

The mating system of the Buff-breasted Sandpiper: lekking and resource defense polygyny

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To date, lekking has been the only reported mating system of the Buff-breasted Sandpiper. Here, we describe apparent resource defense polygyny in this species, and speculate on why it occurs.

The factors affecting the evolution of avian leks are not clearly understood (Bradbury and Gibson 1983). Leks are communal displays where males congregate to display to females, which come to obtain matings (Emlen and Oring 1977). Since a few males on leks account for most of the matings, a lek is a type of polygyny. In another type of polygyny, resource defense polygyny, males obtain matings by defending resources that females require for reproduction (e.g., nest sites, feeding areas). Economic defensibility of resources is thought to be the major ecological factor favoring resource defense polygyny over lekking (Emlen and Oring 1977).

Although males clearly do defend resources in many polygynous species, this does not demonstrate that leks result when resources or females are not defensible (Oring 1982). A comparative study of a species with intraspecific variation in mating system (i.e., lek vs resource defense polygyny) would provide the strongest test of this idea, but there are very few species which exhibit both mating systems. Here we provide evidence for such intra-specific variation in mating system in the Buff-breasted Sandpiper *Tryngites subruficollis*. We demonstrate that Buff-breasted Sandpipers have either geographic or year-to-year variation in mating system, and discuss possible explanations for this observation.

Over much of their breeding range, Buff-breasted Sandpipers have a lek mating system. In their excellent review of the social systems of calidrine sandpipers, Pitelka et al. (1974) classified Buff-breasted Sandpipers as a lekking species, coining the term "exploded lek" to describe the spatial distribution of male territories. This conclusion was based on their own observations made at Barrow, Alaska, where "females nest away from the territories of the males, visiting the display grounds only for copulation". Similarly, Dorogoy (1983) noted that females on Wrangle Island, USSR, do not nest on male territories, and Prevett and Barr (1976) found no tendency for nests to be concentrated near display grounds. However, during our observations of this species on the breeding grounds in the central Canadian arctic, we documented instances of females nesting on male territories, leading us to conclude that in our area, Buff-breasted Sandpiper did not lek.

Between 9 June and 1 August 1984, we observed breeding Buff-breasted Sandpipers on Jenny Lind Island, Northwest Territories (68°43'N, 102°47'W), a small flat island in the Queen Maud Gulf, where Parmelee et al. (1967) previously described their breeding displays. We first noticed male display activity on 13 June, and displays peaked between 18 and 30 June. We found seven nests. The first complete clutch was found on 17 June, and this nest hatched on 10 July. The last nest hatched on 24 July, and extrapolating back from a 24 day incubation period (from nest 1), we determine that mating opportunities for males lasted into early July. No displays were seen after 12 July.

Our observations of unmarked males indicated that displays and activities were confined to a restricted area over at least several days. Some males fought over apparent territory boundaries at an edge of these areas (Fig. 1). Hence, "territory" is used here to denote exclusive and sustained use of space by a single individual for the purpose of display.

We found six of the seven Buff-breasted Sandpiper nests (Fig. 1) early enough to observe displaying males in the vicinity of each (nests 1–6). Our observations were particularly detailed for the territories and nests (nests 2, 4, 5, and 6) in the vicinity of our camp (Fig. 1). Intense male display activity, courtship, and fighting continued on the male territories containing these nests, as well as on surrounding territories. Males were not simply defending egg-laying females, since they continued to hold territories and display after clutches on their territories were complete. These males frequently courted incubating females who had left their nests to feed. Males displayed from the same positions within their territory (Fig. 1) throughout their tenure. Nest 1 was found with 4 eggs on 17 June, within 20 m of the area where on 13 and 15 June two males had been performing ground and paired aerial displays (the latter display performed by males contesting territorial boundaries). Another displaying male was seen within 40 m of nest 3 when it was found on 30 June, with 4 eggs. We also note that the single nest found by Parmelee et al. (1967) in 1962 was "only 40 feet from a displaying male". We conclude that female Buff-breasted Sandpipers nested within territories defended by males. Our observations are not unique. Near Cambridge Bay, NWT, Paulson and Erckmann (1985) also found males displaying near the nest site of an egg-laying female.

