1980). This species is also one of the few shorebird species that do not show a pronounced seasonal shift toward lowland, wet (ponded) sites during brood-rearing (Jones 1980). Habitat use by arctic shorebirds varies within and between years, and may depend on factors such as environmental variation (e.g., weather), changes in shorebird composition and abundance (i.e., presence of competitors for food and nesting areas), season, location (i.e., inland vs. coastal), social organisation, and predator regimes (Myers and Pitelka 1980).

Spring And Fall Migration

In North America, birds frequent short-grass areas such as pastures, golf courses, cemeteries, airports, and lawns (Campbell and Gregory 1976; Paulson 1993; J. Strauch, D. Dekker, personal communication); damp margins of fresh-water lakes, ponds, and lagoons (Campbell and Gregory 1976; Hayman et al. 1986; H.L. Dickson, personal communication); and fields of rice, recently cut alfalfa, cotton, and potatoes (Sutton 1960; T. Collins, J. Strauch, personal communication). In South America, birds are in recently harvested and burned sugar cane fields of Surinam (Haverschmidt 1972); in open, dry fields with short grasses in Brazil (Sick 1981); and on dry sand bars in rivers (southeast Peru; Bolster and Robinson 1990).

**VARIABLE MATING BEHAVIOUR AND
REPRODUCTIVE SUCCESS IN THE LEK-BREEDING
BUFF-BREASTED SANDPIPER, *TRYNGITES SUBRUFICOLLIS***

by

Richard B. Lancot, M.S.

A thesis submitted to the Faculty of Graduate Studies
and Research in partial fulfilment of the requirements for the degree of
Doctor of Philosophy

Department of Biology, Carleton University
Ottawa, Ontario

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**Variable Mating Behaviour
and Reproductive Success in the Lek-breeding
Buff-breasted Sandpiper, *Tryngites subruficollis***

submitted by Richard B. Lancot
in partial fulfilment of the requirements
for the degree of
Doctor of Philosophy

Chairman

Department of Biology

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External Examiner

Carleton University

20 September 1996

ABSTRACT

This thesis summarises data collected during a three-year breeding biology study of the buff-breasted sandpiper, *Tryngites subruficollis*. Buff-breasted sandpipers are one of three shorebirds world-wide that have a lek mating system. The first chapter of the thesis provides a detailed description of the life history of the buff-breasted sandpiper, and thereby provides a framework with which to understand and interpret subsequent sections of the thesis.

The second chapter of the thesis describes variation in male mating behaviour and explores the causes of that variation. Individual male behaviour varied from remaining at a single lek for most of the breeding season or attending multiple leks over the season, to displaying solitarily or displaying both on leks and solitarily. The percentage of males that displayed on leks remained relatively stable (about 75%) and was not affected by changes in the operational sex ratio or the intensity of male-male competition. Rather, male display on leks appeared to be mediated by variable regional ecological conditions.

The third chapter of the thesis investigates whether individual differences among males account for their use of alternative mating tactics. Analyses involving 13 morphological and behavioural traits failed to find any trait that consistently differentiated males using alternative mating tactics. Males using different mating tactics also had similar mating success. An analyses that combined males across mating tactics indicated males with longer lek tenure and fewer wing spots had higher mating success. Disruption and female mimicry were used by both long- and short-term lek males and

enhance the mating opportunities of disrupting males by attracting females away from neighbouring males and allowing copulations to be stolen.

Why females in lek-breeding species continue to mate selectively despite the predicted decrease in additive genetic variance in the preferred male traits is called the "lek paradox". In the final chapter, I combined detailed behavioural observations with paternity analyses using DNA fingerprinting to provide a simple solution to the paradox, i.e. females are less choosy than predicted. I suggest that the resulting low variance in male reproductive success arises from males using alternative reproductive tactics, females mating away from leks, and females mating with multiple males.

ACKNOWLEDGEMENTS

My interest in behavioural ecology began perhaps in what some people might consider an immoral way. When I was 8 years old, my father informed me that it was my duty to rid our farm of the birds (barn swallow, *Hirundo rustica*) and flickertails (thirteen-lined ground squirrel, *Citellus tridecemlineatus*) that inhabited our machine sheds and cattle pastures, respectively. In my father's mind, swallows and squirrels were the pests that dirtied our farm machinery and prevented the grass in our pastures from growing properly. At the time, I thought little about animal rights, and even though I can not once remember wondering how male barn swallows acquire mates or which characteristics reflect a "high" quality male, I was fascinated by their behaviour and wished to learn more about them. At 14 years of age, I discovered the fine art of how hunting from my close friend and mentor Frenchie Vaudrin. The hundreds of hours I spent hunting white-tailed deer (*Odocoileus virginianus*) in Northern Minnesota heightened my interest in wildlife. My biological curiosity was also enhanced by my high school science teacher, Mr. Knudsvig. His knowledge and interest in me probably resulted in my enrolment at the University of North Dakota where I acquired my bachelor's degree in Fish and Wildlife Biology. Like many other outdoor enthusiasts that want to be conservation officers, I was surprised to learn that the field of biology included everyone from cell physiologists to zoo curators. Dov Lank, Connie Smith and Lewis Oring first introduced me to the subdiscipline of animal behaviour during the summer of 1982 when I volunteered to work with them on spotted sandpipers (*Actitis macularia*).

However, it was not until a visit to Costa Rica in the winter of 1983 (and subsequent discussions with Milton and Diana Lieberman) that I became fully aware that there was more to life than managing white-tailed deer on my father's farm. Here began my acute interest in behavioural ecology that led me to study the mating behaviour of the prairie vole (*Microtus ochrogaster*) for my Master's degree and the lekking behaviour of the buff-breasted sandpiper for my Ph.D.

My research on buff-breasted sandpipers began when Dirk Derksen, the Migratory Bird Branch Chief at the Alaska Science Center (ASC) of the National Biological Service, suggested that BP Exploration (Alaska) Inc. (BPX) might be willing to support a research study on this species. In-depth conversations with Chris Herlugson at BPX resulted in seed money for a preliminary field season in 1991 and a full study in 1992. Bob Gill, the shorebird project leader at the ASC, also provided initial start-up funds in 1991, and continued to support the project through the remainder of the study. Other organisations that provided financial and logistical support included the North Slope Borough of Alaska, the Alaska Department of Transportation, ARCO Alaska Inc., Carleton University, Northern Ecological Services of the U.S. Fish & Wildlife Service, and the Natural Sciences and Engineering Research Council of Canada.

Among birds, shorebirds are notoriously difficult to study, and among shorebirds, buff-breasted sandpipers are one of the most enigmatic. Previous research on this species by Bruce Lyon, Phillip Martin, Stephen MacLean, Brian McCaffery, Kate Moitoret, Pete Myers, Stephen Pruett-Jones, Bob Rodrigues, and Declan Troy helped eliminate many potential problems. Conversations with them, as well as Pablo Canevari, Gonzalo Castro,

Ken Kertell, Dov Lank, my supervisor's Pat Weatherhead and Bob Gill, and my two committee members, Hans Daman and Scott Findlay, helped me to develop my study proposal.

