

Seasonal patterns of nest defence by Baird's sandpipers

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Parental Baird's sandpipers increased the intensity of their nest defence through the incubation period. One member of each pair was relatively tame, staying closer to the human "predator" and engaging in more risky behaviours than the other, but both parents increased risk taking as the incubation period progressed. Members of this High Arctic population had little potential for renesting during the short breeding season. There was also apparently no change in either predator persistence or nest conspicuousness during the incubation period. Thus none of these factors can explain the seasonal increase in nest defence. We conclude, therefore, that the observed pattern was most likely due to a decrease in the relative difference between the probabilities of parent and offspring survival as predicted by a recent model.

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Les bécasseaux de Baird qui avaient des petits ont augmenté l'intensité de leur comportement de défense du nid au cours de la période d'incubation. Dans chaque couple, l'un des membres s'est avéré relativement peu farouche: il restait plus près du "prédateur" humain et manifestait des comportements plus risqués que son partenaire, mais les deux parents se sont mis à prendre plus de risques à mesure qu'avancait la période d'incubation. Les oiseaux de cette population du Haut-Arctique avaient peu de chance de refaire un nid durant la courte saison de reproduction. Il n'a pas semblé se produire de changement dans la persistance des prédateurs ou la visibilité du nid au cours de la période d'incubation. Aucun de ces facteurs ne peut donc expliquer l'augmentation du comportement de défense observée au cours de la saison. Ce phénomène est probablement dû à une augmentation de la différence relative entre la probabilité de survie des parents et celle des oisillons telles qu'établies selon un modèle récent.

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Introduction

Naturalists have long known that the intensity of nest defence by parent birds increases with the age of their offspring (Simmons 1955; Armstrong 1965). The earliest attempts to explain the adaptive significance of such seasonal patterns of risk taking invoked the increasing vulnerability of the offspring due to an increase in either nest conspicuousness (Gramza 1967) or predator persistence as the young or eggs get older (Greig-Smith 1980). Thus parents are expected to take more risks as the immediate needs of offspring for protection increase. More recent explanations, however, have all relied on parental investment theory (Trivers 1972), which states that the optimal level of risk expended by a parent on its current brood depends not only on the increased probability of survival of those offspring but also on the concomitant reduction in the parent's ability to invest in other (e.g., future) offspring. Thus a change in nest defence behaviour would be expected even if there was no change in either nest conspicuousness or predator persistence.

Two models based on parental investment theory have been proposed to explain this seasonal increase in risk taking by parent birds. Barash (1975) suggested that, as the nesting season progresses, the diminishing potential for a successful renesting should increase the value of the current brood to the parents because the probability of future reproductive success within that season declines. Andersson et al. (1980), on the other hand, suggested that offspring increase in value simply because the difference between the probabilities of parent and offspring survival decrease with offspring age. As a result, optimal risk taking should increase with offspring age, regardless of the parents' potential for successful renesting in the same season.

Although both models predict an increase in risk taking with offspring age, it would be useful to know whether they can both account for patterns observed in nature. In several species, the probability of offspring survival to independence appears to have an effect on the intensity of nest defence (Andersson et al. 1980; Greig-Smith 1980; Barash 1980). However, no studies to date have examined whether the increasing probability of offspring survival alone could account for the seasonal pattern of nest defence. This could be done by controlling the effects of renesting potential and nest conspicuousness on risk taking (see Weatherhead 1979).

In this paper we describe the seasonal patterns of nest defence behaviour in Baird's sandpipers (*Calidris bairdii*) nesting in the High Arctic. This species allows a clear test of the model by Andersson et al. (1980), since the alternative hypotheses for nest defence behaviour can be eliminated *a priori*, based on the following arguments.

(i) The probability of renesting in Baird's sandpipers is negligible as soon as incubation begins. In four summers of fieldwork in the High Arctic, we have never observed a successful renesting by Baird's sandpipers (or any other shorebird species). Avian nesting is typically highly synchronized at our field site (Montgomerie et al. 1983) and late nesters were easily detected. All but 1 of 24 Baird's sandpiper nests observed in 1981–1984 had completed clutches within 3 days of the median date in any year (Fig. 1). The only outlier (5 July 1981) was probably the only renesting instance we have observed, and all of the young in that nest died during a storm on the day they hatched (26 July). The high degree of synchrony in clutch completion dates within years strongly supports our assumption that the probability of successful renesting, after initial clutch completion, is negligible. Norton (1973) also found no evidence of renesting at Barrow, Alaska.

