



Male traits, mating tactics and reproductive success in the buff-breasted sandpiper, *Tryngites subruficollis*

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ABSTRACT

Buff-breasted sandpipers use a variety of mating tactics to acquire mates, including remaining at a single lek for most of the breeding season, attending multiple leks during the season, displaying solitarily or displaying both on leks and solitarily. We found that differences in body size, body condition, fluctuating asymmetry scores, wing coloration, territory location and behaviour (attraction, solicitation and agonistic) did not explain the observed variation in mating tactics used by males. Which males abandoned versus returned to leks was also not related to morphology or behaviour, and there was no tendency for males to join leks that were larger or smaller than the lek they abandoned. These results suggest that male desertion of leks was not dependent on a male's characteristics nor on the size of the lek he was presently attending. Males did join leks with larger males than their previous lek, perhaps to mate with females attracted to these larger 'hotshot' males. Males at both leks and solitary sites successfully mated. Lek tenure did not affect mating success, although lekking males appeared to mate more frequently than solitary males. Courtship disruption and to a lesser extent, female mimicry, were effective at preventing females from mating at leks, and may offer a partial explanation for female mating off leks. Our analysis that combined all males together within a year (regardless of mating tactic) indicated that males that attended leks for longer periods of time and that had fewer wing spots were significantly more likely to mate. Given some evidence that wing spotting declines with age, and that females inspect male underwings during courtship, the latter result suggests that female choice may play some role in determining male success. We suggest that male buff-breasted sandpipers may use alternative mating tactics more readily than males in other 'classic' lek-breeding species because: (1) unpredictable breeding conditions in this species' high arctic breeding range leads to low lek stability, which in turn hinders mate selection mechanisms mediated by male dominance and female choice; and (2) males are not constrained by morphological markings that indicate status or sex. Both characteristics may reduce the reproductive benefits associated with males adopting one mating tactic and result in a sort of scramble competition in which males switch between tactics as local conditions change.

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Males in a wide variety of animal taxa use alternative tactics to breed (Rubenstein 1980; Dunbar 1982; Arak 1984; Lott 1991). Alternative mating tactics are typically

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attributed to phenotypic or competitive differences among males (e.g. Reeves 1907; Le Boeuf 1974), environmental conditions that favour the use of one mating tactic over another by certain individuals (e.g. Moodie 1972), or more rarely, genetic differences that predispose males to use a particular tactic (e.g. Lank et al. 1995). Considerable study has been directed towards understanding the proximate and evolutionary basis for the existence of such variable mating behaviour.

Alternative male mating tactics have been documented in many avian lek-breeding species. In such systems, males not only defend territories at leks, but display in solitary locations (e.g. Pruett-Jones & Pruett-Jones

1990), share courts with territorial resident males (Hogan-Warburg 1966; McDonald 1989), mimic female behaviour and sneak copulations from other territorial males (Trail 1990; Westcott & Smith 1994) or pursue females off leks (Gibson & Bradbury 1987; Lank & Smith 1987). Few researchers, however, have identified why some males in lek-breeding species use alternative tactics. Exceptions include studies on black grouse, *Lyrurus tetrix*, and yellow-whiskered greenbuls, *Andropadus latirostris*, where solitary males have been identified as juveniles or subordinates (Kruijt & Hogan 1967; Brossett 1982). Similarly, 'beta' males in the cooperatively displaying long-tailed manakin, *Chiroxiphia linearis*, are usually younger, although often heavier, than 'alpha' males (McDonald 1989; McDonald & Potts 1994). In these studies, males changed their mating tactic with age as their competitive abilities or morphological conditions changed. In contrast, mating tactics in male ruff, *Philomachus pugnax*, are fixed for life, depending on the male's genetically derived plumage and behaviour (Lank et al. 1995).

Little information is available on males in lek-breeding species that change mating tactics within years. Previous studies of lek behaviour have focused exclusively on long-term resident males at one or a few leks (e.g. Höglund & Lundberg 1987; McDonald 1989; Gibson et al. 1991; Hill 1991; Petrie et al. 1991). Solitary and short-term resident males were generally dismissed as being juveniles or nonbreeders. This is surprising considering that males have long been assumed to be capable of evaluating their mating opportunities on leks, and if necessary, altering their display location (e.g. moving to larger or smaller leks, or to solitary sites) to maximize their mating chances (see e.g. Alatalo et al. 1992; Höglund et al. 1993; Widemo & Owens 1995).

Buff-breasted sandpipers, are unique among North American shorebirds in having a lek mating system (Lanctot & Laredo 1994). In a previous paper (Lanctot & Weatherhead 1997), we reported that male buff-breasted sandpipers use several alternative mating tactics. About 75% of males display on leks at any given time, while the remainder display at solitary locations. Most males stay at a lek for a day or less before leaving to display elsewhere (i.e. other leks or solitary sites), and a typical lek has one to three long-term (>9 days), one to four intermediate term (2–7 days), and four to 10 short-term (1 day) males resident throughout the breeding season. Males also display alone or with other males near nest sites. In addition to these tactics, males mimic female behaviour, and either disrupt or steal copulations from territorial males on leks (Myers 1979; Pruett-Jones 1988; Lanctot et al. 1997). Such variable mating behaviour provides an unprecedented opportunity to investigate how male traits affect male use of mating tactics, why males change tactics within a breeding season, and how mating tactic influences mating success.

In this study we investigated within- and among-year changes in male mating tactics, and examined whether individual differences among males can explain variation in their use of alternative mating tactics. We then examined the social conditions present when males

altered their mating tactics by comparing the behaviour and morphology of males that abandoned and maintained territories at leks on a daily basis. We also followed individual males through time and compared the social conditions experienced by these males in previous and new display locations. Finally, we investigated how male mating tactics affected reproductive success as determined by observations of copulations and paternity results from a DNA profiling study (Lanctot et al. 1997).

We identified the following male traits as potential variables that may influence a male's use of mating tactics and mating success. (1) Body size and condition may affect a male's ability to establish long-term territories on leks or to mimic female behaviour. (2) Other studies have shown male display to be an important component in female choice (e.g. Gibson & Bradbury 1985; Pruett-Jones & Pruett-Jones 1990). Males with poor behavioural repertoires may be forced to adopt alternative tactics that rely less on their own behaviour to attract mates. This may be especially important in buff-breasted sandpipers because males appear to rely primarily on behaviour (e.g. flapping wings) to attract females to their territories (Lanctot & Laredo 1994). (3) The amount of underwing spotting may also be important to a male's mating success because female buff-breasted sandpipers appear to evaluate a male's wing linings just prior to mating (Myers 1979). Feather spotting has been shown to influence mating success in lekking great snipe, *Gallinago media* (Höglund et al. 1990) and peafowl, *Pavo cristatus* (Petrie & Halliday 1994). (4) Asymmetry in male morphological characters (e.g. wing length and spotting, tarsus length) may also be important in determining whether buff-breasted sandpiper males are able to mate successfully or maintain territories on leks. Individuals with low levels of fluctuating asymmetry are thought to be capable of maintaining developmental homeostasis in the face of stresses during growth and hence be of higher individual quality (e.g. Harvey & Walsh 1993). (5) The location of a male's territory, that is, whether centrally or peripherally located on a lek, may also influence a male's mating success. Males on central territories have relatively higher mating success in many lek-breeding species (Höglund & Alatalo 1995). (6) Finally, the length of time males attend leks has also been shown to influence significantly male mating success (Höglund & Alatalo 1995; Mackenzie et al. 1995). This variable was used to categorize male mating tactics (see below) and was also used as a predictor variable in analyses of male mating success.

METHODS

Study Area and General Methods

Observations of buff-breasted sandpipers were collected on a 16-km² study area of the Prudhoe Bay Oil Field, Alaska (70°12'N, 148°15'W), from late May to July, 1992–1994. Climate and habitat characteristics of the region are described in Lanctot & Weatherhead (1997) and Walker et al. (1980). Adult sandpipers were captured at leks and solitary sites throughout the study area using mist nets. Females were also captured on nests with walk-in traps.

