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Do Savannah Sparrows Commit the Concorde Fallacy?

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Summary. 1. The nest defense behavior of a tundra population of savannah sparrows (*Passerculus sandwichensis*) was examined to determine the relative importance of past investment and future prospects in determining the observed patterns.

2. A comparison of birds initiating nests at various times of the breeding season indicated that the change in renesting potential within a breeding season had little influence on the birds' behavior.

3. For a monomorphic, monogamous passerine the prospective reproductive success for males and females is expected to be quite similar. However, the respective patterns of nest defense behavior differed considerably (Figs. 1 and 2) and most closely reflected past investment. These results are discussed in light of parental investment theory.

Introduction

Trivers' (1972) discussion of the factors influencing the willingness of an individual to continue to invest in existing offspring at the expense of future offspring provided a framework for parental investment theory. More recently, Dawkins and Carlisle (1976) and Boucher (1977) have argued that contrary to Trivers' notion that an individual should act in a manner that will protect its past investments (the Concorde Fallacy of Dawkins and Carlisle), it is future expectations and their costs relative to continued investment in current offspring that will be the determining factor. "The past matters only insofar as it has created one's possibilities for the future" (Boucher, 1977). These arguments have also had recent support from Maynard Smith (1977).

The original aim of parental investment theory was to explain under what conditions mate desertion would be favored for either sex. Barash (1975) has

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shown that its usefulness may also be extended to explain parental defense of the young. Trivers (1972) treats such behavior as another component of a parent's overall investment in its young. However, such behavior can be considered different from other parental care in its predictability and its potential costs to the individual. While the energetic cost of nest defense is probably minor relative to nest building, egg laying, or feeding young, the potential for injury or death by exposing oneself to a predator will be relatively high. Defense behavior may therefore be viewed in the same light as desertion in that the same factors will influence the individual's decision on when such a course of action should be taken. Unlike desertion, however, it is a course of action that can vary in intensity and it is this potentially dynamic side of the behavior that may render it useful in the study of parental investment. The aim of this study is to examine nest defense behavior of savannah sparrows (*Passerculus sandwichensis*) in relation to both past investment and future potential.

Materials and Methods

The study was conducted at the Queen's University Tundra Biology Station, 40 km east of Churchill, Manitoba, on the coast of Hudson Bay. The 20 nests observed were part of a larger group being used for other studies and were selected so that nests from throughout the breeding season were represented. At each nest at least one member of the attendant pair was individually colormarked in order to distinguish the sexes. Observations began with clutch initiation and continued until either nest failure or fledging. A total of 169 trials were conducted.

It was assumed that the proximity of the observer to the nest represented a threat to the nest and that the magnitude of the threat was constant. For each trial, the nest was directly approached on foot and upon arrival the observer knelt within 1 m of the nest. Starting when the observer was in this position, a period of 2 min was allowed for the nest owners to respond. Response was defined as the observer being able to locate the bird either visually or from alarm calls. If a bird was frightened from the nest, which was usually difficult to determine as they moved away on the ground rather than by flying, a response was recorded only if the bird was seen or heard after having left. A bird responding within the 2-min period was observed for 60 s and the number of alarm calls recorded. When both parents were rapidly alarm calling it occasionally became necessary to count the total number of alarm calls and then assign them to individuals on the basis of their estimated relative calling rates. In addition to alarm calls, the closest, furthest, and modal perch distances were estimated with the mean of these three giving the mean distance estimate. A grid of stakes 50 m apart throughout the study area facilitated the estimation of distance.

The scoring of trials in which a bird did not respond proved difficult in the case of the mean distance estimate. If was felt that the lack of response was a meaningful indication of motivation but one that could not be readily quantified. For the purpose of graphical presentation, a distance estimate of 40 m was given, using the reasoning that the maximum distance estimate recorded for any responding bird was 30 m and any distance greater than 40 m would usually place the bird outside its territory. However, the arbitrary nature of this score precluded the distance data from most statistical analysis. Such analysis with distance scores of 40 omitted seemed equally questionable due both to the loss of information and the nonrandom distribution of the omitted scores with respect to the stage of nest development.

