EVOLUTIONARY ASPECTS OF PARENTAL BEHAVIOR: DISTRACTION BEHAVIOR OF THE ALPINE ACCENTOR

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Most animals that demonstrate parental care also engage in behavior that increases their offsprings' chances of survival when confronted by a predator, often at the risk of injury or death to the parent itself. Such "altruistic" parental behavior ranges from concealment and immobility to outright attacks upon the predator. In addition, many birds characteristically perform "broken wing" distraction displays in which the parent lures the predator away from the nest area by apparently feigning injury. Much of the early literature on this phenomenon has concerned controversy as to the motivational state of the animal performing the display (Armstrong 1949), leaving virtually untouched the ultimate questions of evolutionary interest. In fact, these behaviors provide ideal opportunities for analysis using the recently-described concept of "parental investment" (Trivers 1972). This paper describes the distraction behavior of the Alpine Accentor (*Prunella collaris*), suggesting an evolutionary interpretation for the observed pattern and for a general, hypothesized distinction between altricial and precocial species.

METHODS AND RESULTS

I studied two nests of the Alpine Accentor in Vanoise National Park, Savoie, France, during June and July, 1973. The nests were located on the ground in an alpine meadow, 150 m NE of Le Vallon (altitude 2400 m). Nest 1 contained 4 eggs when discovered on 19 June; all hatched between 7–8 July. Nest 2 contained 5 eggs when discovered on 21 June; 4 hatched between 9–10 July (the fifth never hatched). The Alpine Accentor responds to the presence of a human intruder by engaging in a conspicuous distraction display—the female characteristically flies from her nest, settles on the ground at some distance, and occasionally extends one or both wings, quivering them as though injured, often uttering a high-pitched repetitive call. During a series of daily tests, I approached each nest at a slow walk at the same time each day, wearing the same outer garments. I recorded the distance from me to the nest at which the display was elicited (flushing distance) and the distance from the nest at which the bird initially landed immediately prior to performing the display (settling distance). The results are presented in Figs. 1 and 2. Despite some day-to-day variability for each individual and considerable variation in the absolute values from nest to nest, the trend in

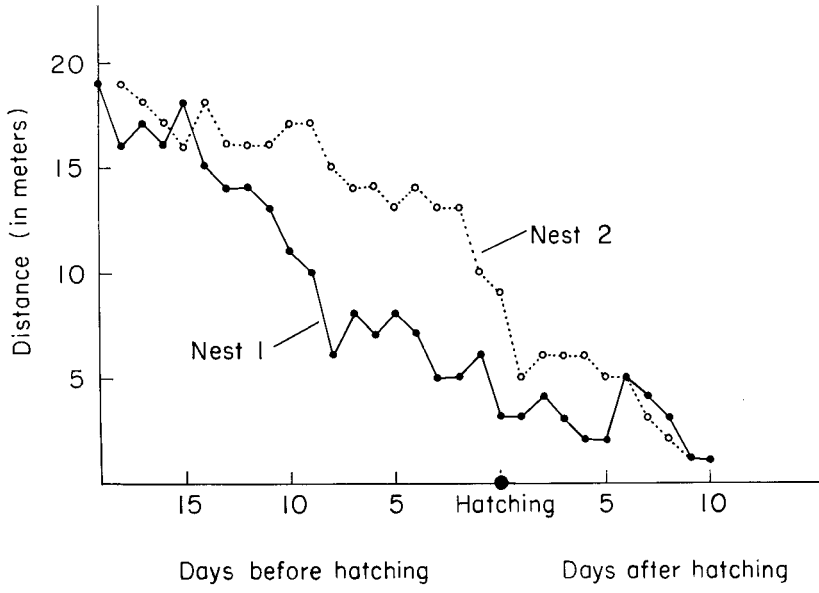

FIG. 1. Flushing distance of adult female Alpine Accentors as a function of clutch age.

both cases is for a progressive decrease in both flushing and settling distances continuing through hatching until observations were discontinued (both nests were destroyed by a red fox, *Vulpes vulpes*, on 18 July, approximately one week before fledging would have occurred).

I also categorized the initial responses of the female after settling as either type A—no wing extension, no threat; type B—one or both wings extended, no threat; or type C—one or both wings extended, threat exhibited. As used here, "threat" involves rapid opening and closing of the mandibles, often (but not necessarily) accompanied by vocalization. As with the decrease in flushing and settling distance described above, the transition from type A to C may be considered a progression of increasing intensity and conspicuousness, involving increased risk to the performer with a corresponding increase in the likelihood of successfully distracting a predator and thus saving eggs or nestlings. Table 1 reveals that as with settling and flushing distances, there is a progressive increase in display conspicuousness with increasing age of the eggs or nestlings. Thus, low initial frequencies of type C responses eventually increase, while high values of type A responses decrease with time. Dividing the sequence into 3 periods—19 to 10 days before hatching, 9 days before hatching to 1 day after, and 2 days after hatching to 10 days after—and combining the data for both nests in each period, I compared