Each bird was weighed, measured and then ringed with unique coloured tarsal bands and a U.S. Fish and Wildlife Service metal band. Six to 25 adults each year (total=12 males, 38 females) were equipped with 1.2 g radiotransmitters and followed daily, when possible (see Lanctot et al. 1997 for details). Because males and females resemble each other (although males are generally larger in most morphological measurements; Lanctot & Laredo 1994), we determined a bird's sex with a discriminant function that involved measurements of the length of the bird's wing, tarsus, culmen and head. Birds that were not captured were sexed based on between-sex differences in size and behaviour (Rowan 1927; Oring 1964; Myers 1979; Lanctot & Laredo 1994). A small number of birds whose sex was unknown (i.e. birds of intermediate size that failed to display sex-specific behaviours) were excluded from all analyses. We located nests by flushing females with ropes dragged across the tundra, by tracking radio-equipped females, by following foraging females back to their nests, and by searching near displaying males.

To document the location of male display sites, we visited the study area daily until the first birds were detected, and then began surveying the area once every 3–5 days until male displays subsided. Variable circular plot (Reynolds et al. 1980) and strip transect surveys were used to locate male display sites (see Lanctot & Weatherhead 1997 for details). Both solitary and lekking males could be easily detected with these techniques because the species' characteristic wing-waving behaviour allow birds to be seen for a kilometre or more (R. B. Lanctot, unpublished data). Strip transects were not conducted in 1992.

Observations of Leks

Up to four observers recorded mating activity daily on two to three leks from late May to mid-June each year. These leks were active for 15–26 days ($\bar{X} \pm SD = 21.3 \pm 4.8$, $N=7$) and averaged between 2.9 and 5.5 males in attendance (average number of males present over all observation days). Thus, these leks represent some of the most stable and largest leks detected during our study (see Lanctot & Weatherhead 1997, for description of leks). Lek territories vary in size throughout the season but generally average less than 200 m². Solitary males, in contrast, frequently have territories that are a hectare or more in size. Individual males (during 1992 and 1993) and females (during 1994) were observed for 30 min or until they disappeared from view. See Lanctot et al. (1997) for more details on how behavioural observations were collected.

Male Mating Tactics

Based on male display location, tenure at leks, and overall movement patterns, we categorized males as exhibiting one or more alternative mating tactics (i.e. solitary, lek, and near nests; see Lanctot & Weatherhead 1997). We also separated males into 'long-' and 'short-

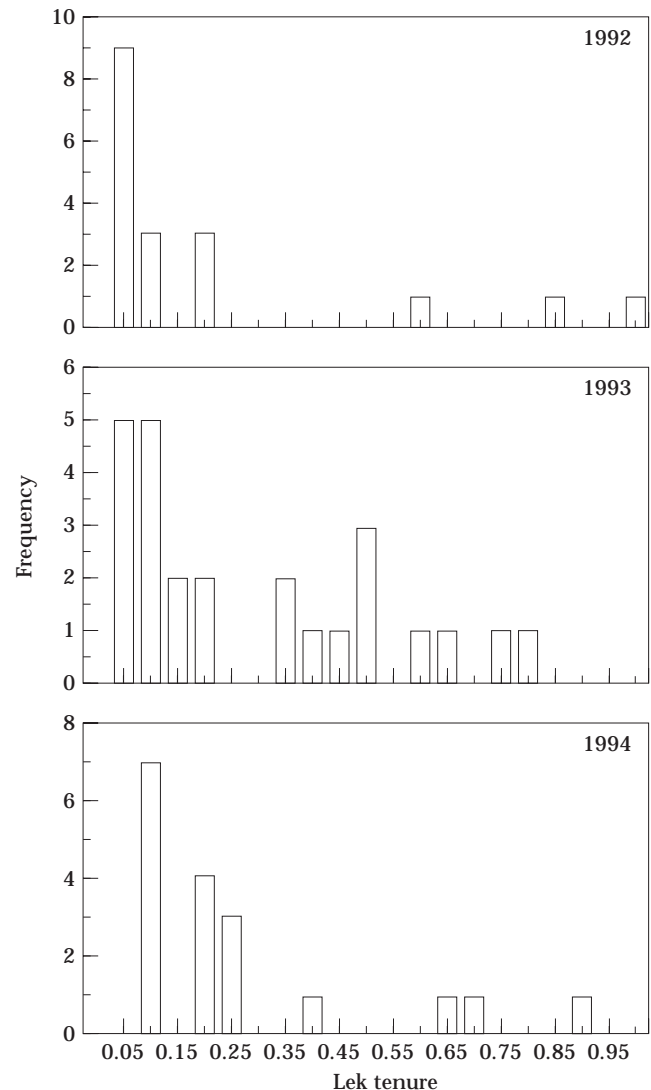


Figure 1. Lek tenure of males marked on two to three intensively studied leks in 1992–1994. Lek tenure was scored as the proportion of daily visits to a lek that a male was observed, beginning with the day the male was banded. For males banded in previous years, we considered all days a lek was visited as possible days a male could be sighted. These values represent minimum estimates because males were present at the lek prior to capture.

term' resident males based on lek tenure. Tenure was scored as the proportion of our visits to a lek that a male was observed, beginning with the day the male was banded. In all cases, leks were active for at least 3 additional days after a male was banded ($\bar{X} \pm SD = 13.8 \pm 4.4$ days). This fact prevented males marked late in the season from being assigned an artificially high score. For males banded in previous years, we considered all days a lek was visited as possible days a male could be sighted. We classified males with a score of 25% or less as short-term residents and males with greater than 25% as long-term residents (Fig. 1). Finally, we classified males seen at the intensively studied leks on a daily basis into those that 'returned' to a lek on the next day and those that 'failed to return' to a lek.

Table 1. Size and fluctuating asymmetry scores for four morphological characters measured on male buff-breasted sandpipers

| Trait* | N | [(R+L)/2]† | | (R-L)† | | | | R-L † | | Nondirectional asymmetry‡ | | Directional asymmetry§ | |
|-----------------|----|------------|------|--------|-------|--------|----------|--------|-------|---------------------------|-------|------------------------|-------|
| | | Mean | SE | Mean | SE | Skew | Kurtosis | Mean | SE | F | P | F | P |
| Wing length | 93 | 136.0 | 0.26 | -0.001 | 0.150 | 0.015 | 0.287 | 1.123 | 0.099 | 2.78 _{91, 179} | <0.05 | 21.78 _{1, 91} | <0.05 |
| Tarsus length | 92 | 32.84 | 0.13 | 0.043 | 0.049 | -0.207 | 0.503 | 0.361 | 0.031 | 1.76 _{90, 177} | <0.05 | 1.36 _{1, 90} | NS |
| Wing darkness | 76 | 0.23 | 0.01 | -0.014 | 0.007 | -0.535 | 2.847 | 0.045 | 0.005 | 4.21 _{75, 179} | <0.05 | 1.98 _{1, 75} | NS |
| Wing spottiness | 76 | 0.197 | 0.01 | 0.000 | 0.005 | 0.229 | 0.543 | 0.036 | 0.003 | 2.56 _{75, 179} | <0.05 | 5.99 _{1, 75} | <0.05 |

'R' and 'L' refer to the right and left side of each trait, respectively. *N* refers to the number of males in the sample.

*See text for description of each trait.

†Wing length and wing spottiness were corrected to a mean of zero to remove directional asymmetry.

‡Tests whether the difference between sides varies more among individuals than would be expected given the size of the measurement error.

§Tests whether one side is significantly larger than the other side on average.