In order to determine the relative energetic costs by sex from rearing young, daily feeding observations from a blind were made at eight nests. Observation time averaged approximately 25 min per nest per day for the period of 2–8 days after hatching. Observations were made between 0800 and 1800 and the order in which nests were observed was varied regularly. Body weights of adult birds captured by mist net were recorded in order that weight loss might be used as another indication of the energetic costs of breeding.

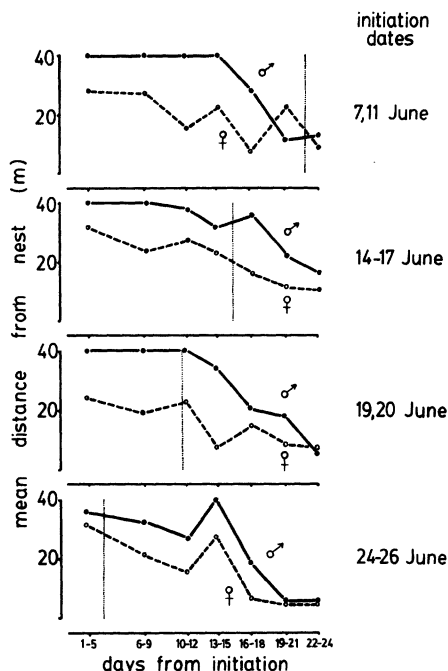


Fig. 1. Mean distance from the nest by parents when the nest was threatened. Vertical line represents the last date for renesting. Nonresponse scores (40 m) are included

Results

Figures 1 and 2 show the changes for males and females in mean distance from the observer and mean number of alarm calls, respectively, from the day of clutch initiation. Due to less frequent nest checks during laying and incubation the observations have been grouped into 3-day intervals from day 10 on only. The results for the first 9 days are presented in two groups, days 1–5, which is the initiation period, and days 6–9, the first 4 days of incubation. Since the most pronounced changes in behavior occur after this time, particularly in the case of alarm calls, it is felt that the larger time intervals early on do not greatly alter the outcome of the analysis.

The nests have been placed in four groups based on their clutch initiation dates to allow comparison on the basis of differential renesting potential. The vertical broken line represents the point at which renesting potential reaches zero and is the date on which the last of 64 clutches found was initiated. Due to the short breeding season at this latitude, renesting by birds losing nests to predators was observed only for early nesting birds losing nests early in the nesting sequence.

Multiple linear regression was used to determine the amount of variation in alarm calling accounted for by the stage of nest development (days from initiation) and the renesting potential. The respective R^2 values for the model for males and females were 0.45 and 0.49. The stage of nest development accounted for 11.8% of the variation explained by the model for males and 53.4% for females. The number of days after the renesting potential had reached

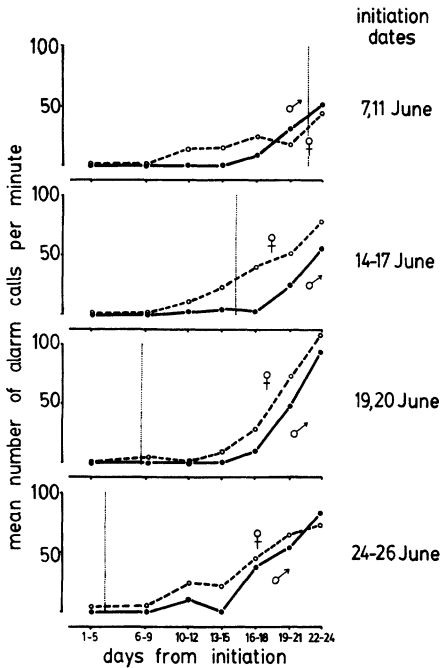


Fig. 2. Mean number of alarm calls by parents when the nest was threatened. *Vertical line* represents the last date for renesting