Very little of this study could have been completed without the work, encouragement, and warm friendship of many field assistants that contributed to this project. These include, in alphabetical order, Connie Adams, Ellen Bentley, Marc Bélisle, An Bleick, Bill Brown, Paul Hess, Bart Kempnaers, Glen Kit, Joanna Klima, Gerry North, Christian Ottke, Carol Ramey, Lynda Ronan, Jason Schraeder, Leslie Slater, Lee Tibbitts, and Bill Wilmoth.

Bart Kempnaers was especially helpful in collecting behavioural data (even though he should have been working on his own Ph.D.) and providing a forum in which I could express my ideas and concerns about the study. My memories of our midnight observation sessions and in-depth discussions of life's questions will always be treasured.

Lynda Ronan was instrumental in coordinating the geographical information system portion of the study, and entered and organised inordinate amounts of data.

Special thanks go to Leslie Slater who provided an immense amount of support and assistance during the initial stages of the project. Paradoxically, the satisfaction I have obtained from completing my Ph.D. program will always be overshadowed by the sadness that accompanied our divorce.

The genetic laboratory work and analyses, which proved to be so instrumental in understanding this species' mating system, was only possible through the skill, guidance, and advice of Kim Scribner, Ray Fields, and Judy Gust. Terry Burke provided advice on

DNA scoring, and along with Olivier Hanotte, provided the single locus minisatellite DNA probes which allowed me to identify sires.

Fellow post-doctorate and graduate students at Carleton University, including Kevin Dufour, Mark Forbes, Monica Mather, Kent Prior, Lisa Venier, and Stephen Yezerinac, provided friendship, advice and assistance throughout my stay at Carleton University. I received similar support from my research associates at the National Biological Service. Colleen Handel, Cindy Hinshaw, Jeff Mason, Lee Tibbitts, David Ward, and Mary Whalen were especially helpful. Bob Gill, my direct supervisor at the ASC, was instrumental in providing administrative support throughout the project. I am grateful to him for stepping away from the project and allowing me to develop confidence in my research abilities and to conduct a research project that was perhaps a bit more esoteric than the usual National Biological Service study.

Numerous other people contributed unpublished information on buff-breasted sandpipers. These include Daniel Blanco, Pablo Canevari, Tom Collins, Dick Dekker, Loney Dickson, Brian Harrington, Lloyd Kiff, Phillip Martin, Mariano Martinez, David McDonald, Kate Moitoret, Robert Montgomerie, R.I. Guy Morrison, Alan Spaans, Misha Stishov, Joe Strauch, Jr., Declan Troy, and Tom Walker. John Pearce translated Russian articles, and Lee Tibbitts, Jacque Lee, and Michelle Watt translated Spanish articles. The Denver Museum of Natural History and the Canadian Museum of Nature allowed access to museum specimens, and the staff of the Borror Laboratory of Bioacoustics, Ohio State University, prepared sonograms. Kevin Karlson generously contributed photographs and Mary Whalen graciously drew sketches of birds for several publications. Ted Swem and

Jacob Höglund gave suggestions on methods for capturing birds. Personnel at the Service Area Ten and Annex 1 housing units provided incredible food and other tangibles during our stay at Prudhoe Bay.

I would like to thank the numerous people who reviewed chapter drafts, including Patty Gowaty, Jacob Höglund, Jerry Hupp, Bart Kempenaers, Dov Lank, Robert Montgomerie, Lewis Oring, Stephen Pruett-Jones, John Reynolds, Kim Scribner, Larry Wolf, Stephen Yezerinac, and the University of Nevada, Reno, and Queen's University discussion groups. I thank my supervisor, Pat Weatherhead, my committee members, Hans Daman and Scott Findlay, and my external examiner, Dave McDonald, for providing constructive criticism on proposals and/or thesis chapters. Pat was especially instrumental in helping me formulate ideas and organise my thoughts during the write-up stage of this project. I leave Carleton University with an increased awareness of the scientific method and manuscript preparation because of Pat's patience and constructive criticism.

Finally, I thank my family. Mom and dad were especially helpful in providing moral and financial support. Their unconditional love and confidence kept me going when times were difficult.

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GENERAL INTRODUCTION

The way males and females interact to obtain mates is referred to as the 'mating system' of a species. This term traditionally includes the number and way mates are acquired, a description of the pair bond, and the pattern of parental care provided by each sex (Emlen and Oring 1977). Lek mating systems are generally distinguished from other mating systems (such as monogamy, polygyny, polyandry) by the following criteria (Emlen and Oring 1977, Bradbury 1981, Oring 1982, Wiley 1991, Höglund and Alatalo 1995):

1. Males aggregate together on arenas or leks to which females come and on which most of the mating occurs.
2. Males provide no parental care and contribute nothing to the next generation except gametes.
3. Male territories provide no resources to the male or visiting females.

A fourth distinguishing criteria, frequently included by researchers (e.g., Bradbury 1981), is that females are free to select their mate. In some species, however, female choice is constrained by males who disrupt the courtship of their neighbours (Foster 1983) and by the establishment of dominance hierarchies among males which influence male display location and ultimately male access to females (Beehler and Foster 1988). Regardless of the mechanism, researchers have detected a pronounced skew in male mating success in

virtually every lek-breeding species studied to date (Wiley 1991, Höglund and Alatalo 1995).

A multitude of breeding biology studies during the past several decades has revealed that lek mating occurs in a variety of taxa, including insects, fish, amphibians, birds, and mammals (Höglund and Alatalo 1995). Lekking has been described in at least 97 species of birds (Höglund and Alatalo 1995), or about 1% of the roughly 9200 bird species in the world (Howard and Moore 1991). Most of the remaining species mate monogamously (Oring 1982). Avian lek-breeding species are primarily either grouse (8), hummingbirds (14), cotingas (18), manakins (18) and birds of paradise (18; Höglund and Alatalo 1995). Lekking has evolved only twice in shorebirds (Family Scolopacidae), including once in the great snipe (*Gallinago media*) and once in the line leading to the buff-breasted sandpiper and ruff (*Philomachus pugnax*, Höglund 1989).

Males are thought to aggregate on leks when either females or the resources they depend upon can not be economically defended (Bradbury 1977, 1981; Emlen and Oring 1977; Oring 1982; Davies 1991). This is most likely to occur when females use widely dispersed resources, resulting in large, undefendable ranges, or when females share a common range and local density is high, resulting in intense male-male competition (Davies 1991). Emlen and Oring (1977) suggested using the operational sex ratio (OSR; i.e., number of fertilisable females relative to the number of sexually active males) as a gauge to predict the level of intrasexual competition and hence the likelihood of males being able to defend resource territories economically. Under intense male-male competition (i.e., when the OSR is skewed toward males), they predicted males would

establish dominance hierarchies on leks and/or demonstrate quality based on display. Few studies, however, have evaluated the strength of this prediction.