Male Traits

Male morphology

We calculated an index of body size for each male using the first principal component score from a principal component analysis using the variance-covariance matrix of linear measurements of the flattened wing chord, tarsus, culmen and head (to the nearest 0.01 mm). Principal component analyses have been shown to represent overall body size better than univariate measurements such as weight or wing length (Rising & Somers 1989). We also calculated an index of body condition for each male by regressing the first principal component score with body weight. Here body condition was equal to the regression residuals, with a positive score indicating a better than average condition and a negative score indicating a lower than average condition for a given body size. A regression analysis of weight against date, standardized for breeding season chronology across years, indicated that capture date did not affect the weight of males and therefore body condition estimates (ANOVA, $F_{1,114}=1.05$, $P=0.3085$). We used averages for all body size and condition calculations when left and right sides (wing chord, tarsus) or replicate measurements were available.

The undersides of buff-breasted sandpiper primary and secondary flight feathers are satiny white with dark brown vermiculation (hereafter called spots, see Lanctot & Laredo 1994). The number of spots and the proportion of the wing that is darkly coloured decreases as juveniles mature, with adult females being more spotted and darker than adult males, but less spotted and lighter than juveniles. It is not known, however, whether wing spotting and coloration continues to change as adults age. To determine the extent and variation of this spotting among males, we photographed both the right and left underwing of each male against a plywood board covered with graph paper. Photographs were taken in a shaded position using a 35-mm camera and flash, converted to CD-ROM images, and digitized and measured using an image analysis system (National Institutes of Health IMAGE version 1.56). We determined the number of spots per unit area and the proportion of black area to white on both the left and right tenth primary feathers on

each male. We restricted analyses to a rectangular area approximately 100 mm² (4 × 25 mm) centred on the ventral side of the inner vane of each feather with the long axis of the rectangle running parallel to the rachis. Within this area, males had between 12 and 33 spots ($\bar{X}=20$, $N=76$) and black covered between 11 and 38% ($\bar{X}=23$) of the area.

We calculated asymmetry values for four morphological characters on males captured in 1993 and 1994 (right and left measurements were not collected in 1992). These included tarsus length, wing length, wing spottiness and wing darkness. For each character, two measurements were taken of the left and right sides. We used a two-way, mixed-model analysis of variance (sides (fixed) × individuals (random)) with repeated measurements to test whether the between-sides variation was significantly larger than the measurement error (Palmer & Strobeck 1986; Palmer 1994). This analysis indicated that all four variables were suitable for fluctuating asymmetry analysis (i.e. between-sides variation was significantly larger than the measurement error; see Nondirectional asymmetry in Table 1). The mixed-model ANOVA also detected slight directional asymmetry in wing length and spot density variables (Table 1). To control for this, we subtracted the (mean[R - L])/2 from the side with the larger mean, and added this same value to the smaller side of all individuals in the sample (after Palmer 1994). The presence of antisymmetry or skew was investigated by plotting the average right minus average left values and testing for departures from normality (via the Shapiro-Wilks or Kolmogorov statistic, SAS Institute 1989). Here, wing length was the only variable not normally distributed. However, removal of a single outlier value resulted in the remaining data being normally distributed. A regression analysis of |R - L| against trait size (R+L)/2 revealed a size-dependent fluctuating asymmetry within males for wing spottiness ($F_{1,75}=5.04$, $P=0.03$) and wing darkness ($F_{1,74}=8.29$, $P=0.005$). We did not correct for this, however, because scaling these variables (|R - L| by (R - L)/2) for the same trait would remove much of the variation due to departure from symmetry (i.e. asymmetry variation was large relative to the variation in the size of the trait; Palmer 1994, page 354). Our final asymmetry scores were, therefore, the

absolute value of the difference between the right and left sides (for wing length and spot density, the R – L values were first corrected to a mean of zero).

Male display and agonistic behaviour

From the behavioural data collected on each male, we determined the mean proportion of the total observation time (termed 'duration') males spent in three behaviour categories: attracting females, soliciting females and male–male aggression. Attraction behaviours included flutter-jumps and wing waves (one or both wings). These behaviours were typically performed by many males at the same time and functioned to attract passing females to each male's territory and the lek in general. Solicitation behaviours, in contrast, were displayed only after females had entered a male's territory, and typically included wing and tail raises that resulted in the female following the male to the centre of his territory where most copulations occurred. We distinguished between attraction and solicitation behaviours because the former may influence relative mating success (i.e. number of female visitors), whereas the latter may influence mating status (i.e. mated versus nonmated; see below). Male–male aggression included paired vertical flights and fights along territorial boundaries, as well as courtship disruptions. Disruptions typically involved intruders flying directly at males on nearby territories and scattering female visitors, or less frequently, 'sneaking' along the ground to gain access to their neighbour's territory. These sneaky males then either disrupted the visiting females prior to copulation, or mimicked female behaviour and attempted to steal copulations by placing themselves between the resident male and soliciting females. Spearman correlation analysis indicated that all three behaviour scores were independent of each other ($P > 0.10$).

To determine whether female presence affected the behaviour exhibited by males (see e.g. Wiley 1973; Avery 1984; Gibson & Bradbury 1985), we used a paired Wilcoxon signed-ranks test to compare male behaviour scores when females were and were not present. Where significant differences existed, we used only that portion of each focal observation when females were present. Regression analyses indicated little or no seasonal change in most behaviour scores (P values > 0.25). The one exception was attraction behaviour, which decreased significantly through time in 1993 ($F_{1,32} = 4.98$, $P = 0.03$). This single significant effect was caused by two high scores at the beginning of the season, which when removed, made the relationship no longer significant. Given the insignificant or weak seasonal effects, we did not restrict the dates of focal observations used in subsequent analyses.

We defined a courtship disruption as any interruption of a precopulatory display (i.e. when a female was inside a male's double-wing embrace) or copulations that led to a decrease in the number of copulations completed by a male (after Foster 1983). For each male, we determined the percentage of female groups visiting each male that were disrupted by other males (this calculation was not possible for males with no female visitors) and the rate (number of disruptions per observation minute) at which the focal male disrupted other males. In both cases, a

value was calculated for each observation day and then averaged over all days a male was observed. Because observations of males mimicking female behaviour and stealing copulations were rare, we simply recorded males as having either exhibited these behaviours or not.

Vocalizations

Buff-breasted sandpiper males utter a series of quiet 'tick' notes during precopulatory display (Lanctot & Laredo 1994). Because the relative importance of these songs for attracting females is thought to be minimal (similar vocalizations are made by males at staging areas during spring migration; Oring 1964), we did not measure this variable in this study.

Territory location

We determined the position of each male's territory on a lek by measuring the distance from the centre of a male's territory to the centre of the lek each day using maps constructed during behavioural observations. These measures were then standardized by dividing by the distance of the most peripheral male on the lek for each day (this controlled for daily changes in lek size). Finally, we determined an average score for each male by averaging standardized values over all days a male was present at a lek. We determined the centre of each lek by enclosing individual male territory centres located within 200 m of each other with a circle or rectangle (depending upon the distribution of male territories). We then used the centre of each circle or rectangle as the lek centre.

Male Mating Success

Male mating success was determined in two ways. First, we categorized males as having mated if they were observed copulating (Behaviour category) with at least one female, or if paternity analyses using DNA typing (Genetic category, see Lanctot et al. 1997 for methods) indicated that the male had successfully sired offspring. Second, we used the number of female visits to a male's territory as an indicator of male mating success. We assumed all visits by unmarked females were by different individuals because females marked prior to nesting were never seen twice at the same lek (although females visited multiple leks, see Lanctot et al. 1997). To generate a male's visitation score, we determined a female visit rate (number/min) for each focal observation and averaged these values across all observation periods. We did not differentiate between females that visited a male's territory and females that interacted with the territorial male (as done by Pruett-Jones 1988) because the two values were correlated (1992: $r_s = 0.45$, $N = 14$, $P = 0.1087$; 1993: $r_s = 0.78$, $N = 18$, $P = 0.0001$; data combined across years: $r_s = 0.60$, $N = 32$, $P = 0.0003$). The rationale for recording both matings and female visits is that it is possible that different variables may affect mating status and relative mating success (after Pruett-Jones & Pruett-Jones 1990). We determined the relative measure of mating success (i.e. female visits) only in 1992 and 1993 when intensive behavioural observations of males were collected.