Table 1. Mean number of feeding visits per hour

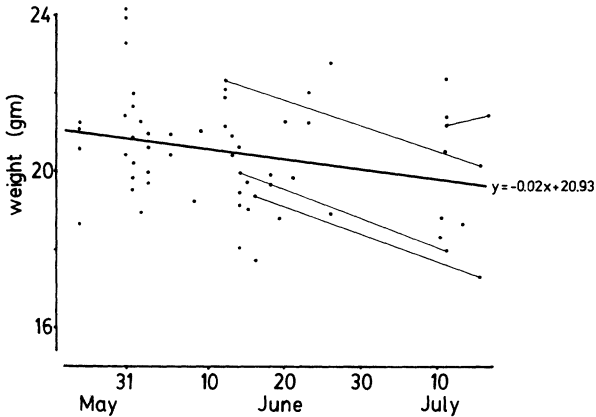
	Days from hatch							Overall mean
	2	3	4	5	6	7	8	
Male	2.0	1.0	4.3	6.3	6.7	7.2	10.5	5.76
Female	6.5	5.6	5.5	4.7	7.1	9.8	9.0	6.90
Time of observation (min)	120	150	230	240	230	160	200	

zero accounted for 85.7% of the variation for males and 44.1% for females. The number of days before the renesting potential had reached zero explained less than 3% of the variation for both males and females. Comparing male and female response directly, in all time periods females alarm called significantly more than males (Wilcoxon test; $P < 0.05$) and in all periods but days 22–24, females approached the observer more closely (Sign test; $P < 0.05$). In the latter analysis, a bird not responding was assumed to be further from the observer than one that did respond.

When conducting the feeding observations the movement of the birds was often too quick to be sure that food was being carried and therefore it has been assumed that any trip to the nest by a bird was a feeding visit (Table 1). Females made significantly more visits to the nest than males on days 2, 3,

Table 2. Mean time spent brooding per hour (min)

	Days from hatch						
	2	3	4	5	6	7	8
Male	0.0	0.0	0.4	3.1	0.0	0.0	0.0
Female	28.5	24.3	19.7	24.8	5.2	7.2	1.8

**Fig. 3.** Changes in male weight over the breeding season. *Fine lines* join two measurements of the same bird

and 7 as well as overall (Mann-Whitney U test; $P < 0.05$). On all other days the number of visits by males and females did not differ significantly.

Brooding was assumed to occur in any nest in which the bird remained at the nest for more than 1 min, since feeding and nest cleaning could both be accomplished in much less than 60 s. From the observations of feeding behavior, it is apparent that nearly all brooding is done by females (Table 2). It should be noted here that mist-netted males had brood patches from 50% to 75% the size of those of females. While checking nests, however, males were never flushed from incubating eggs and on only two occasions from brooding young.

The distribution of adult weights over the breeding season is presented in Figs. 3 and 4 for males and females, respectively. Male weight is significantly negatively correlated with the date of capture ($r = 0.24$, $P < 0.05$) with the regression giving a loss of 0.02 g per day. This equals a total loss of 5.1% of mean male weight during the period 24 May to 15 July. Changes in weight of individuals captured twice, indicated by fine lines joining two points, support the sign of the slope and suggest that its magnitude may be greater than that given by the regression line. Female weight appears to follow a different pattern from that of males. A regression from 1 June to 23 June gives a significant positive correlation with capture date ($r = 0.62$, $P < 0.01$). This increase in weight is probably attributable to follicle growth prior to and during egg laying. A regression excluding birds captured between 10 June and 25 June, the period