Besides displaying on leks, males in many lek breeding species also use a variety of alternative reproductive strategies or tactics to acquire mates (Rubenstein 1980, Dunbar 1982, Arak 1984). Examples of alternative mating tactics include establishing resource defence territories (Clutton-Brock et al. 1988), mimicking female behaviour and attempting to sneak copulations from other territorial males (Trail 1990, Westcott and Smith 1994) or pursuing females off leks (Gibson and Bradbury 1987, Lank and Smith 1987). The presence of alternative reproductive strategies may occur because males differ in some fixed phenotypic feature. A classic example is the resident and satellite strategies seen in ruff where the genetic make-up (which produces dark and light ruffs) of males predisposes them to follow a particular strategy (Lank et al. 1995). Alternative mating strategies may be maintained because: (1) each strategy is adapted to a particular local habitat, (2) the fitness payoff for both strategies is equivalent and frequency dependent (a *mixed-evolutionary stable strategy*), or (3) some animals are forced to adopt an inferior strategy because of a competitive disadvantage (a *conditional evolutionary stable strategy*). Alternatively, males may exhibit different strategies during their life depending upon their phenotype at a particular moment (e.g. body size). These are referred to as *phenotype-limited strategies*. Additionally, some individuals within a species may use different mating behaviours depending on the prevailing ecological (e.g., resource distribution) or social environment (e.g., abundance of competitors and potential mates).

Such mating behaviour flexibility is generally referred to as *mating tactics* as opposed to strategies.

Recent studies of species with alternative mating behaviours have focused on: (1) documenting the costs and benefits to males using each behaviour, (2) identifying the conditions that lead to the use of one mating behaviour rather than another, and (3) determining the origin of these alternative mating behaviours (i.e., are they genetically fixed or conditional) (Rubenstein 1980, Dunbar 1982, Arak 1984, 1988, Gross 1984, Reynolds et al. 1995, Andersson 1994, Lucas and Howard 1995). Research on lek-breeding species where males exhibit alternative male mating behaviours may provide clues to the evolution of lek breeding.

Understanding why females in lek-breeding species exhibit strong unanimity in their choice of mates has been the subject of considerable debate (see e.g., Reynolds and Gross 1990, Kirkpatrick and Ryan 1991). Such unanimity is puzzling because females gain no direct material benefits (e.g., food, nest sites, or parental care; Wiley 1991, Höglund and Alatalo 1995). Males provide only sperm to the reproductive effort. Such strong selection for particular males is predicted to decrease additive genetic variance in the preferred male traits, leading eventually to females having no variability to choose from (Gustafsson 1986, Mousseau and Roff 1987, but see Pomiankowski and Møller 1995). Why females continue to select mates despite the predicted absence of variation in male traits is commonly called the "lek paradox" (Borgia 1979, Taylor and Williams 1982, Reynolds and Gross 1990, Kirkpatrick and Ryan 1991, Wiley 1991).

A number of solutions have been presented to resolve the paradox (see review in Kirkpatrick and Ryan 1991). Unanimity in female choice might be explained if (1) female preference has little or no cost, (2) females benefit from increased fertilisation rates, avoiding harassment, reducing predation risk or decreasing the probability of contracting a disease, or (3) female preferences arise as a correlated response to natural selection (i.e., pleiotropic gene action). In addition, females may benefit from continuing to be choosy if the genetic variance in the system was maintained by random genetic drift, mutation pressure, or through a parasite-host co-evolutionary process. Pomiankowski and Møller (1995) refuted the basic assumption of the lek paradox, asserting that sexually selected traits under long-term directional selection should show higher, not lower, additive genetic variance than non-sexual traits that are under stabilising natural selection. Although this represents a plausible solution to the lek paradox, additional data are needed before definitive conclusions can be made (Turner 1995). Perhaps the simplest solution to the lek paradox is that female choice of mates is not as unanimous as behavioural observations suggest. Indeed, discrepancies between apparent and true reproductive success (as revealed by paternity analyses) have been reported in monogamous, polygynous, polyandrous, and cooperative breeding species (Birkhead and Møller 1992). To date, few studies have evaluated the relationship between apparent and true male mating success in a lek-breeding species.

In this thesis, my primary objectives are to: (1) document the extent and possible reasons for variable male mating behaviour in the buff-breasted sandpiper, (2) investigate whether there are individual differences among males that relate to their use of different

mating behaviours and to their mating success, and (3) examine female choice of males by comparing paternity results obtaining from DNA fingerprinting with behavioural observations of male mating success on leks.

The first chapter of this thesis provides a detailed description of the life history of the buff-breasted sandpiper. Because knowledge of a species natural history is essential to conduct and interpret a behavioural ecology study, it seemed an appropriate first step in the preparation of my thesis. Indeed, the natural history in this instance proved to be essential to understanding why the lekking behaviour of the buff-breasted sandpiper is so atypical relative to other species that have been studied. This chapter was written as part of the *Birds of North America* series, which is a collection of species accounts which detail the life history of each of the roughly 700 bird species that breed in North America. Given the abundance of life history categories, the editors of the BNA series demanded a concise reporting style that at times appears abbreviated and perhaps choppy. Despite this, I felt that the paper was best presented if kept in its published format.

The second chapter of this thesis investigates variation in male mating behaviour in the buff-breasted sandpiper, and attempts to explain that variation by investigating the social context in which various behaviours occur. Previous work on the buff-breasted sandpiper, although suggestive of a variable mating system, was based mostly on anecdotal observations. This chapter summarises variation in male mating behaviour obtained over a three-year period during which a large number of marked individuals were followed over a large area. Thus, it represents the first comprehensive description of this species' mating behaviour. I then tested several predictions made by Emlen and Oring

(1977) regarding when males should display on leks. Specifically, I investigated how the proportion of males displaying on leks changed in relation to the operational sex ratio and the intensity of male competition on leks. I also followed individual males through time to document whether all males responded similarly to changes in the social environment

The third chapter of this thesis investigates whether there are individual differences among males that explains variation in their use of leks, their behaviour on leks, and their mating success. Specifically, I investigated the relationship between male traits (e.g., size, condition, symmetry, and wing coloration), male mating tactics (e.g., long- versus short-term lek tenure, solitary display) and male behaviour on leks (e.g., use of female mimicry, and aggression toward other males). Finally, I examine how male traits and male behaviour relate to male mating success.

The fourth chapter of this thesis attempts to resolve the lek paradox in the buff-breasted sandpiper by combining behavioural observations of male matings on leks with paternity analyses using single locus minisatellite DNA probes. These analyses provide the first evidence from a lek-breeding species that the variance in male reproductive success is much lower than expected based on the observed skew in mating success. I attribute this difference to the use of alternative reproductive tactics by males, females mating with solitary males off leks, and multiple mating by females.

I finish the thesis with a conclusion section that discusses the overall implications of each chapter in relation to understanding the evolution of alternative male mating behaviour in the buff-breasted sandpiper. I then discuss the need and direction for future research on lekking behaviour in general and on the buff-breasted sandpiper in particular

GENERAL METHODS

Study Area

I collected observations on a 16-km² study area on the eastern edge of the Prudhoe Bay Oil Field, Alaska (70°12'N, 148°15'W), from late May through July, 1992-1994 (Figure 1). The Prudhoe Bay Oil Field is part of the Arctic Coastal Plain and is bordered by the Beaufort Sea to the north and the Franklin Bluffs to the south (Hohenberger et al. 1994). The region is characterized by cool summers (mean July temperatures range from 2 to 8° C), little precipitation (May through July cumulative precipitation averages < 1"), elevations that range from sea level at coastal lagoons to 15 m several kilometres inland, extensive networks of rivers and streams, and a large number of wetlands (Bergman et al. 1977, Walker et al. 1980, Derksen et al. 1981, Hohenberger et al. 1994). The 16-km² study area is located between the east and west branch of the Sagavanirktok River. Here elevations range from 1.5-13.8 m ASL, predominant landforms include non- and reticulate-patterned ground, and vegetation types include moist graminoid meadow and dry prostrate scrub (Walker et al. 1980, R.B. Lanctot, unpublished data). A detailed description of the area's geology, climate, landforms, soils, and vegetation is provided in Walker et al. (1980).