Data Analyses

The total time individual males were observed on focal leks during a year ($\bar{X} \pm \text{SD} = 93 \pm 103.3$ min, range 11–417, $N=32$) varied with their tenure on the study area. The amount of time a male was observed did not affect his mating success and behaviour scores when data from each year were analysed separately ($P > 0.05$). Year-by-year analyses seemed most appropriate because female choice and values of fluctuating asymmetry may differ between years within populations (Zhakarov 1981; Zuk et al. 1990; Møller 1993). For some analyses, we pooled male data across all intensively studied leks within years. This seemed justified because there were no differences in male morphology, behaviour and mating success between leks within years.

We generally used univariate nonparametric statistics for analyses because data were either not normally distributed or sample sizes were small. All tests were two-tailed unless otherwise stated and conducted at the 0.05 significance level.

RESULTS

Male Traits

We collected data on male morphology and behaviour on 23, 36 and 57 males in 1992, 1993 and 1994, respectively. Focal behavioural observations were collected on 61 and 44% of these males in 1992 and 1993, respectively, over an average of 3.5 days in each year ($\text{SD} = 4.3$ and 3.0 , respectively). Observations could not be collected for longer periods because of the short tenure of males on leks (see Figure 5 in Lanctot & Weatherhead 1997). Across years, both male morphological and behavioural scores were very similar. Traits with the highest variation included behavioural measures and lek tenure. Aside from maintenance behaviours (e.g. resting, feeding), males spent most of their time soliciting females (average percentage of time males engaged in soliciting females ranged from 15 to 26% across years), followed by attracting females (range 7–11%) and interacting with other males (4% each year). A relatively high percentage of female(s) that visited focal males were disrupted by other males (range 14–41%), and the rate at which individual males performed disruptions ranged from 0.6 to 1.2/h.

Male Mating Tactics

Patterns within and between years

Individual males varied in the number and type of mating tactics used within a year (Fig. 2). The majority of males displayed at a single lek and then left the study area, although few males established long-term territories at a single lek (only 16% of males stayed longer than 8 days, see Lanctot & Weatherhead 1997). Some males displayed at a second, third and even fourth lek within a year, although the percentage of males resighted decreased with lek number (e.g. 93, 20, 7 and 2% of banded males were seen at one, two, three and four leks, respectively, in 1994, see Fig. 2). A few males (2.6 and 6.8% in 1993 and

1994, respectively) were observed only at solitary sites, although these males may have displayed at lek sites prior to being banded or moved to lek sites off the study area. Roughly, 25% of marked males displayed near nests each year (9 of 39 in 1993, and 22 of 59 in 1994). The greater number of alternative mating tactics used by individual males in 1994 relative to 1993 coincided with a longer breeding season in 1994 (23 days in 1994 relative to 13 days in 1993, see Lanctot & Weatherhead 1997).

The number of days males maintained territories at leks did not change significantly with lek number (i.e. first versus second lek and second versus third lek; Wilcoxon paired-sample test: $T_+ = 30$, $T_- = 61$, $N = 18$ males, $P > 0.20$). Male tenure at solitary sites was much shorter than at leks, and generally lasted only 1 day before males began displaying at new locations or left the study area. In each year the number of short-term lek males always exceeded the number of long-term lek males, although the relative proportion of each varied by year (Table 2). Similarly, the number of males that displayed on leks for 1 day generally exceeded the number of males that returned on subsequent days, although the relative proportion of each also varied by year (Table 2).

Males did not always use the same mating tactics from year to year. Two of five males resighted during the study maintained long-term territories at leks in each of 2 and 3 years, respectively, and a third male was a short-term lek resident in 2 years (1992 and 1994). The remaining two males were long-term lek residents in 1 or 2 consecutive years and then became short-term lek residents in later years.

Male Traits and Mating Tactics

Males that displayed in solitary locations did not differ significantly in morphology or behaviour from males observed only on leks (analyses done by year and trait; all NS). Males observed near nests differed significantly in body size from males never seen near nests in both 1993 (Wilcoxon two-sample test: $Z = 2.05$, $P = 0.04$) and 1994 ($Z = -2.50$, $P = 0.01$). However, males seen near nests in 1993 were significantly smaller, whereas males seen near nests in 1994 were larger (Fig. 3). No other morphological or behavioural trait distinguished males that displayed near nests from those that did not.

Female groups visiting short-term lek males were significantly more likely to be disrupted than female groups visiting long-term lek males in 1993 ($Z = 2.61$, $P = 0.009$) but not in 1992 ($Z = 0.31$, $P = 0.76$; behavioural data were not collected on males in 1994). We also found that in 1993, males that visited leks for only 1 day had more symmetrical wing coloration ($Z = -2.83$, $N = 6$, $P = 0.005$ for both categories) and were more likely to have female visits to their territories disrupted ($Z = 2.12$, $N = 10$ for males at lek multiple days, $N = 2$ for males at lek 1 day, $P = 0.03$) than males seen on 2 or more days. Low sample sizes, however, made these relationships potentially unreliable.

Male abandonment of leks

There were no differences in body size, condition, fluctuating asymmetry scores, territory location, or wing

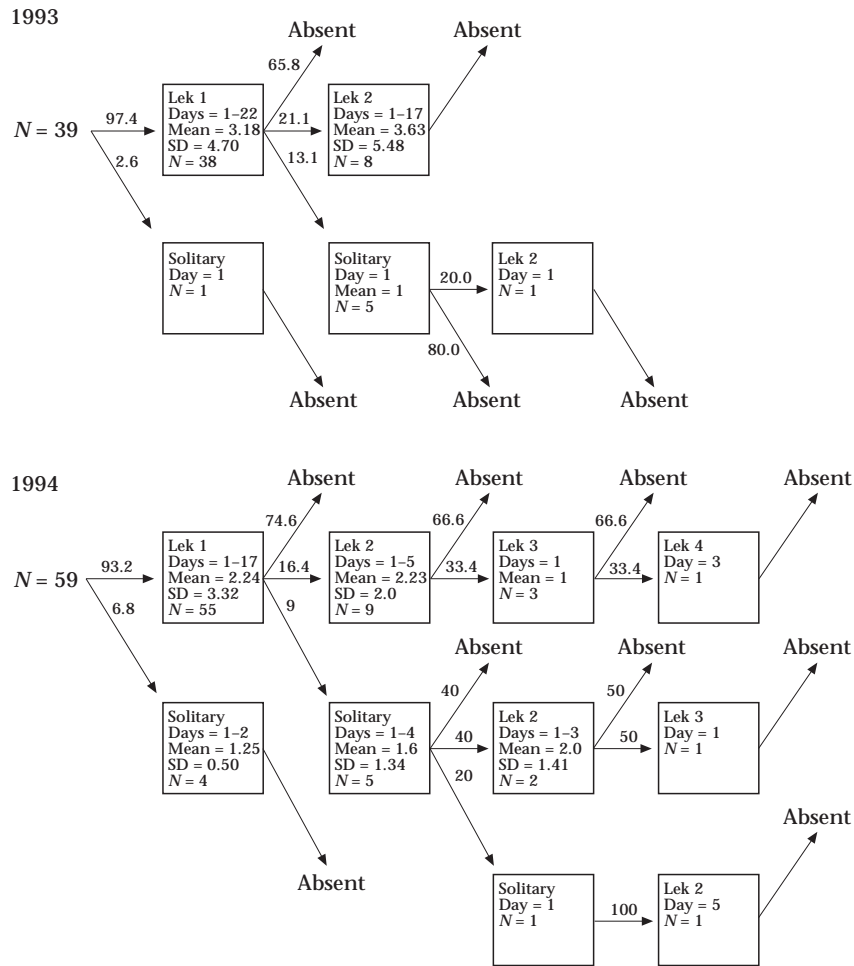


Figure 2. Interdisplay site movements by buff-breasted sandpiper males throughout the 16-km² study area in 1993 and 1994. Number following 'lek' refers to the total number of leks at which a male displayed while visiting a series of sites. Numbers adjacent to arrows indicate the percentage of males that followed each route from the previous site. Summary statistics for male display duration is given in each box. 'Days' refers to the number of days (not necessarily consecutive) a male was observed on a lek. These values were based on study-wide ground surveys conducted every 3–5 days and daily visits to two to three leks per year. 'Absent' refers to males that were not subsequently seen during that field season.

spotting and darkness scores of males that returned to leks on successive days and those that failed to return (Wilcoxon paired-sample one-tailed tests, all NS). Similarly, behavioural data indicated that returning males had similar aggression, attraction, solicitation and disruption scores as nonreturning males.