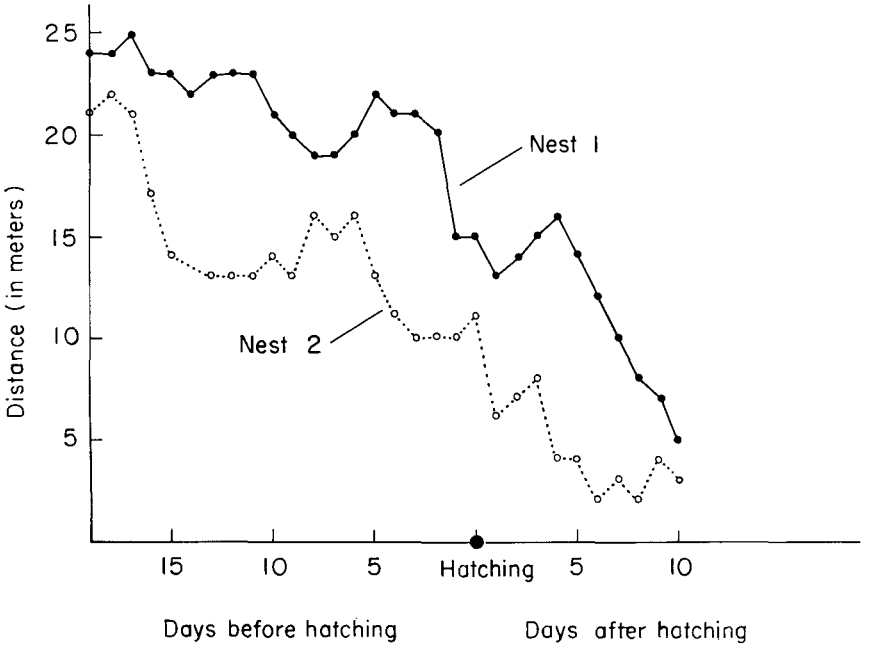

FIG. 2. Settling distance of female Alpine Accentors as a function of clutch age.

the observed frequencies of response types A–C with the frequencies that would be expected assuming equal representation of all 3 responses in each time period. A chi-square test demonstrated that the observed distribution deviated significantly from chance ($p < .01$).

DISCUSSION

Several workers have described a temporal pattern in avian distraction displays, all demonstrating increases in conspicuousness and intensity, peaking when the eggs hatch and declining thereafter (Simmons 1955, Stephen 1963, Gramza 1967). Armstrong (1956) and Gramza (1967) attributed this pattern to the increased conspicuousness of a nest with newly hatched young, reasoning that maximal efforts were required of the defending parent at that time. Armstrong (1956) went on to say that "It is broadly true that in passerines distraction display tends to be most intense when the young leave the nest, although exceptions occur, while in many other groups it is apt to be most accentuated about the time of hatching or when the young are a few days old."

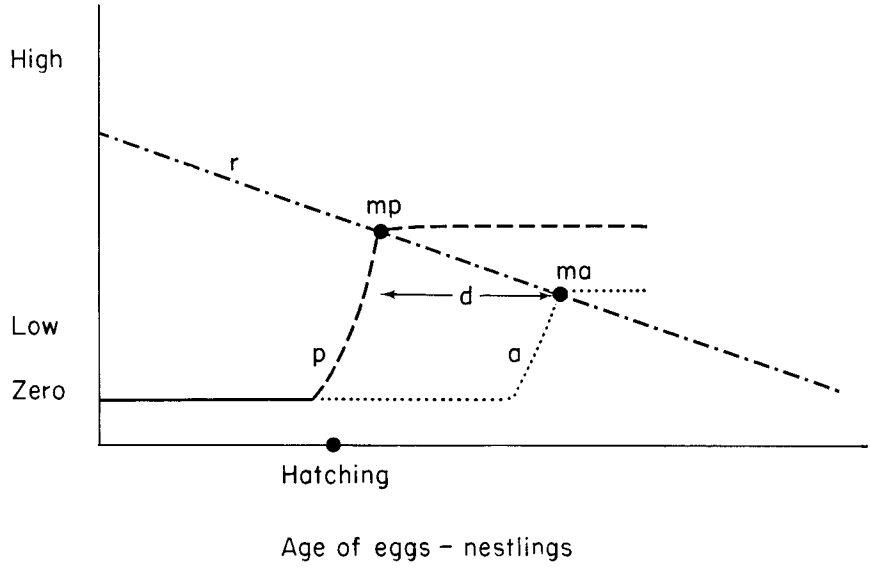

FIG. 3. Schematic representation of the relationship between evolutionary factors influencing distraction displays in precocial and altricial birds. r = probability of successful renesting by the parents; p = relative survival potential of precocial young in the absence of parental investment; a = relative survival potential of altricial young in the absence of parental investment; mp = maximum display by parents of precocial young; ma = maximum display by parents of altricial young; d = difference in time between maximum display by parents of precocial and altricial young. The sum of the ordinate values for "r" and either "p" or "a" at any age of the offspring represents the evolutionary return on the investment of parental distraction displays at that time. For precocial birds this sum is maximum shortly after hatching, while for altricial birds maximum return is received just before fledging.