Capture, Sex Identification and Nesting Chronology

I captured adult buff-breasted sandpipers at leks and solitary sites throughout the study area using mist nets. Females were also captured on nests with walk-in traps during

Figure 1. Location of the 16-km² study area located on the Prudhoe Bay Oil Field, Deadhorse, Alaska.

incubation. Each bird was weighed, measured, and then ringed with unique coloured tarsal bands and a U.S. Fish and Wildlife Service metal band to facilitate identification of individuals. In addition, 1.2 g radio transmitters (Holohil Systems, Ltd.) were superglued to the back of 6-25 adults each year (total = 12 males, 38 females). Radio-equipped birds were located daily when possible with a portable ATS receiver and either a stationary 4-element null-peak or hand-held 3-element single yagi antenna. An omni-directional antenna mounted on the roof of a vehicle and a fixed-wing aircraft outfitted with 2-element H-antennas were used to search for birds that had left the study area.

Because males and females resemble each other, I determined a bird's sex with a discriminant function that involves measurements of the length of the birds' wing, tarsus, culmen and head. To develop the function, I measured the size of 48 buff-breasted sandpiper skins (26 males, 22 females) located at the Canadian Museum of Nature and the Denver Museum of Natural History. The discriminant function correctly identified the sex of 47 of the 48 birds (error rate of 2.1%), and in most instances, produced *a posteriori* probability values that clearly indicated the birds to be either males or females. Birds that were not captured were sexed based on between-sex differences in size and behaviour (Rowan 1927, Oring 1964, Myers 1979). A small number of birds whose sex was unknown (i.e., intermediate sized birds that failed to exhibit sex specific behaviours) were excluded from all analyses.

Nests were located by flushing females with ropes dragged across the tundra, by tracking radio-equipped females, by following females foraging away from their nests, and by searching near displaying males. Twenty and 12 clutches were collected in 1993 and

1994, respectively, as part of a paternity study (Chapter 4). Because most nests were completed before I discovered them, I determined dates of nest initiation by back-dating from subsequent events (e. g., hatch dates, chick weights, egg floatation, and embryo development of collected eggs; R.B. Lanctot, unpublished data). I used a 23 day incubation period (laying of fourth egg to hatching of fourth egg) to determine nest initiation. I considered nests, where no chicks were found, to have failed if the nest was found empty prior to the anticipated hatching date (based on egg floatation scores or dates of egg-laying) or broken eggs, fox scat or scent were found in the nest. Nests were considered abandoned if the eggs were found cold on two consecutive visits spaced 2-3 days apart.

Survey Procedures

To document the location of male display sites and the chronology of male display, I visited the study area daily until the first birds were detected and then began surveying the area once every three to five days until male display subsided. Survey techniques included variable circular plot sampling (Reynolds et al., 1980) and complete coverage strip transects.

Variable circular plot sampling involved one or two observers who recorded the location, number, and behaviour of all birds seen at each of 32 survey points spaced at 500 m intervals throughout two regions of the study area. Birds were recorded during 10-min sampling periods at each point and while walking between points. Locations of all birds were plotted on topographical maps labelled with concentric rings indicating 50 m

distance increments. Data were collected at one of three randomly but equally selected time intervals: 0600-1200, 1200-1800, and 1800-2400. Because this sampling technique covered only a portion of the study area, I used these data primarily to document arrival dates of birds and movement of marked males.

Strip transect censusing consisted of four to six observers simultaneously surveying adjacent 200 m wide transect routes that covered the entire study area. Observers stopped every 300 m along their routes and scanned for birds in all directions for at least 3 min. Bird locations were mapped using a reference grid of stakes spaced at 100 m intervals. Surveys began at 0800 and were usually completed by 1500. Strip transects were not conducted in 1992 because reference stakes were not installed.

Definition and Observations of Leks

For this study, I considered a male to be part of a "lek" if he was located within 200 m of another displaying male. This distance was chosen because males frequently defended territories and exhibited aerial courtship displays over areas of this size throughout the lekking period. Males more than 200 m apart interacted much less frequently. For comparisons of male display behaviour among years, I considered males detected alone to be part of a lek if a previous or subsequent survey detected multiple males in the same area. I classified leks as "stable" if males were present in the same area for at least two surveys within a year and as "unstable" if males were only present during a single survey.

Up to four observers recorded mating activity daily on 2-3 leks from late May to mid-June each year; males at the remaining leks and in solitary locations were observed less frequently. Observations were made throughout the day and arctic sunlit night for about 3-6 hrs per day. Individual male (1992 and 1993) and female (1994) buff-breasted sandpipers were observed for 30 min or until they disappeared from view. Focal observations were recorded onto tape cassettes by one or two people. When a single observer was present, s/he made a continuous record of the focal bird's behaviour and its interactions with other males and females. The second person, always present in 1993 and 1994, monitored the location and movements of other birds (e.g., adjacent and resident males, visiting females) on the lek. The location and identity of displaying males were plotted on topographical maps using grids of stakes, placed at 25 or 100 m intervals, as reference points.

Data Analyses

Tape recordings of focal observations were translated and summarized with The Observer software package, version 2 (Noldus, 1990). All statistical analyses were performed using the SAS® Statistical Package for Windows (version 6.08 or 6.10) and followed Sokal and Rohlf (1981) or Zar (1984) for all analyses. In most cases, small sample size required the use of non-parametric statistics. Analyses were restricted to 1993 and 1994 if tests required standardised survey techniques that included the entire 16-km² study area. All tests were two-tailed and conducted at the 0.05 significance level. Means are reported as $\pm$ SD unless otherwise stated.

CHAPTER 1.**NATURAL HISTORY OF THE BUFF-BREASTED SANDPIPER
(TRYNGITES SUBRUFICOLLIS)**

This chapter formed the basis of a paper published in *The Birds of North America* (No. 91) and co-authored by Claudio D. Laredo.

SUMMARY

The buff-breasted sandpiper is a medium-sized shorebird that breeds sporadically along arctic coasts from central Alaska to Devon Island, Canada. It winters in South America on the pampas of Argentina, Uruguay, and Paraguay where individuals frequent heavily grazed grasslands and grasslands adjacent to wetlands. Northward migration proceeds through central South America, across the Gulf of Mexico, and through the central United States and Canada before the birds reach the arctic coast. Southward migration follows a similar route, but over a much broader front.

Buff-breasted sandpipers are unique among North American shorebirds in having a lek mating system. Males defend relatively small territories that provide no resources for females and are simply display sites to which females can be attracted. Females select a mate and then leave to nest and raise their chicks elsewhere.

Once abundant, the population decreased substantially in numbers owing to commercial hunting in the late 1800s and to loss of habitat along its migratory route in the central United States and its wintering grounds in South America. The extreme tameness of the buff-breasted sandpiper and its tendency to return to a wounded flock member made these birds especially vulnerable to hunting. Recent surveys on the migration corridor suggest this species may still be declining, although more study is needed to accurately determine the size of its population.