To test whether male movement between leks was associated with male size or condition, we compared the morphology of resident males at the first lek that moved to that of residents at the lek the moving male subsequently visited. Males on second and third leks were larger on average than males located on first leks (9 of 10 comparisons, $P=0.02$). No other variables differed significantly in this analysis. We also found that males were just as likely to move to leks with more males as leks with fewer males relative to the size of their first lek (Wilcoxon paired-sample test: $T_+ = 93.5$, $T_- = 77.5$, $P > 0.5$).

Table 2. Number of male buff-breasted sandpipers observed using different mating tactics

| Category* | Year | | | |
|----------------------|------|------|------|--------------|
| | 1992 | 1993 | 1994 | Combined (%) |
| Lek tenure | | | | |
| Short-term | 15 | 14 | 14 | 43 (69.4) |
| Long-term | 3 | 11 | 5 | 19 (30.6) |
| Site fidelity to lek | | | | |
| Did not return | 12 | 13 | 10 | 35 (56.5) |
| Returned | 6 | 12 | 9 | 27 (43.5) |

*Males were categorized first by their lek tenure and second by their site fidelity. Long-term residents of leks had tenure scores above 0.25 (see text for calculation of lek tenure). Males observed at the same lek on at least 2 different days were classified as having 'returned', whereas males observed on only 1 day were classified as having 'not returned'. Information is only presented for males captured on our intensively studied lek sites.

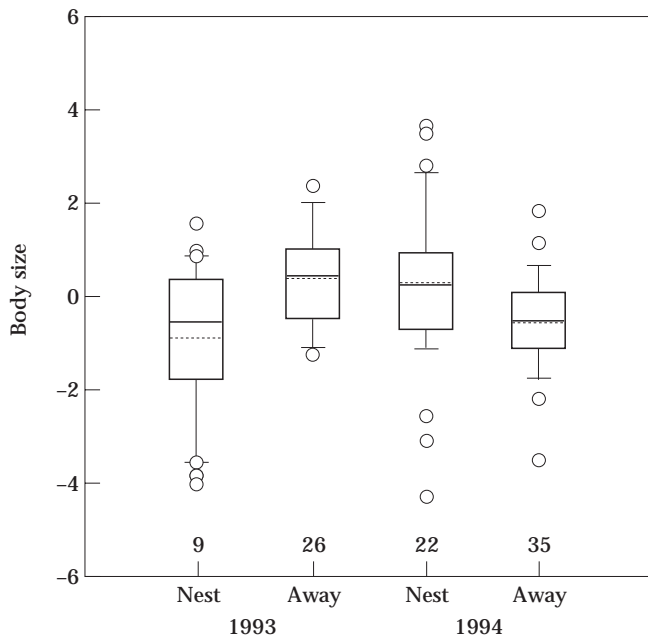


Figure 3. Body size (first principal component score) of males observed near nests relative to males not seen near nests in 1993 and 1994. See text for a description of body size calculations and how males were categorized as being near nests. Sample sizes are above the X-axis. Box plot boundaries represent the 25th and 75th percentiles, solid lines inside the box represent the medians, dashed lines inside the box represent the means, capped bars indicate the 10th and 90th percentiles, and circles represent all data outside the 10th and 90th percentiles.

Courtship disruption and female mimicry

We documented 57 and 38 female visits to males on leks in 1993 and 1994, respectively. Only 12 female visits resulted in copulations, including five of 54 visits (9%) that were not disrupted by other males, and seven of 41 visits (17%) that were disrupted. Almost half of the 41 visits with disruptions involved repeated intrusions by one or more males. Females responded to disruptions by staying on the resident male's territory (67.6%), leaving the territory of the male or the entire lek (17.1%), following the disrupter back to his territory (12.6%), or mating with the intruder on the disrupted male's territory (2.7%). In no instance did we document females mating with a disrupting male after following him to his territory (data limited to 1994 when female focal observations were conducted). Whether intruders disrupted males by flying in or sneaking did not significantly affect the response of females (likelihood ratio $\chi^2_3=7.09$, $P=0.07$), although all three stolen copulations occurred when males sneaked into a territory and mimicked female behaviour. Two of three stolen copulations occurred when the intruder placed himself between the resident male and female, and the third occurred while the resident male was chasing a second intruder out of his territory. Males also frequently disrupted neighbouring males when no other birds ($N=52$) or only other intruding males were present ($N=12$). In the first case, males appeared to be looking for

females that may have been feeding in the surrounding vegetation, because these males typically left when no females were detected. In the latter case, intruding males frequently entered the precopulatory embrace of the resident male. Occasionally, intruding males ran behind the embracing resident male and mounted him. Simultaneous mountings by three to four males occurred at least three times.

Behavioural observations of marked males on leks in 1993 indicated that 42% of males disrupted their neighbours, and 58% of males were disrupted by other males ($N=19$ males). About 42% of all males were both disrupted and disrupted others. A similar number of long- and short-term lek residents were disrupted, disrupted others, or were both disrupted and disrupted others (likelihood ratio: $\chi^2_2=1.69$, $P=0.43$; data restricted to 1993 when two observers were present and males were the focus of behavioural observations). Two of the stolen copulations were by long-term lek males and the third was by a short-term lek male.

Male Mating Success and Mating Tactics

We found no significant differences in female visitation rate between solitary and lekking males, between males located near nests and those that were not, or between those males that returned to a lek on a subsequent day and those that did not (all P values were >0.08). Short-term lek males, however, had significantly higher female visitation rates than long-term lek males in 1993 ($Z=2.80$, $P=0.005$, long-term: 0.01 visits/min, $N=9$; short-term: 0.06 visits/min, $N=5$) but not in 1992 ($Z=0.0$, $P=1.0$).

Paternity analyses and behavioural observations indicated that both solitary and lek (short- and long-term) males successfully mated (Table 3). The number of successful lek males was significantly higher than the number of successful solitary males in 1994 (likelihood ratio: $\chi^2_1=9.49$, $P=0.002$) but not in 1992 ($\chi^2_1=0.52$, $P=0.47$) or 1993 ($\chi^2_1=1.21$, $P=0.27$). Mating success was distributed relatively evenly among each mating tactic in 1992 and 1993, whereas in 1994, short-term lek males were more successful. When the 3 years were combined, short- and long-term lek males had relatively equal mating success and solitary males were the least successful (Table 3). Long-term lek males appeared to have mated more frequently with multiple females (Table 3) and sired more full clutches than short-term lek males (number of full and partial clutches sired by solitary males=1, 1; short-term lek males=2, 7; long-term lek males=7, 3), although neither of these relationships was significant when compared across mating tactics (multiple mating: $P=0.51$; clutches: $P=0.10$). A comparison of the mating success of males that returned to leks and those that failed to return indicated that returning males were significantly more likely to have mated (sign test: 16 of 20 comparisons, $P<0.05$). Males were never observed copulating with females whose nests they displayed near but DNA typing indicated they successfully fertilized eggs in two of 47 clutches analysed (Lanctot et al. 1997).