We reject the notion that the presence of nests within

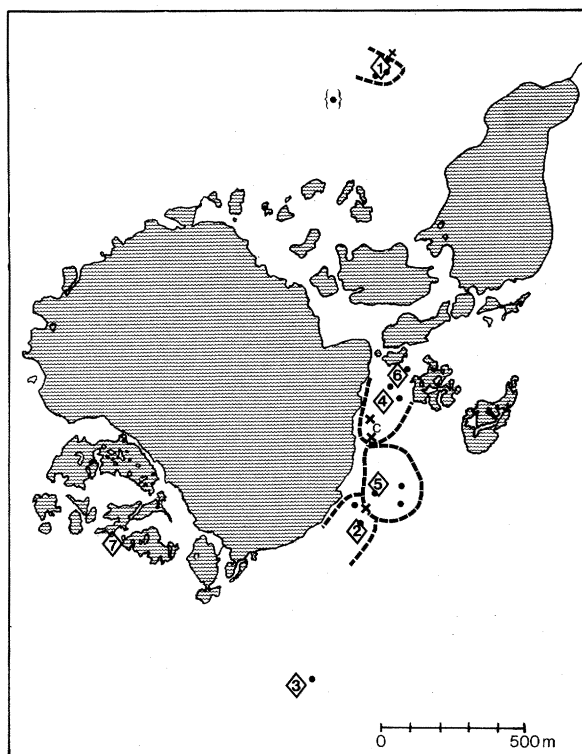


Fig. 1. Buff-breasted Sandpiper nest and male territory locations on Jenny Lind Island, NWT. Nests are identified by numbers in diamonds, male display areas by dots, male territorial fights by crosses, territory boundaries (estimated coarsely by observing the movements of focal males over 0.5–2 h periods) by dotted lines, and the location of our camp with a “c”. North is at the top of the figure. The bracketed dot denotes the marsh region in which early displays by two males occurred (see text). Shaded areas are water bodies.

male territories was coincidental. In the course of searching for nests of many sandpiper species, we thoroughly and systematically explored all habitats within a roughly 1 km radius of our camp. In spite of the intensive search effort in this main study area, each nest that we found was within the territory of a displaying male (true for all six nests found during the period of male display), although we observed male display activity in locations where we later did not find nests (largely through lack of searching effort in these more remote areas).

Males restricted their displays largely to the dry and flat habitats characterized by short vegetation and *Carex rupestris* – precisely those in which females nested. However, during the first few days of rapid snow melt (beginning 13 June), but generally before clutch initiation, we noticed two males displaying in a marshy area, within 200 m of nest 1 (bracketed dot in Fig. 1). The shifts in display grounds used by males noted by Parmelee et al. (1967) may have resulted from a similar move from marsh to nesting habitats. We must stress, though,

that this early observation of male display in a non-nesting habitat was minor when compared with the intense male display activity observed later in nesting habitats. Further, it occurred only early (i.e. 13–15 June) in the egg-laying phase (which itself spanned 14 June to early July). It may therefore have been functionally similar to display on migration (see Oring 1964).

It is conceivable that males actually followed females to nesting areas, i.e., defending territories in snow-free areas before laying, then shifting these to nesting areas when females began laying. Our early observation of a display away from a nesting area hints at this. However, we feel that the bulk of mating occurred on the nesting areas, for the following reasons: (1) males were common on nesting areas by 18 June, and the peak in male display activity for any location – not just those with known nests – was between 18 and 30 June, and (2) apart from nest 1 (where we have already established male proximity at egg-laying), clutches with known completion dates were in late June (27 and 30 June for nests 7 and 6, respectively). Further, we saw females attending small, non-flying chicks on 22 and 24 July, which would place the clutch completion dates for these sometime in late June. All of this suggests that most females were laying during the period of maximum male display: that during which male territories were known to contain nests. After 13 June, we found no displaying males away from appropriate-looking nesting habitat, suggesting that if other males were indeed forming “classical” leks, they were doing so outside of a 3 km radius of our camp.