DISTINGUISHING CHARACTERISTICS

Medium-sized plover-like shorebird (18-20 cm long, male 57-78 g, female 46-66 g). Face and underparts strongly buff in all plumages; bright yellow-ochre legs; short, dark, pigeon-like bill. In flight, upperwing buffish, underwing axillaries gleaming white and contrasting with buff flanks and belly and dark bar at tips of under primary coverts. Upperwing also has indistinct buffish bar that poorly contrasts with rest of upperparts. Sexes similar in plumage, but males average larger, difficult to reliably classify sexes in field. Juveniles similar to adults but distinguishable at close distance. Juvenile ruff similar, but much larger (20-25 cm long for female) with dull-coloured legs and white wingbar and sides to rump. Upland sandpiper (*Bartramia longicauda*) also buff-coloured but larger (28-32 cm long) with longer neck and tail. Baird's sandpiper (*Calidris bairdii*) has black legs with the buff of the breast cut off sharply from white of abdomen. Similar to eurasian

dotterel (*Charadrius morinellus*) in flight, but dotterel has conspicuous black-and-white tail tip and prominent pale supercilium (Hayman et al. 1986, Paulson 1993).

DISTRIBUTION

The Americas

Breeding range. See Figure 1-1. High arctic (66°-76°N) including Alaska (Point Barrow and Atkasuk eastward), Yukon (Herschel Island, Blow River to Clarence Lagoon), Mackenzie (Anderson River to Horton River, Franklin Bay, Rasmussen Basin Lowlands), Banks Island (south of Bernard River, Sach's Harbor, De Salis Bay), Melville Island (Polynia Lake, Winter Harbor), Bathurst Island (Cape Cockburn, Polar Bear Pass), Devon Island (Truelove Lowland, Cape Sparbo), Victoria Island (Cambridge Bay, Prince Albert Sound, Richard Collinson Inlet), Jenny Lind Island, King William Island, Prince of Wales Island (Crooked Lake), Boothia Peninsula (Wrottesley Valley), and Somerset Island (Creswell River; Manning et al. 1956, Höhn 1959, Alliston et al. 1976, McLaren and Renaud 1977, McClaren et al. 1977, Salter et al. 1980, McLaren and Alliston 1981, Am. Ornithol. Union 1983, McWhorter et al. 1986, Godfrey 1986). Courtship also observed near Cape Woolley, Seward Peninsula in western Alaska (Kessel 1989).

Winter range. See Figure 1-2. Southern South America (19°-38° S) including Argentina (Buenos Aires, Córdoba, Formosa, Misiones, Corrientes, Sante Fe, Jujuy, and Entre Ríos provinces), Uruguay (Canelones, Maldonado, Montivideo, and Rocho provinces), and Boquerón and Central provinces of Paraguay (Stempelmann and Schulz

Figure 1-1. Breeding range of the buff-breasted sandpiper in North America.

Figure 1-2. Breeding and wintering ranges and key migration routes of the buff-breasted sandpiper.

1890; Wetmore 1926, 1927; Hellmayr and Conover 1948; Teague 1955; Cuello and Gerzenstein 1962; Myers and Myers 1979; Contreras 1981; De La Peña 1988; Narosky 1988; Hayes et al 1990; Blanco and Canevari 1992; Devesa et al. 1992; Blanco et al. 1993; Rilla 1993, F. Moschione, personal communication). Altiplanos of northwest Argentina and southwest Bolivia (C. Laredo, unpublished data). Use of mouths of Colorado and Negro rivers in northern Patagonia as winter areas (Wetmore 1927) is unsubstantiated.

Outside the Americas

Breeding range. Wrangel Island and Western Chukotka, Russia, from Aion Island east to Ekryratap River Valley (Dorogoi 1983; Stishov 1989, personal communication).

Winter range. Regular visitor to Ireland and Great Britain (Sharrock and Sharrock 1976) and accidental to most parts of continental Europe, Africa, Japan, and Australia (Hayman et al. 1986).

Historical Changes In Distribution

Breeding range in Western Chukotka, Russia, may be relic of a larger range during the time of the Bering Land Bridge in the late Pleistocene (Stishov 1989). Although reported to include Paraguay, primary winter range seems to be farther south in Argentina (Hayes et al. 1990). Recent wintering records in northwest Argentina (Narosky 1988) and

southwest Bolivia (C Laredo, personal observation) may be a result of habitat modification in principal wintering habitat in eastern Argentina

Fossil History

No available data.

SYSTEMATICS

Geographic Variation

None reported.

Subspecies; Related Species

Kessel (1989) suggested a western population breeds in western Chukotka and migrates along the coast of the Pacific Ocean (in contrast to the interior of North America), but no banding, morphometric, or genetic studies have been conducted to define the differences between western and eastern populations.

Strauch (1976) suggested merging *Tryngites* with the *Calidris* genus based on anatomical features. Although chicks from the two genera also have similar downy patterns, *Tryngites* has unique juvenile and adult plumages, and its displays lack song flights present in *Calidris*. *Tryngites* may thus be intermediate between *Calidris* and *Philomachus* genera (Johnsgard 1981). Larsen (1957) suggested *Tryngites* and

Philomachus may be sister taxa that diverged in the Miocene. Their similar social systems support this hypothesis, or may be due to convergent evolution.

MIGRATION

Nature Of Migration In The Species

Large variation in annual densities in staging areas and on breeding grounds (see Demography and Populations: population status) may coincide with changes in local food abundance and conditions on the migratory route (Pitelka et al. 1974, Dekker 1991). Sightings of birds in Saskatchewan throughout summer (1 May - 5 October; H.L. Dickson, personal communication) and at Beaverhills Lake, Alberta, into mid-June (D. Dekker, personal communication) suggest some birds "short-stop" migration and fail to reach the breeding grounds. Information on these individuals is needed.

Timing And Routes Of Migration

Most birds depart Buenos Aires Province in Argentina by early February, although some birds, primarily females, remain into late March (see Figure 1-3; Myers and Myers 1979). Northward migration is via central Amazonia/Pantanal flyway (Antas 1983), through Brazil in March (Campbell and Gregory 1976), and through Venezuela, Guyana, and Surinam in April (Bent 1927, Haverschmidt 1972, Thomas 1987). Birds arrive in Texas and Louisiana late April to early May after flying over the Gulf of Mexico (Hall 1960; C. Collins, B. Harrington, personal communication). Migration in North America

Figure 1-3. Annual cycle of migration, breeding, and molt of the buff-breasted sandpiper .

Thick lines show peak activity, thin lines off peak.

follows a narrow corridor (94°-100°W) through states and provinces such as Oklahoma (9-12 May; Oring 1964), southern Kansas, eastern Nebraska (8 May; J. Strauch personal communication), Iowa, Missouri, Saskatchewan and Alberta (12 May; Dekker 1991, personal communication). Birds arrive at southern edge of breeding grounds by late May and at remote sites by the second week in June (Campbell and Gregory 1976, R. Lanctot, personal observation). Males precede females from wintering grounds (Myers and Myers 1979) and through Oklahoma (Oring 1964) and Alberta (Rowan 1927), but both sexes arrive simultaneously on breeding grounds (R. Lanctot, personal observation). Virtually unseen on Atlantic or Pacific coasts during the spring (Bent 1927, Campbell and Gregory 1976).