Table 3. Number of male buff-breasted sandpipers that successfully mated at least once relative to mating tactic

| Year and measure* | Lek | | | |
|-------------------|----------|------------|-----------|----------|
| | Solitary | Short-term | Long-term | Unknown† |
| 1992 | | | | |
| Behaviour | 3 | 1 | 2 (1) | 3 |
| 1993 | | | | |
| Behaviour | 1 (1) | 1 | 3 | 1 (1) |
| Genetic | 2 | 1 (1) | 3 | 0 |
| 1994 | | | | |
| Behaviour | 0 | 1 | 1 (1) | 1 (1) |
| Genetic | 0 | 6 | 2 (2) | 0 |
| Subtotal | | | | |
| Behaviour | 4 (1) | 3 | 6 (2) | 5 (2) |
| Genetic | 2 | 7 (1) | 5 (2) | 0 |
| Total‡ | 6 (1) | 10 (1) | 10 (4) | 5 (2) |

Number of males that mated with multiple females in parentheses. Males were either observed copulating with females during focal behavioural watches (Behaviour) or were determined to have sired offspring via single-locus minisatellite DNA typing (Genetic). Because many males on the study area were unmarked and could not be identified from day to day, we were unable to determine the total number of unsuccessful males using each tactic.

*DNA typing was not conducted in 1992.

†We could not determine the lek status of these males because they were unmarked.

‡Individual males were never observed copulating in more than 1 year so combining males across years for analyses (see text) does not violate assumptions of independence (Hurlbert 1984). The total number of males in the long-term category in 1993 is one less than the behaviour and genetic subtotals would indicate because one male was observed mating on a lek and also shown to have genetically sired young from a brood. In all other cases, males observed to copulate and those confirmed to have sired young by DNA typing were different.

Comparisons of male tactics and mating success were potentially confounded by small sample sizes and uneven sampling of males. For example, the majority of our behavioural data were collected on males at leks. This may have resulted in an artificially low number of matings being observed at solitary sites. Similarly, long-term lek males may be sampled more frequently than short-term or solitary displaying males (long tenure provides more capture opportunities) and thus be identified as fathers in our subsequent genetic analyses more often. This is consistent with our inability to identify the sires of 83 and 71% of the clutches sampled for paternity in 1993 and 1994, respectively (Lancot et al. 1997). It seems likely that many of these unidentified fathers were solitary or short-term lek males.

In a final analysis, we combined males together within a year and investigated the effect of 13 predictor variables on male mating status (i.e. mated and nonmated). Data were available for 7, 13 and 10 variables in 1992, 1993 and 1994, respectively. These analyses indicated that male attraction behaviour and lek attendance significantly predicted a male's mating status in 1 year of the study (Table 4). Because data from different years were collected on different males (only five males were resighted among years, three of which were recaptured), we treated each year as an independent test of the

relationship between the predictor variables and mating status, and combined probabilities across years to generate a more robust test of each relationship (Sokal & Rohlf 1981). This process indicated that males that attended leks for longer periods of time and had fewer wing spots were significantly more likely to mate (Table 4, Fig. 4). Male attraction behaviour also remained significant after combining probabilities across years, but was related to mating status differently in each year (i.e. males with higher attraction scores were more likely to mate in 1992 but less likely to mate in 1993).

Interestingly, our two measures of male mating success (i.e. female visitation rate, and number of matings observed and inferred from paternity analyses) were not correlated with each other when analysed separately by year, or by year and lek (all $P > 0.05$). This may be because fewer than 10% ($N = 120$) of the females that visited males were observed to copulate. Thus a male's ability to attract females may not reflect his ability to copulate with these females.

DISCUSSION

Our results indicate male buff-breasted sandpipers within one population used several alternative mating tactics and regularly switched between tactics within and among breeding seasons. Observations of marked or radio-equipped males indicated that some males used one tactic almost exclusively, while other males switched between tactics (see Fig. 2 and Lancot & Weatherhead 1997). The extent to which males used multiple tactics was difficult to determine, however, due to limitations associated with following males away from our study area. We suspect the large number of males that disappeared (i.e. denoted as being 'absent' on Fig. 2) continued to be sexually active because resighted males were almost always involved in courtship display, and males continued to display occasionally near nests after clutches were completed despite the high energetic costs and low probability of females remating (see Lancot & Weatherhead 1997). These results contrast with previous descriptions of the buff-breasted sandpiper's mating system (Pruett-Jones 1988; Cartar & Lyon 1988; see explanation for differences in Lancot & Weatherhead 1997) and with most descriptions of avian lek-breeding systems in which a majority of males follow a single strategy (e.g. long-term display at a single lek; Wiley 1991; Höglund & Alatalo 1995). The presence of alternative mating tactics in other avian lek-breeding species has been attributed to variation in individual male qualities such as male size, age and phenotypic quality (see introduction in Höglund & Alatalo 1995). For example, Lank & Smith (1987) suggested that male ruff that have a 'true lekking' tactic (i.e. stable lek residents) are older, while males that have a 'following' tactic are younger. Contrary to these patterns, however, we failed to find any relationship between male morphology or behaviour and the mating tactic used by a male. We believe buff-breasted sandpipers may differ from other species in this regard because of where they breed (i.e. the high arctic) and their lack of sexual dimorphism (see below).

Table 4. Morphological and behavioural traits of successful and unsuccessful male buff-breasted sandpipers during 1992–1994

| Variable* | Year | No matings | | | Matings | | | Wilcoxon two-sample test† | | Combined probability <i>P</i> |
|------------------------------|------|------------|--------------|----------|---------|--------------|----------|---------------------------|----------|-------------------------------|
| | | Median | Range | <i>N</i> | Median | Range | <i>N</i> | <i>Z</i> | <i>P</i> | |
| Male morphology | | | | | | | | | | |
| Body size | 1992 | 0.434 | -2.715–3.322 | 20 | 1.133 | 0.116–1.212 | 3 | 0.59 | 0.55 | |
| | 1993 | -0.399 | -3.977–1.616 | 26 | 0.030 | -1.187–2.440 | 9 | 1.26 | 0.21 | |
| | 1994 | 0.029 | -4.274–3.582 | 48 | 0.284 | -0.993–3.727 | 9 | 0.49 | 0.62 | NS |
| Body condition | 1992 | 1.81 | -4.28–9.16 | 20 | 0.48 | -0.20–1.75 | 3 | -0.68 | 0.49 | |
| | 1993 | 1.05 | -8.59–7.80 | 26 | -0.96 | -4.11–5.95 | 9 | -1.34 | 0.18 | |
| | 1994 | -0.38 | -4.26–14.72 | 48 | -2.29 | -8.63–6.48 | 9 | -1.11 | 0.27 | NS |
| Wing spot density | 1993 | 0.201 | 0.160–0.335 | 15 | 0.187 | 0.154–0.244 | 6 | -1.25 | 0.21 | |
| | 1994 | 0.197 | 0.125–0.294 | 47 | 0.178 | 0.125–0.285 | 8 | -1.22 | 0.22 | <i>P</i> <0.05 |
| Wing darkness | 1993 | 0.22 | 0.12–0.37 | 15 | 0.25 | 0.167–0.362 | 6 | 0.90 | 0.37 | |
| | 1994 | 0.22 | 0.11–0.35 | 47 | 0.21 | 0.132–0.380 | 8 | 0.0 | 1.00 | NS |
| Wing asymmetry | 1993 | 1.16 | 0.16–3.66 | 28 | 1.34 | 0.16–3.34 | 8 | 0.0 | 1.00 | |
| | 1994 | 0.66 | 0.16–3.84 | 48 | 0.66 | 0.34–2.16 | 9 | 0.39 | 0.70 | NS |
| Tarsus asymmetry | 1993 | 0.30 | 0–1.05 | 26 | 0.15 | 0.10–1.25 | 9 | -0.51 | 0.61 | |
| | 1994 | 0.35 | 0–1.25 | 48 | 0.25 | 0.05–0.65 | 9 | -1.28 | 0.20 | NS |
| Wing spot asymmetry | 1993 | 0.030 | 0.008–0.128 | 15 | 0.028 | 0.009–0.039 | 6 | -0.51 | 0.61 | |
| | 1994 | 0.029 | 0–0.127 | 47 | 0.043 | 0.010–0.068 | 8 | 1.47 | 0.14 | NS |
| Wing darkness asymmetry | 1993 | 0.022 | 0.003–0.087 | 15 | 0.035 | 0.005–0.246 | 6 | 1.09 | 0.27 | |
| | 1994 | 0.029 | 0–0.196 | 47 | 0.045 | 0.007–0.126 | 8 | 0.64 | 0.52 | NS |
| Male behaviour scores | | | | | | | | | | |
| Attraction | 1992 | 0.048 | 0–0.221 | 11 | 0.078 | 0.047–0.090 | 3 | 0.62 | 0.53 | |
| | 1993 | 0.122 | 0–0.467 | 10 | 0.000 | 0–0.185 | 5 | -1.93 | 0.05 | <i>P</i> <0.05 |
| Solicitation | 1992 | 0.124 | 0.002–0.271 | 8 | 0.154 | 0.084–0.297 | 3 | 0.68 | 0.49 | |
| | 1993 | 0.228 | 0.043–0.442 | 10 | 0.292 | 0–0.707 | 5 | 0.55 | 0.58 | NS |
| Aggression | 1992 | 0.007 | 0–0.282 | 11 | 0.009 | 0.002–0.014 | 3 | 0.0 | 1.00 | |
| | 1993 | 0.013 | 0–0.221 | 11 | 0.020 | 0–0.111 | 5 | 0.06 | 0.95 | NS |
| Distance from lek centre | 1992 | 3.404 | 2.04–5.60 | 15 | 3.838 | 3.46–4.81 | 3 | 0.83 | 0.41 | |
| | 1993 | 4.444 | 1.61–5.87 | 19 | 3.244 | 2.08–4.21 | 6 | -1.43 | 0.15 | |
| | 1994 | 3.243 | 0–5.80 | 15 | 2.774 | 2.17–5.71 | 4 | -0.35 | 0.72 | NS |
| Lek tenure | 1992 | 0.060 | 0.05–0.85 | 15 | 0.570 | 0.09–1.0 | 3 | 2.05 | 0.04 | |
| | 1993 | 0.140 | 0.04–0.77 | 19 | 0.500 | 0.06–0.75 | 6 | 1.70 | 0.09 | |
| | 1994 | 0.140 | 0.08–0.70 | 14 | 0.225 | 0.17–0.88 | 4 | 1.36 | 0.17 | <i>P</i> <0.05 |