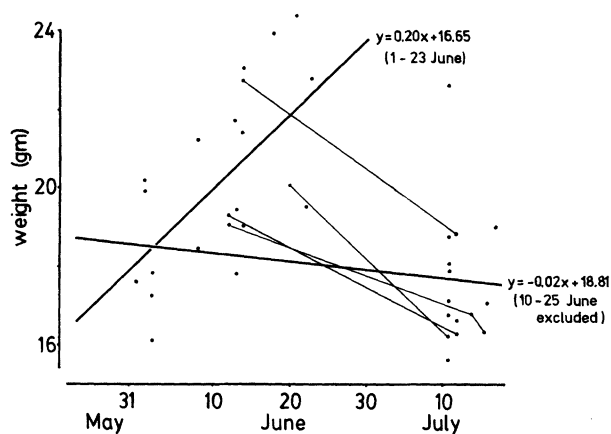


Fig. 4. Changes in female weight over the breeding season. *Fine lines* join two measurements of the same bird

during which 95% of all clutches found were initiated (Weatherhead, 1979), gives a negative correlation between weight and capture date. This correlation is not significant ($r=0.26$, $P<0.05$) but is based on a rather limited sample size. It is interesting to note, however, that the slope obtained is identical to that for males (-0.02 g/day) and in this case represents 5.8% of mean female body weight, again excluding weights taken between 10 June and 25 June.

Discussion

From Trivers (1972), Barash (1975), Dawkins and Carlisle (1976), and Boucher (1977), two general factors may potentially affect parental defense behavior at a given point in time. The first is the total investment to date. The second is the cost of continued investment balanced against the potential gain by successfully completing the current nesting attempt, relative to the cost of renesting. This latter cost will be strongly influenced by the potential for successfully renesting both within the breeding season and in future breeding seasons.

Barash (1975) suggests that renesting potential of the parents will have a 'profound effect' on their defense strategy. The importance of this factor should be indicated by the relative strength of response when renesting potential is zero. If it is of paramount importance one would expect a maximum response to be reached and maintained once this threshold is crossed. If renesting potential is of a least some consequence, then the expected pattern would be that, within a given population, later nesting birds should begin approaching maximum response levels sooner in the nesting sequence than those individuals nesting earlier. An examination of the data for both approach distance and alarm calling gives little evidence of such a trend. For neither males nor females was the number of days before renesting potential reached zero an important influence on their response. Rather, it was the stage of nest development and, particularly in the case of males, the number of days after renesting potential

was zero that explained most of the variation in defense behavior. It therefore seems that at least in this population the potential to renest had little influence on the defense strategy of the parents.

An examination of sexual differences in defense behavior indicated that females respond sooner than males with respect to the stage of nest development and that their response is nearly always stronger. In no case did male response significantly exceed female response. Other evidence to support these differences was found coincidentally in another study that was being conducted simultaneously. Eight males were removed within 2 days of their young hatching in order that unaided female performance could be assessed. In all eight cases females continued to feed young and did so at rates far exceeding those of normal females, thereby probably incurring serious costs energetically. Two instances were also observed in which males were left to care for the young alone; one due to removal of the female and the other due to female abandonment after being nest-trapped. In both cases the young were at least 2 days old. Within 24 h (when the nests were revisited) all the young had died. Both males were still on their territories but behaviorally had changed from nest defense to territory advertisement. One interpretation is that the males abandoned their young when 'deserted' by the female, in spite of their being both physiologically (as evidenced by brood patches) and behaviorally capable of brooding and feeding young. Although no observations were made to determine whether only females brood the young at night, were this the case then males may lack the behavioral flexibility to assume this role. Only one night without brooding would certainly be sufficient to kill young nestlings and therefore this result might not be a true reflection of the male's response to desertion. Welsh (1975) reports an observation of a male savannah sparrow rearing a brood alone. However, his mate did not disappear until the fifth day after hatching, by which time brooding is much reduced (see Table 2).

A possible basis for the difference in behavior between males and females could be that males have a much higher probability of successfully reproducing in the future. Future here would have to refer to future breeding seasons, since in a monogamous population with very limited renesting potential within seasons the latter would be essentially equal for males and females. To explain the difference in defense response and possibly abandonment behavior in terms of future reproduction requires a substantial difference in longevity between the sexes. One should then expect differences in return rates and sex ratios. In the case of return rates, one must assume that there is either no emigration or equal emigration of both sexes. The strong site tenacity by returning birds of both sexes in this population as well as similar observations from another population (Stobo and McLaren, 1975) suggest that the assumption of no emigration is not unreasonable. Several estimates of return rates are available from birds banded in 1976. For all birds banded, 22 of 39 (56%) males and 8 of 25 (32%) females were resighted or recaptured in 1977. However, considering only birds whose nests were known in 1976; 12 of 23 (53%) males and 8 of 23 (35%) females had known nests again in 1977. Females are very secretive (also see Potter, 1972), except when defending a nest, while males are much more obvious due to territorial advertisement prior to nest defense. This renders