The critical distinction between resource defense polygyny and lekking is whether or not mates or critical resources are economically monopolizable (Tab. 1 in Emlen and Oring 1977); lek-type mating systems evolve when mates or resources are not monopolizable. One simple way to distinguish the two is to compare the distribution of nests with those of male territories. Nest distributions should be random with respect to male territories in the case of male dominance polygyny, and should be clustered with male territories in the case of resource/mate defense polygyny. As noted earlier, Buff-breasted Sandpipers were classified as lekking precisely on the basis of females nesting away from male territories (Pitelka et al. 1974, Prevet and Barr 1976, Dorogoy 1983). Our observations therefore indicate that Buff-breasted Sandpipers on Jenny Lind Island did not lek, but instead defended nesting territories. Sanderling *Calidris alba* also show geographic variation in their mating system; birds in the Canadian high arctic are serially polygamous (Parmelee and Payne 1973), while those in eastern Greenland are monogamous (Pienkowski and Green 1976).

Interestingly, Parmelee et al. (1967) concluded that Buff-breasted Sandpipers on Jenny Lind Island did have a lek-type mating system (despite the single nest that they found in 1962 being close to a displaying male).

Population densities noted by these authors were similar to those noted by us. If we accept their conclusion of lekking, this suggests temporal – in addition to geographic – variation exists in the Buff-breasted Sandpiper's mating system.

Why don't Buff-breasted Sandpipers on Jenny Lind Island lek? We suspect that suitable nesting habitat is scarce, and was therefore economically defendable. We could easily identify nesting habitat, having found some nests (nests 3 and 7) simply by searching appropriate-looking patches of habitat far from our camp, and there is no reason to suppose that Buff-breasted Sandpiper males would have had greater difficulty. Defense of resources may therefore be possible under these conditions of low nest habitat availability, allowing resource/mate defense polygyny, not leks, to arise (Oring 1982). It would be interesting to know whether Buff-breasted Sandpiper habitat elsewhere (Alaska, Yukon, Wrangel Is.) is more homogeneous, and therefore more difficult for males to defend. Alternatively, other population densities may be so low that males cannot predict where females will nest. In either case, the evolution of leks could be favored. Buff-breasted Sandpipers therefore offer a unique opportunity for within-species comparisons to evaluate current models of lek evolution.

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Effects of nest failure and spread of laying on counts of breeding birds

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If breeding failure occurs and there is variation in the time of egg-laying by individual females, then even accurate counts of occupied nests during the peak of the breeding season will underestimate the total population of breeding pairs. It is shown that breeding failure, the spread of egg-laying and the frequency of counting interact in their effects on estimates of breeding bird populations based on nest counts.

Counts of incubating birds or occupied nests are often used to estimate the size of breeding populations. Wanless and Harris (1984) recently investigated the effects of date and sampling error on the accuracy of estimates of the numbers of breeding gulls (*Larus argentatus* and *L. fuscus*) obtained by counting nests. They recom-

mended that regular sample counts be carried out to determine the date on which the maximum number of nests is present, or that the count be delayed until the end of incubation of the first-laid clutches. They recognised that some nests could fail or hatch before the date of the maximum occupied nest count and allowed for this by including the numbers of complete nests without eggs in the count. However they did not consider the consequences of nest failure and the spread of egg-laying in detail. It is obvious that, if nests fail, then even an accurate count of the peak number of nests with eggs or incubating adults will underestimate the number of pairs attempting to breed. In this paper we quantify this effect by means of a simulation model and identify an interaction between nest failure and the spread of egg-