*See text for a description of each trait.

†Normal approximation with continuity correction of 0.5.

Abandonment of Leks: When to Leave and Where to Settle?

Several studies have concluded that there may be a reproductive advantage for males to attend larger leks because the number of female visits and copulations increase with lek size (Alatalo et al. 1992; Höglund et al. 1993; Widemo & Owens 1995). It has also been suggested that there is a reproductive cost to being on large leks, as males on larger leks have to expend more energy to maintain their territory and repel disrupting neighbours. For example, Alatalo et al. (1992) found that less competitive males preferred smaller leks because of lower levels of disruptions. Thus, we predicted that males that showed high lek fidelity within a year should be more competitive (e.g. larger, better condition). Contrary to our predictions, however, we detected no differences in male morphology and behaviour between males that deserted leks and those that returned on successive days. Furthermore, there was no tendency for males to join leks that were larger or smaller than the lek they abandoned. These results suggest that abandon-

ment of leks was not dependent on a male's characteristics nor on the size of lek he was presently attending. The fact that males joined leks with larger males gives some support for males settling near more attractive males and thereby parasitizing the 'hotshot' male's abilities to attract females (Beehler & Foster 1988; Höglund & Robertson 1990). This seems especially likely in the buff-breasted sandpiper because smaller males can mimic female behaviour and steal copulations from other males (see below). The fact that males that returned to leks were more likely to have mated than those that abandoned leks suggests that a male's previous mating success may influence his decision to leave or stay. In a similar way, Lank & Smith (1987) found that lek ratio in ruff (males at leks/total males) was significantly correlated with the previous day's copulation rate. It seems likely that other factors, such as changes in female distribution (Bradbury et al. 1986), differences in the per capita male copulation rate among leks (Widemo & Owens 1995) or level of relatedness among males at leks (Kokko & Lindström 1996), may also be important.

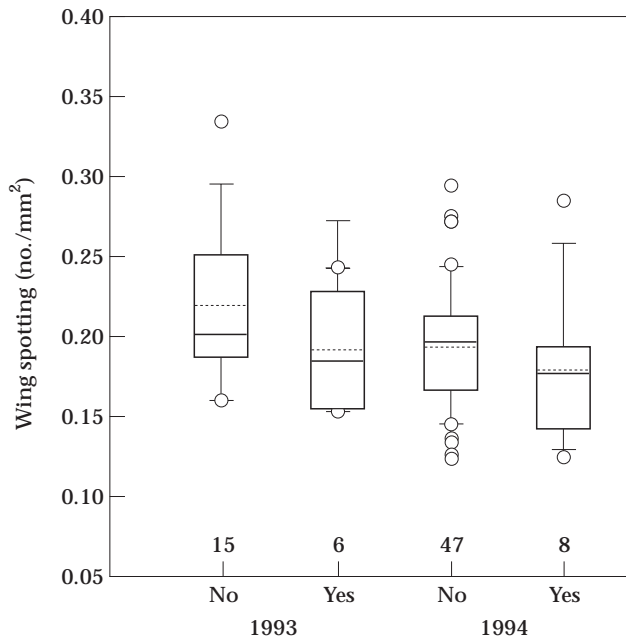


Figure 4. Number of wing spots per mm^2 on male outer primary feathers relative to mating status (mated=yes, unmated=no) in 1993 and 1994. See text for a description of how spots were counted. Figure designations are the same as those listed in Fig. 3.

Courtship Disruption and Homosexual Mounting

Our study indicated that courtship disruption and to a lesser extent, female mimicry, altered female choice of mates. Indeed, nearly half of the female visits documented in this study were disrupted and only about one-tenth of all female visits resulted in a copulation. Similar findings, in terms of the percentage of female visits that resulted in disruptions and copulations, were reported in two earlier studies on buff-breasted sandpipers (Pruett-Jones 1988; P. Myers & F. Pitelka, personal communication). Such high disruption frequencies are rather rare in lek-breeding birds (see Trail & Koutnik 1986; Widemo 1997), with most species having 10% or fewer of copulation events disrupted. We had little evidence to suggest that disrupters were able to redirect copulations to themselves. In the three instances where they were successful, the disrupters mimicked female behaviour and sneaked copulations without leaving the disrupted male's territory. Courtship disruption has also been reported to be ineffective at increasing a male's mating success in the lek-breeding Guianan cock-of-the-rock, *Rupicola rupicola* (Trail & Koutnik 1986), golden-headed manakin, *Pipra erythrocephala* (Lill 1976), sharp-tailed grouse, *Tympanuchus phasianellus* (Gratson et al. 1991), sage grouse, *Centrocercus urophasianus* (Gibson & Bradbury 1987) and black grouse (Alatalo et al. 1996). Although disruption appears to be ineffective at increasing an individual's mating success directly, it may offer a partial explanation for why females occasionally mate with males off leks.

The presence of homosexual mounting in buff-breasted sandpipers represents a conundrum. The fact that male-

male mounting frequently occurred between males that occupied adjacent territories suggests that such behaviour may function in establishing dominance and perhaps acquiring territories or additional matings. Male intrusions and/or homosexual mounting has also been documented in the sexually monomorphic lek-breeding ochre-bellied flycatcher, *Mionectes oleagineus* (Westcott & Smith 1994) and razorbill, *Alca torda* (Wagner 1996). Intruding flycatchers were primarily inexperienced, mostly immature, males that appeared to be either observing (or practising) courtship or evaluating the vigour of the territorial male. In contrast, intruding razorbill males appeared to use male-mountings as a fighting tactic to obtain additional copulations. Here, males that mounted other males obtained the highest mating success, while males that were mounted the most were less likely to return to the lek. The flycatcher explanation seems unlikely for buff-breasted sandpipers because mountings occurred between mature adults and occasionally included several males at a time. Although we did not directly test the razorbill explanation, the available evidence suggest it is also unlikely. Male-male mountings rarely resulted in a territory take-over (on one occasion the resident male abandoned his territory to follow a visiting female), and such mountings were typically used by most males at a lek. The evolution of such behaviour may be related to the potentially high reproductive rewards associated with stealing copulations and the negligible costs associated with homosexual mounting.

