Animal Behaviour 84 (2012) 835–842

Contents lists available at SciVerse ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Shorebird incubation behaviour and its influence on the risk of nest predation

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ARTICLE INFO

Article history:
Received 9 March 2012
Initial acceptance 25 April 2012
Final acceptance 20 June 2012
Available online 9 August 2012
MS. number: A12-00188R

Keywords:
biparental incubation
incubation
nest predation
nest survival
predation risk
shorebird
uniparental incubation

Both nest survival and incubation behaviour are highly variable among shorebirds (Charadrii), and we tested whether more conspicuous incubation behaviour increased the risk of nest predation. During 2000–2006, we monitored nest fate at 901 shorebird nests at three study sites across the circumpolar Arctic. Using miniature video recorders and nest temperature sensors, we obtained 782 days of behavioural data for 161 nests of 11 species. We related nest fate to the rate and duration of adults' nest absences or restless movements on the nest, as well as the total proportion of each day that adult birds engaged in these activities. Nest predation was positively related to the proportion of time that each species left the nest unattended. After controlling for species effects, the likelihood of a successful nesting attempt was lower for individuals that spent more time off the nest, but among failed nests, the number of days that a nest survived prior to depredation was not significantly predicted by measures of incubation behaviour. To control for weather or seasonal effects, we paired observations from nests that were ultimately depredated with observations from successful nests of the same species on the same day. In this paired sample (dominated by two species: red phalaropes, *Phalaropus fulicarius*, and little stints, *Calidris minuta*), both incubation recesses and restless movements were more numerous among failed versus successful nests. Our results suggest that more conspicuous incubation behaviour is indeed related to a higher risk of nest predation, and that this relationship may underlie patterns of nest survival within and among shorebird species.

Parents must balance the costs of providing care with the benefits to their offspring of being cared for (Clutton-Brock 1991; Stearns 1992). A fundamental parental care behaviour among birds is the incubation of eggs, and because a large proportion of eggs do not survive until hatch in most species (e.g. Ricklefs 1969), parent birds could realize benefits by increasing their investment in incubation. In most previous studies of incubation behaviour, the costs to parents are measured in terms of time and energy, and balanced against the need to maintain the eggs at a suitable temperature for embryonic development (Mallory & Weatherhead 1993; Williams 1996; Tulp & Schekkerman 2006). However, because predation is the primary cause of nest failure in almost all avian species studied to date (e.g. Martin 1993), incubation behaviour also may be modified to reduce the risk of nest predation.

Increased activity of parent birds around the nest can increase the risk of predation if predators locate nests by sight (Skutch 1949). For species where one mate feeds the other while on the nest (i.e. 'incubation feeding'), more frequent feeding trips have been linked to reduced nest survival, and feeding trips are suspended when parents are faced with an immediate risk of nest predation (Martin & Ghalambor 1999; Ghalambor & Martin 2002; Martin et al. 2000). For species without incubation feeding, more frequent incubation recesses may increase the risk of predation (Cresswell et al. 2003; Smith et al. 2007a), but this effect has not yet been demonstrated directly.

Shorebirds do not perform incubation feeding, but do vary dramatically in their incubation behaviour. Within days or throughout the season, shorebird incubation behaviour has been shown to vary in response to environmental conditions and energetic demands (Norton 1972; Cartar & Montgomerie 1987; Cresswell et al. 2004; Tulp & Schekkerman 2006; Smith et al. 2012). However, incubation behaviour is constrained at a higher level by mating system; ecologically similar species breeding in sympatry show strategies ranging from completely uniparental incubation, by females or by males, to incubation shared evenly or unevenly between the sexes (Pitelka et al. 1974; Székely & Reynolds 1995; St Clair et al. 2010). Uniparental incubators leave the nest more frequently to feed than do members of a biparental pair (e.g. Norton 1972; Reneerkens et al. 2011), and some previous studies suggest that uniparental birds may suffer higher rates of nest predation in most

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0003-3472/$38.00
http://dx.doi.org/10.1016/j.anbehav.2012.07.004

years (Smith et al. 2007a; Smith & Wilson 2010). There is considerable variation in incubation behaviour even within groups of species with uni- or biparental incubation (Tulp & Schekkerman 2006; Reneerkens et al. 2011), and how this variation may contribute to interspecific variation in nest survival remains unknown.

We simultaneously monitored the nest survival and incubation behaviour of shorebirds to determine whether more conspicuous behaviour increases the risk of nest predation both within and among species. Data were collected on the rate and duration of incubation recesses, as well as the rate and duration of restless movements on the nest for 11 shorebird species varying widely in incubation behaviour, with both uniparental and biparental incubation systems. We related patterns in behaviour among species to interspecific patterns in nest survival. Within species, we asked whether successful and failed nests differed in the conspicuousness of adult behaviour on the nest. We then paired observations from nests that eventually failed with observations from successful nests of the same species on the same day to evaluate behavioural differences while controlling for seasonal or weather-related variation in incubation behaviour.

METHODS

Study Area

Fieldwork was conducted between 2000 and 2006, at three sites across the circumpolar Arctic. At Coats Island, Nunavut (62°51′N, 82°29′W; Fig. 1), work was carried out from the beginning of June until the end of July, 2004–2006. At East Bay, Nunavut (63°59′N, 81°40′W; Fig. 1), we worked from late May until late July in 2002, 2005 and 2006. At both of these sites, workers searched for nests over an area of 12 km^2 in wet lowlands, upland heath tundra, raised beach ridges and coastal habitat types typical for these latitudes. The third site was located at Medusa Bay, on the Taimyr Peninsula, Russia (73°20′N, 80°30′E; Fig. 1). Work here was carried out from early June to early August, 2000 and 2001, in a 4 km^2 area of hilly tundra interspersed with wet sedge meadows and scattered, stony ridges. The physiography of the field sites are described in more detail elsewhere (Canada: Smith et al. 2007a; Siberia: Tulp 2007).

The sample includes behavioural data from 11 species: semipalmated plover, *Charadrius semipalmatus*, black-bellied plover, *Pluvialis squatarola*, American golden-plover, *Pluvialis dominica*, red phalarope, *Phalaropus fulicarius*, ruddy turnstone, *Arenaria interpres*, dunlin, *Calidris alpina*, curlew sandpiper, *Calidris ferruginea*, semipalmated sandpiper, *Calidris pusilla*, white-rumped sandpiper, *Calidris fuscicollis*, little stint, *Calidris minuta*, and pectoral sandpiper, *Calidris melanotos*. The relative abundance of nests found at each of the sites and the composition of the sample of behavioural data appear in Table 1. At the Canadian sites, we collected behavioural data for all of the species that breed in significant numbers, together representing more than 95% of all breeding individuals. At Medusa Bay, behavioural data were collected only for species with uniparental incubation (see below), and thus some abundant species are not represented in the

Figure 1. Study sites at (a) East Bay, Nunavut, Canada, (b) Coats Island, Nunavut, Canada and (c) Medusa Bay, Russia.