Significantly, all of the above recent quantitative studies were concerned with non-passerine species having relatively precocial young, and all supported Armstrong's generalization by revealing an inverted U-shaped temporal pattern of display conspicuousness. My study involved a passerine, altricial species and demonstrated a different pattern, again consistent with Armstrong's generalization: display conspicuousness increased with increased age of the egg-nestling unit. This apparent difference in temporal patterning of display conspicuousness between precocial and altricial species may be interpreted as follows.

Trivers (1972) has defined "parental investment" as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence, reproductive success) at the cost of the parent's ability to invest in other offspring." Insofar as increased conspicuousness

TABLE 1

RESPONSE TYPES OF FEMALE *PRUNELLA COLLARIS* AS A FUNCTION OF AGE OF HER CLUTCH (SEE TEXT FOR DESCRIPTION OF CATEGORIES)

	Days Before Hatching																			Days After Hatching										
	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0	1	2	3	4	5	6	7	8	9	10
Nest 1	A	A	A	A	B	A	B	A	B	B	A	B	A	A	B	B	B	B	B	C	B	C	C	B	C	C	C	C	C	C	C
Nest 2	–	A	A	A	A	B	B	A	A	B	A	B	B	B	B	B	B	B	B	B	B	B	C	B	B	C	C	B	B	C	–

of a distraction display renders the performer more likely to be preyed upon while increasing the chances of its offspring's survival, performances of such behavior can be considered a form of parental investment. One might expect that the amount of such investment worth expending on any particular clutch would be to some degree a function of the amount already invested, and the older the egg-nestling unit, the greater parental investment it represents. This is especially true since the older the egg-nestling unit, the lower the probability of renesting by the parent whose distraction display was unsuccessful—perhaps because of insufficient conspicuousness (i.e., risk) by the defending parent. In effect, as their offspring grow older, even parents capable of renesting find their eggs increasingly placed in the one basket at hand. The parallel increase in display conspicuousness with increasing age of the offspring presented here for *Prunella collaris* is consistent with this interpretation.

But *P. collaris* is an altricial species, in which the chances that offspring will survive without parental assistance are virtually zero, with essentially no change until fledging. By contrast, shortly after hatching the offspring of precocial species have a finite chance of survival without parental assistance, and this survival potential increases rapidly within a few days. Thus, although young of precocial species resemble altricial young in that they represent accruing parental investment as they get older, this increasing investment is to some extent counteracted by their rapidly-acquired ability to survive without further parental investment.

Whereas the optimum time for maximum parental investment in altricial species should occur just before fledging, with progressive increases leading up to that maximum, the optimum time for maximum parental investment in precocial species should be just after hatching, when the young are old enough to represent a large investment, but not so old that they no longer benefit from further investment. As precocial young become increasingly mobile and able to secure their own protection, the ultimate parental risk involved in protecting them would exceed the return in protection received

and a progressive decline in such parental investment would therefore be expected (Fig. 3). The differing temporal patterns of distraction displays reported for precocial and altricial species thus conforms to the predictions of evolutionary theory, using the concept of parental investment as a guide.

Possible habituation of the animals to the experimenter must also be considered. However, it would not explain the differential responses of precocial and altricial birds here reported. In addition, the progressive increase in response intensity shown in Table 1 runs counter to the expected performance of habituating animals. Thorpe (1951) has suggested that rapid habituation to a potential predator would be clearly maladaptive, and Gramza (1967) has proposed that repeated withdrawal of a human intruder might actually reinforce distraction behavior, just as the normally-occurring withdrawal of an owl is believed to reinforce mobbing of chaffinches (Hinde 1954). Finally, the very complexity of the human stimulus configuration plus the 24 hour interval between exposures both probably mitigate further against habituation.

Many considerations must influence the particular behavior patterns demonstrated by each species and broad generalizations may be deceptive. For example, the renesting capability of each species would have a profound effect upon its strategy of optimum parental investment. This factor is currently being investigated.

SUMMARY

The distraction display of the Alpine Accentor, a ground-nesting altricial species, increases progressively in conspicuousness and risk to the parent as the egg-nestling unit grows older. By contrast, precocial species appear to reach maximum display intensity around the time of hatching with progressive declines thereafter. This difference in temporal pattern is consistent with an evolutionary interpretation of behavioral strategies serving to maximize return on "parental investment."

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