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MALE RESPONSE TO APPARENT FEMALE ADULTERY IN THE MOUNTAIN BLUEBIRD (SIALIA CURRUCOIDES): AN EVOLUTIONARY INTERPRETATION

If a phenotypic trait has some genetic component, we can expect it to be selected so as to maximize the inclusive fitness of its possessor. Behavior—even complex social behavior—should be no exception, and indeed we might expect that the adaptive significance of animal behavior should be particularly apparent with regard to the constellation of reproductive and parental behavior shown by each species (Trivers 1972). Males, for example, should be strongly selected to avoid being cuckolded, thus ensuring that "their" females are not carrying strangers' genes. Predictably, this characteristic would be especially well developed among single-brooded, monogamous species and those in which males make a substantial investment in the success of their offspring. The present report describes one aspect of such behavior in the mountain bluebird, Sialia currucoides.

I studied mountain bluebirds at two nests in Mount Rainier National Park, Washington, during the summer of 1974. This species is double brooded where possible (Power 1974) but is apparently single brooded in alpine environments on Mount Rainier. The species is sexually dimorphic, with bright blue males and relatively drab, gray brown females. The two nests were 1 km apart in Berkeley Park, elevation 2,200 m. Both nests were located in small holes (probably made by woodpeckers) at 2 m height in krummholtz alpine fir (Abies lasiocarpa). I began observations while nests were being constructed, 11 and 9 days before egg laying, and continued until 2 days after hatching. In one case, the male attended the nest during brief absences by the female during incubation; members of each pair appeared to participate equally in provisioning the nestlings. The experimental treatment involved attaching a model male bluebird (a mounted study skin with wings slightly open and the feet at a 30° angle from the body axis) 1 m from each nest while the resident male was foraging, so that he encountered the model in proximity to his female upon returning. This treatment was continued at each nest for 2 consecutive days on three

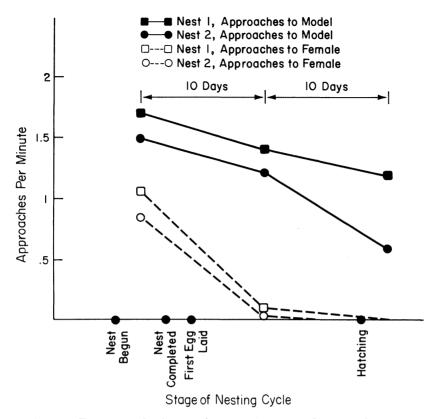


Fig. 1.—Frequency of resident-male approaches toward both model and mated female during first 10 min following male's return to nest. Each data point represents mean of 2-h observation periods on consecutive days (based upon data from table 1).

separate occasions, each set intersecting a different stage of the nesting cycle. In each case the model was removed 2 h after the male's return. Observations concentrated on the behavior of the male toward the model and toward his female during the first 10 min immediately following his discovery of the model.

An aggressive display of the mountain bluebird involves a 2–3-sec aerial hover 5–25 cm from another animal, with feet and bill oriented toward the other animal, while the bill is vigorously snapped and a staccato, high-pitched vocalization is occasionally uttered (Power 1966; and personal observation). When directed at another bird, it generally results in either retreat by the opponent or a brief aerial fight. The frequency of these approaches performed by the resident males during the initial 10 min of each observation period is presented in figure 1. The two males initially directed a high frequency of aggressive approaches toward both the model and their own mates. Although no direct physical contact was observed between the males and the models, on the second day of model exposure, the resident male at nest 1 pulled an undetermined number of primary feathers out of his mate's wing. Two days

later, this female was replaced by another female with whom the resident male successfully reared a brood. The second series of model exposures, 10 days later, was followed by a great reduction in aggressive approaches toward the mate (t test, P < .01) but an insignificant reduction in such approaches toward the model. The final exposure, another 10 days later, elicited no change in the previously low frequency of approaches to the female and a nonsignificant decrease in the previous high frequency of approaches toward the model. A significant decrease in approaches toward the model is apparent, however, when the initial and final series of exposures are compared (t test, P < .01). As a control for the effects of novelty upon the males' behavior, I presented a mounted male robin ($Turdus\ migratorious$) at each nest 4 days after the initial presentation of the bluebird model. No aggression was apparent from the males toward either this model or the females.

These results are consistent with the expectations of evolutionary theory. Thus aggression toward an intruding male (the model) would clearly be especially advantageous early in the breeding season, when territories and nests are normally defended. Since the availability of appropriate nest sites is a major factor limiting mountain bluebird populations (Miller 1970), a high level of male-male aggressiveness could well be related to nest-site scarcity and the resultant competition for this resource (Power, personal communication). The continuation of a relatively high level of aggression can be explained on a proximate basis by the operation of a releaser contained in the model and ultimately by the presumed advantage to reducing encroachment by strange males at any stage of the nesting cycle. The initial, aggressive response to the mated female is also adaptive in that, given a situation suggesting a high probability of adultery (i.e., the presence of the model near the female) and assuming that replacement females are available, obtaining a new mate would enhance the fitness of the male.