Male Mating Success and Mating Tactics

Research on lek-breeding species has shown that the relative payoffs of males using alternative tactics may differ considerably (Lank & Smith 1987; Kruijt & de Vos 1988; Fiske et al. 1994; McDonald & Potts 1994) or be similar (e.g. Pruett-Jones & Pruett-Jones 1990; Westcott & Smith 1994). Here, using behavioural observations and DNA typing, we found that a similar number of males that established short- and long-term territories on leks mated each year. Males that displayed at solitary sites also mated, although less frequently, and males located near nests only rarely fertilized eggs in the nest near which they displayed. Our analyses also indicated a weak, but nonsignificant trend for long-term lek males to mate with multiple females and to fertilize entire clutches of eggs more frequently. Further study is needed to substantiate this trend because of problems associated with uneven sampling of males using different tactics and the difficulties associated with assessing a male's mating success throughout the breeding season.

An analysis that combined males across mating tactics indicated that male lek attendance significantly influenced a male's mating success. Pruett-Jones (1988) failed to find a relationship between lek attendance and mating success in his study on buff-breasted sandpipers, although his measures of lek attendance and mating success differed from ours. Numerous other researchers have found significant relationships between lek attendance and male mating success (e.g. Gibson & Bradbury 1985; Höglund & Robertson 1990; Hill 1991; Fiske et al. 1994; Höglund & Alatalo 1995). Such positive relationships

may result from females visiting leks repeatedly, and mating with males that maintain territories for the longest period of time (males with the highest tenure are ascertained to be of highest quality, Hill 1991) or mating with males observed to copulate on previous days (i.e. delayed copying). Neither of these scenarios seems likely in buff-breasted sandpipers given that females breed within several days of arrival (Lanctot & Weatherhead 1997) and are not known to visit the same lek more than once (Lanctot et al. 1997). The most parsimonious explanation may be that long-tenure males have higher mating success because they are present longer and are selected by more females simply by chance. Initially, we suspected males that maintained long-term territories would pay an energetic cost (e.g. poor body condition) as suggested previously by Pruett-Jones (1988) for buff-breasted sandpipers, and as documented in the great snipe (Höglund et al. 1992) and sage grouse (Vehrencamp et al. 1989). Our analyses, however, failed to find a relationship between mating tactic and body condition. It seems likely that lek attendance by males is mediated by initial fat reserves, ability to forage for short periods off leks, and level of display and disruption occurring on leks (see Vehrencamp et al. 1989 for discussion of this topic).

The number of spots males had on their outer primaries was also weakly correlated with male mating success. Males that successfully mated in both 1993 and 1994 had fewer wing spots than males that were unsuccessful. Preliminary information on spot maturation suggests that successful males may be older (Lanctot & Laredo 1994). More data are needed to document how wing spotting changes with age to test this hypothesis adequately. Experimental manipulations of wing spots are also needed to confirm that this relationship is not an artefact of another unidentified variable that is correlated with wing spotting. If wing spotting is an important determinant of mating success, it seems likely that female choice, as opposed to male-male competition, is the driving force (as seen in studies on great snipe and peafowl, Höglund et al. 1990; Petrie & Halliday 1994). Indeed, female buff-breasted sandpipers frequently refused to mate with males even though their courtship was not disrupted by other males.

The role male behaviour plays in obtaining mates is less clear. Although male attraction displays were shown to influence male mating success in both years, the relationship varied between years in both its direction and strength. It seems likely that this relationship was spurious, possibly resulting from the small number of males observed during the study and the limited amount of time some males were observed. It is important to note, however, that female buff-breasted sandpipers also have a limited amount of time to evaluate and compare male behaviour (females lay eggs 4–7 days after visiting males on leks, see Lanctot & Weatherhead 1997), making male behaviour potentially unreliable as a mate selection cue.

Ecological and Morphological Explanations for Male Mating Patterns

The results of this study, in terms of the use of alternative mating tactics by males, the inability to distinguish

between males using alternative tactics based on morphological or behavioural attributes, and the lack of cues to indicate when males should abandon and settle on leks, may be partially explained by the breeding location and migratory nature of the species, and the lack of morphological markings to separate males from females. Climatic conditions in the high arctic make the timing and duration of breeding seasons unpredictable both within and across years. This variability appears to have led to extremely low lek stability, short tenure of males at leks, and males displaying at numerous locations across the arctic landscape (Lanctot & Weatherhead 1997). Such instability undoubtedly hinders the establishment of male dominance hierarchies and may explain the high levels of fighting and disruptions observed in this study (see discussion in Pruett-Jones 1988; Widemo 1997). Studies on great snipe and ruff also indicate that males within these species may move regularly between leks and display low site fidelity within and between years (Cramp & Simmons 1983; Lank & Smith 1987; Höglund & Robertson 1990). The short breeding seasons and high turnover of males at leks may also prevent females from visiting males repeatedly or copying the mate selection of other females. The reduction of male dominance-mediated mating (Robel & Ballard 1974; Foster 1983; Beehler & Foster 1988; Gratson et al. 1991; Hovi et al. 1995) and female mate selection mechanisms (see review in Kirkpatrick & Ryan 1991), commonly reported in other lek-breeding species (Höglund & Alatalo 1995), may reduce the benefits associated with males adopting one particular mating tactic and result in a sort of scramble competition in which males switch between tactics as conditions change (e.g. number of females visiting leks, number and quality of males on the occupied and adjacent leks).

Buff-breasted sandpipers are also unique in that they show only a slight size dimorphism and little plumage dimorphism between the sexes (Lanctot & Laredo 1994). We suggest these characteristics are maintained because of the reproductive advantages each accrues to males. For example, intense male-male competition, which occurs during territory establishment and disruptions, may favour the evolution of larger bodies, while benefits associated with female mimicry (i.e. sneak copulations) may favour the maintenance of plumage monomorphism and smaller bodies. Indeed, phylogenetic evidence suggests that the slight size dimorphism present in buff-breasted sandpipers today is a remnant from the species' past when less extreme forms of polygyny led to its evolution (Höglund & Sillén-Tullberg 1994). This hypothesis is not at odds with the hypothesis that wing spotting may have evolved as a male quality advertisement to females, because spots are only visible during the final precopulatory stages, and then, only to approaching females (sneaky males open their wings so that the inside surface faces away from the resident male). Further supporting evidence comes from studies of other monomorphic lek-breeding birds in which males frequently display sexual mimicry, and there is low lek stability and high male turnover within or between breeding seasons (Trail 1990; Westcott & Smith 1994). The end result of

maintaining plumage monomorphism is that male buff-breasted sandpipers are able to use multiple mating tactics more readily than males in other lek-breeding species. Alternative explanations for the absence of plumage dimorphism may include reducing predation costs (Höglund et al. 1992) and the evolution of alternative signals, such as acoustic or behavioural displays (Höglund 1989). The importance of monomorphic plumage in reducing predation is difficult to determine given the potential role plumage coloration plays in so many life history traits (e.g. predation on the wintering grounds and during migration). The evolution of alternative signals seems unlikely, however, given the limited vocal repertoire of the species, and the absence of a significantly positive relationship between male behaviour and male mating success as would be predicted if male behaviour was the target of selection. Further information on the effects of body size and plumage variation on the occurrence of disruption and female mimicry is needed to substantiate these ideas. Perhaps most valuable (but exceedingly difficult to obtain for this species) would be information on how males use different mating tactics throughout their lives.

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