The negligible renesting potential in this species can readily be accounted for by the relatively short High Arctic growing

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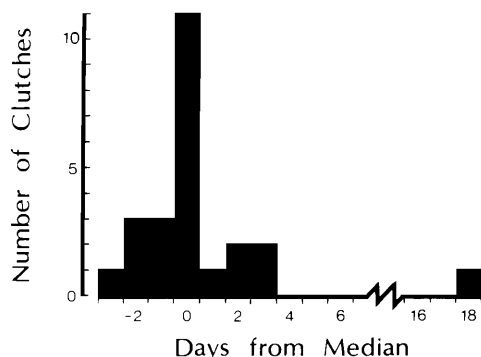


FIG. 1. Clutch completion dates of Baird's sandpipers relative to the median each year. Median dates were 17, 24, 16, and 22 June for the years 1981–1984, respectively.

season and the high costs of egg production. At our study site, the entire period available for pairing, nesting, and raising young to fledging is <60 days (Montgomerie et al. 1983). Since the minimum time required from laying to fledging in Baird's sandpipers is about 45 days (Parmelee et al. 1967) following a 1-week pairing period (unpublished data), there is little time for renesting even if a clutch is lost early in the incubation period. Based on our sample of clutch completion dates, it is clear that even the earliest nesting bird losing its clutch on the day of clutch completion would have only 3 days to begin a new clutch and have it completed within the observed egg-laying period (Fig. 1). Most important, both the relative clutch mass (117% of female body mass) and energy content of eggs (7.61 kJ/g) in Baird's sandpipers are among the highest known in birds (Walsberg 1983). Thus, the energy costs of renesting would be very high, especially considering the time constraints and the need to replace energy lost during the initial nesting attempt.

(ii) Nest conspicuousness and predator persistence can also be excluded as variables influencing nest defence behaviour by Baird's sandpipers. Nest conspicuousness remains constant, since offspring leave the nest immediately upon hatching and parent incubation patterns do not vary at least until the day before hatch (Norton 1972). Vegetation changes, potentially affecting nest visibility, are also minimal in the nesting habitat. Predator persistence was kept constant in this study by using a human "predator."

Thus any increase in nest defence during the incubation period of Baird's sandpipers is probably due to the increasing probability of offspring survival relative to that of the parents (Andersson et al. 1980). This study constitutes the first explicit test of this model.

Methods

Our study site was at Sarcpa Lake, Melville Peninsula, Northwest Territories, Canada (68°33' N, 83°19' W) where Baird's sandpipers are one of the common breeding birds (about 7 pairs/km²; Montgomerie et al. 1983). Baird's sandpipers return to this site as soon as the snow begins to melt in early June (Montgomerie et al. 1983). The breeding activities of all pairs are quite synchronous, with egg laying completed by the last week of June and hatching occurring during the middle 2 weeks of July. Males and females share equally in incubation duties except that males appeared to incubate more than females for the first day or two (unpublished data). Young fledge and begin southward migration in late July and early August.

Predators of sandpiper nests at Sarcpa Lake were mainly arctic fox (*Alopex lagopus*), long-tailed jaegers (*Stercorarius longicaudus*), ermine (*Mustela erminea*), and arctic ground squirrel (*Citellus*

parryi). All but ground squirrels also prey on adult birds. In our study area, predation accounted for the loss of 5 of 25 (20%) Baird's sandpiper nests whose fate was known (data from 1981–1984). In other parts of their range, predation pressure can be more intense; Norton (1973) reported a 44% nest predation rate for Baird's sandpipers over 4 years in Alaska.