Males and non- and failed-breeding females leave breeding grounds after nest initiation during mid-June to early July (R. Lanctot, personal observation). Females that breed successfully, and their broods, depart late July to early September (Campbell and Gregory 1976, R. Lanctot, personal observation). Birds generally follow the same route south (as their northerly route in spring) but travel over wider corridor: from British Columbia (25 July - 8 October; Campbell and Gregory 1976) to Nova Scotia (22 July - 22 September; G. Morrison, personal communication). Small numbers move east before flying south along the western side of Hudson Bay (14 July - 17 August, Jehl and Smith 1970), across the Great Lakes, and through the New England states (1 August - 1 November, B. Harrington, personal communication; Campbell and Gregory 1976, Cramp and Simmons 1983). Migration in South America retraces the Central Amazonia/Pantanal

flyway (Antas 1983) but covers a broader front than northward migration (Blake 1977).

Birds reported in every South American country except from Chile (C. Laredo, unpublished data). Birds arrive on wintering grounds in Argentina during second week of September; numbers grow through mid-October and remain constant through January (Myers and Myers 1979).

Based on collection location and age of museum specimens, adults thought to migrate south via Central Flyway, whereas juveniles may use east and west coasts of North America more frequently (Campbell and Gregory 1976; J. Strauch, personal communication). Adults also thought to precede juveniles through prairie provinces (last 3 weeks of August versus September; Rowan 1927).

Highest concentrations of this species in North America found (March - April?) east of Houston, Texas (flocks of 500); York Co., Nebraska (100s and 1000s each year); and Beaverhills Lake near Edmonton, Alberta (flocks of 300 - 2000; Rowan 1927, D. Dekker 1991, personal communication; J. Strauch, personal communication). A flock of 2200 near Saskatoon, Saskatchewan, in May 1985 indicated this may be an important staging area (Gollop 1985). Migration distance from United States indicates a staging area should exist in northern South America (J. Strauch, personal communication). Besides one 500 bird flock near Meta, Columbia, in March 1977 (B. Harrington, personal communication), no large concentrations have been observed. Myers (1980) estimated as many as 2000 birds wintered on the 11,000 ha Estancia Medaland ranch in Buenos Aires Province, Argentina, in 1973.

Migratory Behaviour

Birds commonly observed as singles or pairs, occasionally in flocks of ≤ 5 ; suspected of being nocturnal migrants (Rowan 1927, Hall 1960, Oring 1964). Species use the same fields from year-to-year (Oring 1964; Abbott 1982; H.L. Dickson, D. Dekker, J. Strauch, personal communication). Given suitable environmental conditions (Dekker 1991), birds may concentrate at particular locations, but often in only one field despite the availability of others; feed in small, evenly distributed territories (Hall 1960, see Behaviour: spacing).

Control And Physiology Of Migration

Birds shot in Nebraska (J. Strauch, personal communication) and Alberta (Rowan 1927) were extremely fat (Table 1-1). No information available on rate of weight gain prior to or during migration. Post- and failed-breeders spend the majority of time feeding.

HABITAT

Breeding Range

Breeding restricted to tundra ecoregion (Bailey 1980). Habitat use depends on sex and breeding stage; males display in first snow-free areas, typically along barren ridges, creek banks, and raised, well-drained areas with reticulate-patterned ground and scant vegetation (e.g., *Dryas* sp.; Parmelee et al. 1967, McWhorter et al. 1986, Pruett-Jones 1988). Within 3-5 days, most males display together (see Breeding:

Table 1-1. Mass (g) of adult buff-breasted sandpipers from breeding, wintering, and staging areas.¹

Location	Sex ²	Mean	SD	Range	N
<i>Breeding</i>					
Alaska ³	M	68.5	3.6	57.5-77.5	67
	F	56.3	3.7	46.0-65.3	58
Northwest and	M	71.1	8.8	61.2-78.0	3
Yukon territories ⁴	F	55.0	0	55.0	1
Victoria and	M	70.5	—	63.0-94.0	10
Jenny Lind Island ⁵	F	51.0	0	51.0	1
<i>Migration: Spring</i>					
Brazil ⁶	F	65.0	—	—	1
Surinam ⁷	M	61.0	11.3	53.0-69.0	2
Nebraska ⁸	M	101.0	9.4	79.8-117.0	24
	F	72.6	6.1	61.6-81.2	17
<i>Migration: Fall</i>					
Ontario ⁴	M	54.0	9.5	47.2-60.8	2
	F	60.9	2.0	59.5-62.3	2
Surinam ⁷	M	51.3	8.8	43.0-60.5	3

Table 1-1. Continued.

<i>Winter</i>					
Argentina ⁶	M	61.0	--	--	1

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¹ Weights during fall migration may be from hatching-year birds.

² Female weights include only non-laying individuals for Alaska and Victoria Island.

Data from Northwest Territories may not take this into account.

³ Lanctot, unpublished. data.

⁴ Canadian Museum of Nature study skins.

⁵ Parmelee et al. (1967)

⁶ Laredo, unpublished. data

⁷ Haverschmidt (1972)

⁸ J. Strauch, personal communication

mating system) in moist, graminoid meadows with *Carex aquatilis* and *Eriophorum angustifolium* as dominant vegetation types. Display areas tend to be on non-patterned ground with closely-spaced tussocks about 20 cm high and 25-50 cm in diameter (Prevett and Barr 1976, R. Lanctot, unpublished data), often with dwarf willow thickets (*Salix glauca* and *S. lanata*; Dorogoi 1983). Within 1-2 weeks, most males abandon these sites and begin displaying around nest sites. Nests are on dry slopes with numerous sedge tussocks (Prevett and Barr 1976), on moss-willow-varied grass tundra (Dorogoi 1983), and in moist or wet sedge-graminoid meadows on non-patterned or strangmoor (series of aligned tussocks) ground. Females on incubation breaks found primarily along stream banks in non- and reticulate-patterned ground with scant vegetation. Females with broods seen primarily in moist and emergent vegetation along or in stream beds (R. Lanctot, personal observation). Presence and interconnectiveness of these habitats may affect suitability of area for breeding.

Buff-breasted sandpipers are considered part of the "upland species" guild (with American golden plovers [*Pluvialis dominica*], dunlin [*Calidris alpina*], and baird's sandpipers) because of their dependence on drier, sloping areas or tundra with many polygons (many sided ponds/enclosures with either dry, elevated ridges and wet, depressed interiors [1-2 m deep] or dry, elevated interiors and wet depressed borders). "Lowland species" guild (e.g., semipalmated sandpipers [*Calidris pusilla*], pectoral sandpipers [*C. melanotos*], red and red-necked phalaropes [*Phalaropus fulicaria* and *P. lobatus*]) use flat areas with few or no polygons, and/or areas adjacent to lakes (Jones

1980). This species is also one of the few shorebird species that do not show a pronounced seasonal shift toward lowland, wet (ponded) sites during brood-rearing (Jones 1980). Habitat use by arctic shorebirds varies within and between years, and may depend on factors such as environmental variation (e.g., weather), changes in shorebird composition and abundance (i.e., presence of competitors for food and nesting areas), season, location (i.e., inland vs. coastal), social organisation, and predator regimes (Myers and Pitelka 1980).