In this regard, it would certainly be desirable to know the actual availability of replacement females. Driving away a "suspected" female would be maladaptive if replacements were scarce; on the other hand, in an area of restricted nest-site availability (as Mount Rainier appears to be), surplus females might be present. The decline in male-female aggressiveness during incubation and fledgling stages could be attributed to the impossibility of being cuckolded after the eggs have been laid. In addition, animals inhabiting a high-elevation environment with a short growing season experience a rapid decline in the probability of successful renesting as the breeding season progresses, thus making it increasingly advantageous to remain with the original mate, despite the chance of having been cuckolded. Indeed, males are actually susceptible to being cuckolded only during a restricted period at the time of egg laying (Power, personal communication). It is at present uncertain to what extent natural selection will restrict male responsiveness to the precisely appropriate times.

On a proximate level, the possibility of habituation should be considered. However, the 10-day interval between test pairs should make the subjects unlikely to habituate, and in any case habituation would not in itself account

TABLE 1											
Approaches per M	MINUTE DURING	First	10 Min	OF EACH	OBSERVATION	PERIOD					

Approaches	NEST CONSTRUCTION		Incubation		FLEDGLINGS	
	Day 1	Day 2	Day 1	Day 2	Day 1	Day 2
To model:						
Nest 1	1.9	1.5	1.8	1.1	0.9	1.7
Nest $2 \dots \dots$	1.8	1.2	0.8	1.7	1.1	0.3
To female:						
Nest 1	1.4	0.8	0.1	0.1	0	0
Nest $2 \dots \dots$	0.6	1.0	0	0	0	0

for the distinction between male-model and male-female approaches on days 10 and 20. A slight reduction in both male-model and male-female approaches is apparent on the second of each pair of days (table 1); however, this tendency is neither consistent nor statistically significant.

Further work along these lines could employ live intruding males rather than models and is now being attempted by H. W. Power (personal communication). In addition, the response of the mated female might well be significant—sexual interest in the intruding male might be expected, but only if he increased the likelihood of her eggs being successfully fertilized and her offspring reared. Given a probable aggressive response by the mated male toward an adulterous female, it might also be adaptive for the female to vary her interest in a possible consort as a function of whether her mate is likely to find out! The female might also assess the prospects of cooperating with a stranger to oust the original territorial male (Power, personal communication), presumably as a function of the ultimate effects of such action upon the fitness of the female (relevant factors here would include the chances for success and the consequences of failure as well as the relative merits of the two males).

The responses of both male and female to model (and/or real) intruding females would also be worth examining. Again, many predictions could be made—the data are needed. In continuing the present paradigm, I hope to enlarge the sample and avoid possible confounding by exposing each subject only on 1 day (1, 10, or 20). Thus far, however, the results are consistent with an evolutionary interpretation. In addition, the term "adultery" is unblushingly employed in this letter without quotation marks, as I believe it reflects a true analogy to the human concept, in the sense of Lorenz (1974). It may also be prophesied that continued application of a similar evolutionary approach will eventually shed considerable light on various human foibles as well.

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CAN EVOLUTIONARY THEORY PREDICT?

Peters (1976) refers to evolutionary theory as a tautology and asserts its putative resultant inability to predict. The implications of such a view are grave. Popper (1974) has concluded from this same predictive incapacity that evolutionary theory is untestable and thus not a scientific theory at all; rather, according to Popper, it is a metaphysical research program. Prediction is crucial in Popper's verdict: "Thus Darwinism does not really predict the evolution of variety. It therefore cannot really explain it" (Popper 1974, p. 136). Mayr (1968, p. 50) agrees with Peters to the extent that evolutionary theory "can describe and explain phenomena with considerable precision, but it cannot make reliable predictions." Mayr is solely interested here in prediction of the future course of the evolution of species; selective attention prevents him from considering other possible kinds of neo-Darwinian prediction. This letter questions the conclusion of the above writers that evolutionary theory cannot predict.

In a paper in which frequent appeals are made to formal logical considerations, Peters (1976) uses the term "tautology" in a manner entirely different from that employed in formal logic. A tautology is technically defined as a statement "that excludes no logical possibilities" (Nagel and Newman 1958, p. 52), or, more precisely, as a statement that "is true on every truth-value assignment to its atomic components" (Leblanc and Wisdom 1972, p. 28). Peters's usage