This study was done in 1982 when we conducted tests on 10 pairs during the breeding season. To distinguish individuals, one member of each pair was marked early in the incubation period. In most cases, a bird was marked while it was incubating by spraying a spot of permanent yellow dye (picric acid) on its breast. The sprayer was set within 4 cm of the nest and was controlled from a blind about 10 m away. This technique was used instead of colour-banding to minimize desertion by the birds as a result of handling and also to keep both members of a pair equally inexperienced with humans, since a person was later used in experiments to simulate a predator. There were two exceptions to this protocol: in pair 9, which was found at a later stage of incubation, both members were individually colour banded before any tests were done, and in pair 10, one adult was banded before testing. Neither of these pairs behaved differently from the others.

Because we used a plumage dye rather than colour bands, identification of individuals was only possible at close range. This hindered our ability to sex most marked individuals by their behaviour, but we did positively identify three males by their territorial activities early in the season. Most adults were banded and measured just before hatch, but the large overlap in male and female size (Prater et al. 1972) prevented sexing by measurements.

Experiments

In our experiments, a person was used to simulate a predator for several reasons. In 1981 we observed that our presence near Baird's sandpiper nests elicited particularly vigorous distraction displays. Thus this species, like many others (Barash 1975; Andersson et al. 1980; Greig-Smith 1980; Wiklund and Stigh 1983), appeared to respond to humans as potential predators. A predation attempt or trial consisted of an observer (the "predator") slowly approaching the nest (about 1 m/s) beginning at a distance of 60–100 m and ending about 1.5 m from the nest where the observer remained until the end of the trial. The starting point was the same for all trials at a given nest and was chosen so that the observer could see most of the area around the nest during a trial. All trials were conducted by the same observer wearing the same clothing.

Each trial lasted 5 min and began when the observer left the starting point. At 5-s intervals (timed with a metronome), the behaviour of the "on duty" bird and the number of each vocalization (Alarm, Breep made during the preceding interval were recorded (see Table 1 for behaviours observed). The distance from the bird to the observer was also estimated at each 5-s interval. Flush Distance was determined by dropping a marker at the moment of flushing the incubating bird and measuring the distance from the marker to the nest after the trial.

We tested most birds at 3- to 7-day intervals (mean = 4.9, SD = 1.7, range 2–10). One bird was tested five times during incubation but all others were tested four times or fewer. For a given individual, trials were usually conducted at approximately the same time each day (± 2 h). Because the nest-attendance schedules of the male and female within each pair were relatively consistent throughout incubation, we could usually predict which individual would be on the nest at a given time of day. This helped us to avoid testing individuals more often than we had scheduled.

In 12 of 82 trials we noticed the presence of another Baird's sandpiper in addition to the bird "on duty" (see Drury 1961 for a similar observation). Two of these 12 birds simply watched silently, 5 gave a few Alarm calls, and the remaining 5 performed a few distraction displays, all from a distance. Thus nest defence was performed only by the "on duty" bird each time and mate protection does not appear to be one of the functions of nest defence in this species (cf. Shields 1984).

Analysis

Following previous workers, we assumed that displays resulting in

TABLE 1. Changes in behaviour and distance variables between early and late halves of the incubation period of Skittish and Tame birds. The number of birds for which each variable increased or decreased is shown

	Skittish		Tame	
	Increase	Decrease	Increase	Decrease
Risky behaviours				
Crouched Run	1	2	2	4
Rodent Run	3	1	5	5
Squat	3	1	4	3
Flutter-attack	0	0	6	* 1
Other behaviours				
On Nest	6	3	2	7
Stand	1	5	1	2
Alert	4	3	4	6
Run	4	4	6	4
Fly	2	* 5	5	4
Displacement	2	4	3	2
Out of Sight	6	3	3	2
Vocalizations				
Alarm Calls	7	* 1	5	5
Breep Calls	4	2	4	2
Distances				
Flush Distance	1	* 7	4	6
Distance to predator	3	6	6	4
No. of birds tested	9		10	

NOTE: For some birds there was no change in the frequency of a variable between early and late halves of the incubation period (not shown). Displacement includes feeding and preening.