Spring And Fall Migration

In North America, birds frequent short-grass areas such as pastures, golf courses, cemeteries, airports, and lawns (Campbell and Gregory 1976; Paulson 1993; J. Strauch, D. Dekker, personal communication); damp margins of fresh-water lakes, ponds, and lagoons (Campbell and Gregory 1976; Hayman et al. 1986; H.L. Dickson, personal communication); and fields of rice, recently cut alfalfa, cotton, and potatoes (Sutton 1960; T. Collins, J. Strauch, personal communication). In South America, birds are in recently harvested and burned sugar cane fields of Surinam (Haverschmidt 1972); in open, dry fields with short grasses in Brazil (Sick 1981); and on dry sand bars in rivers (southeast Peru; Bolster and Robinson 1990).

Winter Range

Primarily the pampas biome of South America (F. Vuilleumier, personal communication). Species relies heavily on flooded pampas region in eastern Argentina where cattle ranching predominates (<25% land cultivated). Frequents wet grassland areas (average height 14 cm) heavily grazed by sheep, cattle, and attine ants, but with little human activity and few roads (Myers and Myers 1979, Blanco et al. 1993, R. Straneck, personal communication). Predominate vegetation includes *Distichlis* sp. and *Stenotaphrum secundatum* (Blanco et al. 1993). Also in vegetative communities dominated by *Spartina ciliata* and *Salicornia ambigua* (Chani 1986), short grasses near rivers and marshes (Blanco et al. 1993), and shrub- and grassland areas adjacent to wetlands in Altiplano of northwest Argentina and southwest Bolivia (C. Laredo, unpublished data).

FOOD HABITS

Feeding

Main foods taken. Few data; observations of spring migrants show mostly terrestrial invertebrates, including spiders; insect adults, larvae, and pupae; and plant seeds (Rowan 1927). Copepods, crane-flies, and gammarid crustaceans in fall (Johnsgard 1981).

Microhabitat for foraging. On breeding grounds, primarily areas of dry, elevated tundra with sparse vegetation (e.g., *Dryas* sp.; Sutton 1967). Incubating females feed on

banks of rivers and streams (R. Lancot, personal observation). In contrast to most arctic shorebirds, buff-breasted sandpipers (and other species such as baird's sandpiper and American golden plover) remain in upland areas throughout the breeding season, rather than switching to lowland marshes during brood-rearing (Holmes and Pitelka 1968, Jones 1980). Species uses short-grass areas, margins of water bodies, and agricultural fields during migration (see Migration). During stop-overs in Texas, often seen feeding in rice fields with upland sandpipers and American golden plovers (T. Collins, personal communication). On wintering grounds, birds forage almost exclusively in short-grass uplands < 3 cm high and move to local water sites for drinking and bathing (Myers and Myers 1979).

Food capture and consumption. Short bill and poor development of the porous structure of the upper mandible require species to collect food from surface (Dorogoi 1983). Feeds in deliberate stop-and-go fashion, plover-like, searching intently for prey while standing still, followed by quick spurts to capture prey. Females feed rapidly during incubation breaks, running and pecking in fast succession. Males feed casually on display areas, usually interspersing 1-2 pecks with brief alertness. When first arrive on wintering grounds, forage in flocks up to 100; flocks reduce to 5-6 birds before establishing feeding territories (Myers and Myers 1979).

Diet

Major food items. Poorly documented. Diet of six breeding birds from Wrangel Island included *Tipula* sp. imagoes, pupa, and larvae; *Muscidae* imagoes, *Chironomidae* imagoes, *Chrysomela wrangelii* imagoes and larvae, *Pezomachus* sp. imagoes, lemming bones, and small pebbles (Dorogoi 1983). During spring migration in Alberta, Rowan (1927) found 40% *Coleoptera* adults and larvae, 50% *Diptera* larvae and pupae, and 1% seeds of *Polygonum*, *Potamogeton* and *Eleocharis* in 17 stomach samples; also spider and insect remains.

Comparative food studies of arctic shorebirds indicate most species switch from a diet of freshwater zooplankton, insect larvae and adults during nesting to a diet of oligochaetes, insect larvae on mudflats, and marine zooplankton (Holmes 1966, Holmes and Pitelka 1968, Connors et al. 1979, Jones 1980). Because buff-breasted sandpipers do not move from upland to lowland sites, they remain dependent on insect larvae and adults and feed less on *Chironomidae* larvae and other wetland invertebrates.

Nutrition And Energetics

No information.

Metabolism And Temperature Regulation

No information.

Drinking, Pellet-casting, And Defecation

Species visits local water sites in Argentina (Myers and Myers 1979), ponds in Oklahoma (Sutton 1960), and rivers in Alaska (R. Lanctot, personal observation) for drinking and bathing. Drinks by repeated bouts of dipping the bill in water and tilting head back. Does not cast pellets and no information on defecation.

Food Selection And Storage

No information on recognition and choice of food or on caching

SOUNDS

Vocalisations

Development. No information.

Vocal Array. Very quiet sandpiper. Most characteristic sound is a series of "tick" notes (like two stones hitting together) by males while displaying during spring migration and on breeding grounds (Figure 1-4, Rowan 1927, illustrated in Miller et al. 1988). Although described as a call sequence (Miller et al. 1988), seems to function like a song because only males make the note and only during courtship. Tick notes carry short distances and lack the rhythmically repeated calls common in many other sandpipers (Miller et al. 1988). Accompanying ticks are quiet buzzing noises, perhaps made by ruffling wing feathers and a light pitter-patter sound from stamping feet (R. Lanctot, personal observation). Adults also make low rolling trills 'pr-r-r-reet', 'prriht', 'trrruu'

(Cramp and Simmons 1983) when mildly alarmed (Palmer 1967). Males also make a short "churh" call as females fly over or leave a display area (Figure 1-4). This may be similar to calls by flushed adults staging in Oklahoma ('chuh') and wintering in Argentina ('chwup'; Wetmore 1926). Females make distinct but quiet 'chup' or 'chook' calls during nest defence and brood-rearing (Sutton 1967). Alarmed chicks make series of sharp notes (Figure 1-4). Birds of the year said to have very different call from spring adults, described as similar to the pectoral sandpiper's but shorter and less harsh (Cramp and Simmons 1983).

Phenology. 'Tick' notes by males during courtship while migrating northward and on breeding grounds until females initiate nests (Rowan 1927, R. Lanctot, personal observation).

Daily pattern of vocalising. 'Tick' notes occur throughout day and sunlit Arctic nights; made when males lift both wings (see Behaviour: sexual behaviour) at territory boundaries when alone and at display sites in presence of females (R. Lanctot, personal observation).

Place of vocalisation. 'Tick' notes made primarily at small depressions in tundra near centre of display territory that serve as copulation sites (see Behaviour: sexual behaviour). Fewer notes when males raise both wings at boundaries of territories (R. Lanctot, personal observation).

Figure 1-4. Sonogram of buff-breasted sandpiper vocalisations (recorded June-July 1993, Prudhoe Bay, Alaska, by R. Lanctot). Top (a): male display "tick" notes. Middle (b): "churh" call made by males to females flying over or leaving lek. Bottom (c): chick distress call.

Ground alarm calls by most late-incubating females when flushed from nest. Calls intensify after hatching and may occur from the ground and while female flies circles around area with young.

Repertoire and delivery of songs. No information.

