, two on the second, and one each on the third and fourth days. One female consort was first seen on the second day after collection, but the other not until on eggs of her own 52 days after collecting the original female and after fledging of the original young and their disappearance from their home territory.

Table 1. Experimental design.

Group	Young per nest*	Adults per nest	Sex of attendant adults	Nests (No.)	Single birds (No.)†	Consorts No.	Consorts Sex
1	6‡	2	M and F	7			
2	6	1	M	6	12	1	F
3	6	1	F	6		5	M
4	3	2	M and F	6			
5	3	1	M	7	13	1	F§
6	3	1	F	6		3	M

*Normal brood size was five or six; half of the broods were culled to three young. †Single birds remained after collection of their mates. ‡One nest had only five young. §This female behaved altruistically (see text).

Three male consorts were seen to attempt copulation but were repulsed by courted females; otherwise, females exhibited no discernible hostility toward male consorts even when they were around nests.

All male consorts were reproductively selfish: none fed young, cleaned nests, or generally gave alarm notes when young appeared endangered. They sometimes gave alarm notes if female parents became excited about apparent danger to their young, but seemingly only in response to the females' excitement. They did not defend young against me although female parents did so vigorously; for example, when I checked nests to see if young had fledged. By contrast, the collected fathers had fed their offspring, cleaned their nests, and vigorously defended their young as often and fiercely as their mates.

The silence of consorts may imply a nonnegligible predation risk incumbent on calling (*3, 4, 10*). Alternatively, predation risk may be trivial but silence may increase the probability of offspring death and thus bring the courted parent quickly into condition for mating with the consort.

Insofar as they took no risks and provided no services, male consorts clearly were not altruistic. But R. D. Alexander suggested to me that they might be considered altruistic insofar as they neither killed nestlings nor interfered with mothers' services to them. This suggestion is serious because some male mammals, such as lions (*11*) and langurs (*12*), kill the young of vanquished males. Male consorts probably did not harm young because this could have prevented pair bond formation. Females are approximately the same size as males and thus can be expected to successfully defend young and resist copulation. Because they cannot be forced into a parental role, females must be courted.

Male consorts sometimes succeeded in nesting with widowed females, forming pair bonds, and gaining territories and nest sites usable in the same or succeeding season, even with different mates. These courtship benefits accrued to two male consorts which had broods by the birds they courted in 1972; and one male consort in 1970 which courted a female after her original mate broke a wing and eventually died, and which had a brood by her later the same season and two more the next.

Of the two females replacing collected birds, one was not seen until incubating her own eggs, so I do not know whether she was even exposed to the young of her eventual mate. The other female cared for the three nestlings of the male she courted after an interval of 5 days during which she provided them no services; she successfully nested with that male later in the season.

Assuming that the second female consort was not closely related to the young she aided (which is reasonable if outbreeding is favored), her behavior could be alternatively considered truly altruistic, reciprocally altruistic, or a reproductive error. I dismiss true altruism because her long hesitation in providing care suggests that she was not oriented toward aiding young so much as she was being reproductively primed by them. A truly altruistic bird could be expected to provide care immediately. Indeed, the stepwise hormonal preparation necessary for carrying out the successive stages of nesting in birds (*13*) is probably a proximate expression of ultimate selection for reproductive selfishness, making altruistic errors infrequent.

Reciprocal altruism (*4*) is a possible but unlikely explanation. It is considered because the female consort may have increased her chances of nesting by helping her prospective mate. Only three of the ten birds obtaining consorts had additional broods that year, and two of these had only three young in their original brood rather than the usual five or six. Even this small sample suggests the possibility that single birds with normal size broods either cannot or ordinarily will not attempt a second brood. Insofar as helping a prospective mate rear its young leads to successful future nestings more often than not, parental care by consorts might be favored provided it does not also exhaust the consort. But helping rear the young of other birds probably has little influence on their decision to renest because neither two of the three experimentally occurring consorts of 1972, nor the naturally occurring consort of 1970, all of which renested, provided care to the young of their prospective mates. Thus reciprocal altruism does not appear to play an important part in the occasional fostering of apparent nonrelatives in bluebirds.

Williams (*2*) considered cases similar to the behavior of the consort female as reproductive errors made possible by the unrewarded benefactor having had its own reproduction interrupted at a stage of nesting similar to that of the benefiting bird. Such interruption would place the bird in the proper hormonal state to be stimulated into misdirected parental behavior by the offspring of the aided adult. Paradoxically, selection to avoid altruism could occasionally almost inevitably result in altruistic error because at rare intervals a bird may be confronted with a concatenation of stimuli, more or less inducing it to provide parental care even though those stimuli emanate from other birds' young rather than its own, which otherwise always would be the case and would cause the bird to care only for its own young. That only one of 11 naturally and experimentally occurring consorts in 1970 and 1972 provided care, and that she hesitated 5 days before providing this care, suggests that altruistic behavior is rare and best interpreted as an occasionally inevitable reproductive error.

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References and Notes

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14. I thank R. D. Alexander, G. F. Estabrook, R. B. Payne, D. R. McCullough, and L. L. Wolf for support and advice during and after this work.

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Orientation of Gull Chicks Exposed to Project Sanguine's Electromagnetic Field

Abstract. *Birds tested on clear days in the normal geomagnetic field showed a significant clustering of headings about a predicted bearing corresponding with the direction of migration. Individuals tested when a large antenna was energized dispersed randomly. Magnetic fields associated with such conductors may be sufficient to confuse orienting birds.*

Publication of Yeagley's (*1*) findings almost three decades ago generated a continuing controversy regarding the possible existence of an avian ability to use geomagnetic cues for migrational orientation. Recently Keeton (*2*), Southern (*3*), Walcott (*4*), and Wiltschko and Wiltschko (*5*) have recorded changes in the direction-finding ability of pigeons (*Columba livia*), ring-billed gulls (*Larus delawarensis*), and European robins (*Erithacus rubecula*) when the birds are subjected to disturbances in the geomagnetic field, superimposed d-c fields (*6*), or simulated fields

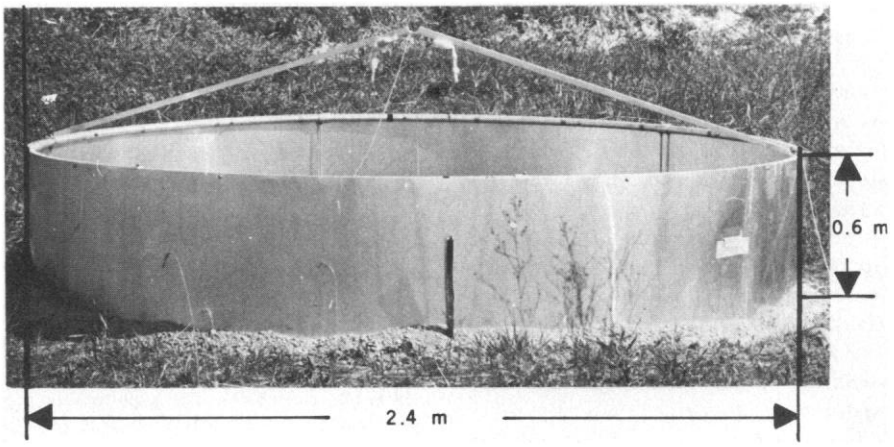

Fig. 1 Orientation cage.