* $P < 0.05$; Wilcoxon matched-pairs signed ranks test, one-tailed.

the parent being closer to, or more visible to, the predator were riskier (Curio 1975; Barash 1975; Weatherhead 1979; Andersson et al. 1980; Siegelmann and Curio 1983; Buitron 1983). We also assumed that there is a positive relation between the intensity of nest defence behaviour and riskiness such that a behaviour is more risky (by the preceding definition) if it is performed more frequently. Thus, Flutter-attack was probably the most risky behaviour because the bird leapt aggressively at the observer from close range (< 2 m). The distraction behaviours (Crouched Run, Rodent Run, and Squat; see Simmons 1955 and Gochfeld 1984) were also risky because they drew attention to the displaying parent and were usually performed relatively close to the predator. On Nest was an increasingly risky behaviour as the predator moved toward the nest and this usually resulted in shorter Flush Distances. All other behaviours were considered less risky because they were usually performed at some distance from the predator and they did not tend to draw attention to the parent.

Baird's sandpipers often made Alarm Calls when performing non-risky behaviours. These were two-note vocalizations ("toowee"; see also Drury 1961) that we could hear up to 200 m away. Since these vocalizations would attract the attention of predators, they were also risky. In addition, the birds made Breep Calls, low trills that could not be heard from more than 50 m. We considered these less risky than Alarm Calls because they were much harder to hear at a distance.

Since the members of each pair exhibited distinctly different intensities of nest defence, we identified these as "Tame" and "Skittish" individuals. Tame birds spent more time < 10 m from the observer once they left the nest, and gave more Alarm Calls than Skittish birds. Skittish birds left the immediate nest area when disturbed and often watched the observer silently from a distance. The three birds positively identified as males were Tame, so it is possible that all Tame birds were males and Skittish birds were females (see also Gochfeld 1984). Since all individuals studied could be readily assigned to one of these two categories, we analyzed Tame and Skittish birds separately.

In all cases one-tailed significance tests were used because we were testing the hypothesis that risk taking increases during the incubation

TABLE 2. Percent of time spent in risky behaviours (Crouched Run, Rodent Run, Squat, and Flutter-attack) during experimental trials in early (E) and late (L) halves of the incubation period

Pair	Skittish		Tame	
	E	L	E	L
1	0	0	35	8
2	0	0	5	26
3	23	13	75	6
4	0	0	58	59
5	13	24	9	0
6	3	36	15	33
7	—*	16	38	47
8	8	62	2	22
9	0	0	7	25
10	75	0	18	61
Mean	13.2	15.0	26.2	38.4

*The Skittish member of pair 7 was not tested in the early half of the incubation period and is not included in the calculation of the mean.

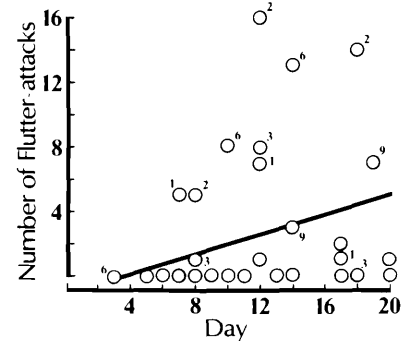


FIG. 2. Seasonal patterns of Flutter-attacks by Tame birds during the incubation period. Some pairs are numbered as in Table 2 to show intraindividual variation. Trend lines were fitted by Bartlett's three-group regression (see Sokal and Rohlf 1981, p. 551).

period. We initially looked for correlations between each variable and day of incubation, using Kendall's coefficient of rank correlation (τ). However, because there was considerable interindividual variation in behaviour (Reid and Montgomerie, unpublished manuscript), we also analyzed each individual separately, simply scoring whether the mean score for each variable increased or decreased between first and second halves of the incubation period (days 1–11 and 12–21, where day 1 is the day after clutch completion). We then determined whether a significant proportion of the individuals changed behaviour using the Wilcoxon matched-pairs signed ranks test (Siegel 1956, p. 75).