females more difficult to resight except at a nest and is borne out by the fact that of the 8 females resighted in 1977, all 8 had known nests while the same was true for only 12 of 22 males.

If males live longer than females a large unmated male population should exist. Over 2 years 65 territories were accurately mapped and well searched for nests (Weatherhead, 1979). In only five (7.7%) of these were no nests found and in several cases it was suspected that this reflected an inability to locate a well-concealed nest rather than the male being unmated. In general then it seems that if males live longer than females in this population, the difference is not large enough to explain the observed behavioral differences.

Dawkins and Carlisle (1976) and Boucher (1977) have convincingly argued that expected returns rather than the amount invested should determine further parental investment. In a monogamous population both members of a pair have an identical expected return from their nest. Given an equal and low likelihood of renesting within a breeding season and a limited number of future breeding seasons for both members of a pair one would expect that, overall, males and females should be equally willing to risk themselves in defense of a nest. However, the observed patterns more closely reflect the respective past investment by each sex. The data on weight change indicate that, overall, a female's costs are slightly higher, particularly as some of the energy expended by males will certainly go toward activities such as attempting to court other females and therefore have nothing to do with the male's nest. This difference in investment is similar to the overall difference in the degree and number of risks taken by males and females in defense of the nest.

An examination of the timing of investment relative to defense response further points to a strong correlation between the two. Male investment in the nest is not substantial until the eggs hatch and he begins feeding nestlings, approximately 15–16 days from initiation. It is at about this time that males begin to respond consistently to the presence of an observer at the nest. Male response was strongly correlated with the number of days after renesting potential had reached zero and, for the majority of nests, this period coincides with the nestling stage; 11 of 20 nests (55%) reached zero renesting potential between 13 and 16 days after initiation. Females, on the other hand, have already accumulated a substantial investment by day 15 and have also been responding to the observer from the time of initiation. Given similar absolute investment from hatch to fledging, the males' investment relative to that of females is higher for that period since, unlike females, males have little previous investment. That the increase in the male's defense response is faster than the female's from hatch to fledging further indicates that response is governed by investment.

It appears difficult to reconcile these results with the apparently sound arguments presented by Dawkins and Carlisle (1976) and Boucher (1977). Resolution of this paradox may lie in an examination of an assumption implicit in parental investment theory. It is never questioned that animals must possess a very acute innate ability to weigh a number of factors pertaining to future events in order to behave in an optimal manner. The decisions of when and how much to invest or when to desert must be based on how much has been invested relative to expected costs of continuing or renesting, balanced by the probability

that a new nest would be successful and the expected number of nestings attempts available in an individual's lifetime. These factors will vary with the age and condition of the individual, through the breeding season, and from one breeding season to another. This alone suggests the need for a sophisticated analytical ability. However, add in a high degree of unpredictability for some of the factors and the problems may be insurmountable. While this is an admittedly anthropomorphic view of the situation, the theory appears to demand it.

At high latitudes such as the location of the present study, the quality and duration of the breeding season will be quite variable one year to the next and can even change rapidly within one season. As well, the predictability of survival for a small passerine migrating considerable distances is probably quite low. Given all these problems, the most reliable way an individual can assess future gains may be by direct feedback from past investment. The more that an individual invests in a nest, the greater will be the expected returns. To base defense behavior entirely on past investment seems inefficient but unless an individual can accurately assess future costs and benefits it may be the most likely way for selection to operate in determining parental investment. If this hypothesis is valid, the degree to which parental defense behavior deviates from that predicted solely by past investment will be directly correlated with the predictability of future events.

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