Results

Both members of each pair performed some risky behaviours (distraction displays or Flutter-attacks; Tables 1, 2) and (or) Alarm Calls, but there were few clear seasonal changes in the frequency of any behaviour or vocalization during the experimental trials. Tame individuals were characterized by relatively intense nest defence (Table 2), with a seasonal change in riskiness due mainly to a significant correlation between the frequency of Flutter-attack and day of incubation ($\tau = 0.25$, $P = 0.04$, $n = 33$; Fig. 2), and a significant increase in the frequency of this behaviour between early and late halves of the incubation period (Table 1). Since Flutter-attack was the most risky behaviour, this seasonal pattern indicates an important

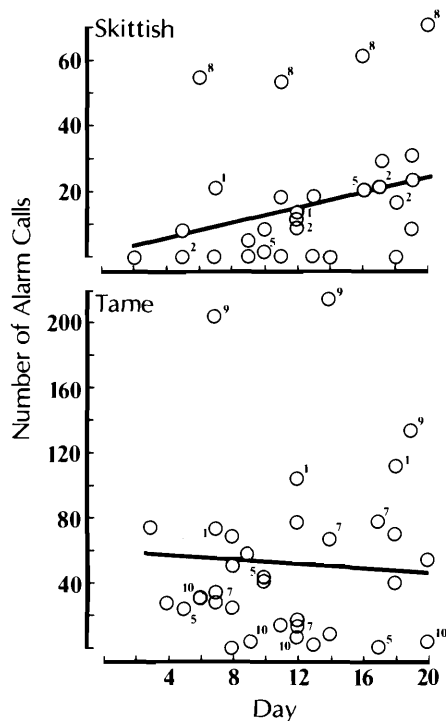


FIG. 3. Seasonal patterns of Alarm Calls by Skittish and Tame individuals during the incubation period. Trend lines were fitted as in Fig. 2.

increase in risk taking, despite considerable interindividual variability (Fig. 2).

Skittish birds, on the other hand, never engaged in as much distraction display as Tame birds (Table 2), and none of the changes in risky behaviours were significant (Table 1). However, Alarm Calls increased significantly with day of incubation ($\tau = 0.37$, $P = 0.0008$, $n = 32$; Fig. 3), and a significant proportion of the birds decreased in Flush Distance and increased the number of Alarm Calls between early and late halves of the incubation period (Table 1).

The mean time spent in all risky behaviours together also increased from early to late halves of the incubation period for both Tame and Skittish birds. Although these trends were not significant, possibly because of small sample sizes, they corroborate our findings based on the individual variables.

Discussion

Our experiments showed that both Tame and Skittish Baird's sandpipers increased the intensity of their nest defence behaviour through the incubation period. Although there was considerable variability among individuals (see Table 2 and Figs. 2, 3), some of the trends toward increased risk taking were statistically significant (Table 1). Moreover, there were no significant trends that could be interpreted as a decrease in risk taking through the incubation period (Table 1 and correlation analyses). Since other explanations for a seasonal increase in nest defence were ruled out *a priori* (see Introduction), we conclude that the model of Andersson et al. (1980) best explains this pattern of nest defence. Thus the optimal level of risk taking by parents in defence of their offspring increases because the probability of offspring survival during incubation increases faster than that of the parent.

The seasonal change in nest defence behaviour of Baird's sandpipers seems to be less pronounced and less consistent

among individuals (see Table 2 and Figs. 2, 3) than that described for other species (Curio 1975; Greig-Smith 1980; Weatherhead 1979; Lemmetyinen 1971) using similar methods and based on sample sizes comparable to ours. Although interspecific comparisons must be made with caution, this may indicate that reneating potential (Barash 1975) has a much larger effect on risk taking than the changing relative probabilities of parent and offspring survival (Andersson et al. 1980). Intraspecific comparisons may shed more light on the relative importance of these two variables. In a preliminary study of two subspecies of white-crowned sparrow (*Zonotrichia leucophrys*), for example, Barash (1980) showed that an observed difference in the intensity of nest defence was related to the difference in their reneating potential; individuals with little reneating potential took more risk.

In conclusion, we showed that the model of Andersson et al. (1980) can explain seasonal increases in nest defence behaviour. Its importance relative to other hypotheses (reneating potential, nest conspicuousness, predator persistence) explaining changes in risk taking by parent birds remains unknown and warrants further investigation.

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- ANDERSSON, M., C. G. WIKLUND, and H. RUNDGREN. 1980. Parental defence of offspring: a model and an example. *Anim. Behav.* **28**: 536–542.
- ARMSTRONG, E. A. 1965. Bird display and behaviour: an introduction to the study of bird psychology. Dover, New York.
- BARASH, D. P. 1975. Evolutionary aspects of parental behavior: distraction behavior of the alpine accentor. *Wilson Bull.* **87**: 367–373.
- . 1980. Predictive sociobiology: mate selection in damselfishes and brood defense in white-crowned sparrows. In *Sociobiology: beyond nature/nurture?* Edited by G. W. Barlow and J. Silverburg. AAAS Selected Symposium No. 35. Westview Press, Boulder. pp. 209–226.
- BUITRON, D. 1983. Variability in the responses of black-billed magpies to natural predators. *Behaviour*, **87**: 209–236.
- CURIO, E. 1975. The functional organization of anti-predator behaviour in the Pied Flycatcher: a study of avian visual perception. *Anim. Behav.* **23**: 1–115.
- DRURY, W. H., JR. 1961. The breeding biology of shorebirds on Bylot Island, Northwest Territories, Canada. *Auk*, **78**: 176–219.
- GOCHFELD, M. 1984. Antipredator behavior: aggressive and distraction displays of shorebirds. In *Behavior of marine animals: current perspectives in research*. Vol. 5. Shorebirds. Breeding behavior and populations. Edited by J. Burger and B. L. Olla. Plenum Press, New York. pp. 289–377.
- GRAMZA, A. 1967. Responses of brooding nighthawks to a disturbance stimulus. *Auk*, **84**: 72–86.
- GREIG-SMITH, P. W. 1980. Parental investment in nest defence by stonechats (*Saxicola torquata*). *Anim. Behav.* **28**: 604–619.
- LEMMETYINEN, R. 1971. Nest defence behaviour of common and arctic terns and its effects on the success achieved by predators. *Ornis Fenn.* **48**: 13–24.

- MONTGOMERIE, R. D., R. V. CARTAR, R. L. MCLAUGHLIN, and B. LYON. 1983. Birds of Sarcpa Lake, Melville Peninsula, Northwest Territories: breeding phenologies, densities, and biogeography. *Arctic*, **36**: 65–75.
- NORTON, D. W. 1972. Incubation schedules of four species of Calidridine sandpipers at Barrow, Alaska. *Condor*, **74**: 164–176.
- . 1973. Ecological energetics of Calidridine sandpipers breeding in northern Alaska. Ph.D. thesis, University of Alaska. Fairbanks.
- PARMALEE, D. F., H. A. STEPHENS, and R. H. SMITH. 1967. The birds of southeastern Victoria Island and adjacent islands. *Natl. Mus. Canada Bull. No. 222*. pp. 1–229.
- PRATER, A. J., J. H. MARCHANT, and J. VUORINEN. 1972. Guide to the identification and ageing of holarctic waders. *British Trust for Ornithology, Field Guide* 17.
- REGELMANN, K., and E. CURIO. 1983. Determinants of brood defence in the great tit *Parus major* L. *Behav. Ecol. Sociobiol.* **13**: 131–145.
- SHIELDS, W. M. 1984. Barn swallow mobbing: self-defence, collateral kin defence, group defence, or parental care? *Anim. Behav.* **32**: 132–148.
- SIEGEL, S. 1956. *Nonparametric statistics for the behavioral sciences*. McGraw-Hill, New York.
- SIMMONS, K. E. L. 1955. The nature of the predator-reactions of waders towards humans; with special reference to the role of the aggressive-, escape- and brooding-drives. *Behaviour*, **8**: 131–173.
- SOKAL, R. R., and F. J. ROHLF. *Biometry*. 2nd ed. W. H. Freeman and Co., San Francisco.
- TRIVERS, R. L. 1972. Parental investment and sexual selection. *In* *Sexual selection and the descent of man*. Edited by B. Campbell. Heinemann, London. pp. 136–179.
- WALSBERG, G. E. 1983. Avian ecological energetics. *In* *Avian biology*. Vol. 7. Edited by D. S. Farner, J. R. King, and K. C. Parkes. Academic Press, New York. pp. 161–220.
- WEATHERHEAD, P. J. 1979. Do savannah sparrows commit the Concorde fallacy? *Behav. Ecol. Sociobiol.* **5**: 373–387.
- WIKLUND, C. G., and J. STIGH. 1983. Nest defence and evolution of reversed sexual size dimorphism in snowy owls *Nyctea scandiaca*. *Ornis Scand.* **14**: 58–62.