Social context and presumed functions of vocalisations. 'Tick' notes clearly associated with courtship but also made during spring migration when females not present (Oring 1964). 'Tick' notes absent after nest initiation and not reported to occur during fall migration or on wintering grounds (Myers 1980). Alarm calls by females flushed from nests and near broods probably function to distract predators.

Nonvocal Sounds

Low buzzing sound accompanying "tick" notes may be made by ruffling wings, but not verified. Feet stamped on ground during courtship make quiet pitter-patter sound.

BEHAVIOUR

Locomotion

Walking, hopping, climbing, etc. Gait described as high-stepping (Hayman et al. 1986, Pringle 1987); walks or runs between pecking attempts during feeding. Birds often stand on one foot to roost and occasionally hop on one foot (R. Lanctot, personal observation).

Flight. Low, fast, and in tight flock formation (Hudson 1951, Palmer 1967); rapid flight with many turns and zigzag movements; when near the ground turn frequently to reveal white underparts (description of birds arriving at decoys, Mackay 1892 *in* Bent 1927).

Swimming and diving. Young or adults not reported to swim and dive.

Self-maintenance

Preening, head-scratching, stretching, bathing, anting, etc. Species perform all but anting. Males preen extensively on breast and underwings after fighting with other males (see agonistic behaviour below). Extending wings common in males and females. Bathes at water's edge by dipping head below water and raising to splash water over back. Often accompanies American golden plovers when visits water sites to bathe in Argentina (Myers and Myers 1979, Myers 1980).

Sleeping, roosting, sunbathing. Males on display territories roost (by placing bill and front of head under scapulars), especially during morning (01:00-05:00) and when no females present, for ≥ 30 minutes. In Argentina, birds from broad area arrive in flocks of 5-20 (average flock size = 16) to form monospecific roosts (600-1000 birds in 500x300 m area) that form shortly before sundown and break up at sunrise. Spaced ≥ 20 cm apart, individuals roost in grass depressions or behind grass tufts (Myers 1980). No information on sunbathing.

Daily time budget. Not well quantified. On breeding grounds, resident males are on display territories throughout day and night, but frequently leave to feed. See Breeding: incubation, for female attentiveness to nest.

Agonistic Behaviour

Physical interactions. Males defend breeding territories by aerial displays, ground attacks, and vertical flights (Pruett-Jones 1988); stakes are high because, as a lekking species, successful male may mate with multiple females. In ground fights, males rush at each other with lowered heads, ruffled back feathers, and held-in wings. Birds peck each other on breast and back and hit each other with their feet; fights may last 10 or more minutes, interrupted by short breaks (R. Lanctot, personal observation). Males in vertical flights fly up at a 45° angle while fluttering wings and dangling feet, ascend slowly to 10-15 m before flying off in different directions (Parmelee et al. 1967). Birds that fly near or into male territories are aerial-chased by territorial owner; also ground-chase each other while holding up one or both wings (Rowan 1927, Myers 1980). Males may chase females that leave nests for incubation breaks. Females mildly defend brood territories. Males and females defend foraging territories during migration and on winter grounds (Rowan 1927, Myers 1980).

Communicative interactions. Threat displays. Males erect both wings at territory boundaries (often twice in succession) when alone and occasionally to each other. A similar double wing raise functions in courtship (see sexual behaviour). Females also raise

both wings and flutter-jump (jump in the air and snap wings downward) when young are approached by humans.

Appeasement displays. Territorial neighbours (during migration and on breeding grounds) erect back feathers and depress tail while moving slowly near their mutual boundary; one or both may crouch, oriented parallel to one another and the boundary line for short time (2-3 min) before continuing agonistic encounter. One neighbour eventually flies or walks away (Myers 1980).

Attraction displays. Males Flutter-jump (Pitelka et al. 1974) and wave one or both wings at conspecifics and heterospecifics (e.g., pectoral sandpipers, semipalmated sandpipers, stilt sandpipers [*Calidris himantopus*], American golden plovers, black-bellied plovers [*Pluvialis squatarola*]; Parmelee et al. 1967, Sutton 1967, R. Lancot, personal observation), landing in or flying over breeding territories. May display to humans. Raised wings and tail solicit female to mating post where courtship begins (Myers 1979, see sexual behaviour). Females also Flutter-jump and wave wings at chicks when separated; both behaviours may be used to reunite brood (R. Lancot, personal observation).

Spacing

Individual distance. Roosting members maintained minimum of 20 cm on wintering grounds (Myers 1980).

Breeding territoriality. Lek territories range from 10-50 m² during the first few days of display (Pitelka et al. 1974), but may increase in size as breeding season progresses (Pruett-Jones 1988).

Winter territoriality. Winter foraging territories established gradually; average size 0.04 ha (SE = 0.002, N = 29). Birds defend territories but flush in unison in loose flock in response to predators and then return to territories (Myers 1980). Similar foraging territories established during migration with birds scattered evenly over field.

Interspecific territoriality. May nest close to American golden plovers and black-bellied plovers (Paulson and Erckmann 1985; D. McDonald, personal communication); these species occasionally chase females but do not elicit aggression.

Dominance hierarchies. No direct evidence although a few males on each lek receive more female visits and copulations (Pruett-Jones 1988). Although dominance is often a function of a male's ability to acquire and maintain a lek territory in other lekking species (Wiley 1991), females copulated with males on and off leks and with males in peripheral and central territories. Also, reproductively successful males were just as likely to be disrupted by neighbours (Pruett-Jones 1988).

Sexual Behaviour

Mating system. Only North American shorebird to exhibit true lek behaviour (Johnsgard 1981). Referred to as having an 'exploded' lek mating system because of large size of display territories (0.25-4 ha contra ruffs' 1-2 m², Hogan-Warburg 1966). For size

and dynamics of lek territories, see spacing (above). Locations of most leks vary from year-to-year, although they may occur at traditional locations along river bends and junctions. Number and identity of males on leks change daily. Maximum number of males at 2 leks at Prudhoe Bay, Alaska, were 8 and 11, but up to 21 males have been seen on a lek (Pruett-Jones 1988). Of 18 and 36 males captured at leks in 1992 and 1993, respectively (Prudhoe Bay, Alaska), 38 and 61% were not seen again, 18 and 22% were seen 2-5 days, and 10 and 16% were seen > 10 days later. Males may display several km apart on successive days (R. Lanctot, personal observation).

Males also display in solitary locations away from leks; searches often reveal the presence of one or more nests in proximity to these males. As lek activity decreases, virtually all remaining males display toward females at nest sites. Pruett-Jones (1988) suggested these males are waiting for renesting opportunities, but timing of display in relation to nest phenology indicates males are attempting to nest with egg-laying females (chapter 2). Whether males display on leks or in solitary locations may depend on geographic location, habitat distribution, sexual availability of females, and other factors (Emlen and Oring 1977, Cartar and Lyon 1988, Pruett-Jones 1988).

Lekking behaviour is extremely rare among shorebirds; besides buff-breasted sandpipers only great snipe and ruffs form leks. Most shorebird species are monogamous. Individuals within these species may maintain long-term pair-bonds (often over several years) and establish and defend territories to ensure access to food and nest sites. Other species form only short-term pairbonds (e.g., serial polygamous species), form several

pairbonds simultaneously (polygynous species), or fail to form pairbonds altogether (e.g., lekking species). How individuals within species space themselves and care for their offspring may be related to cross-seasonal interactions between migration distance, breeding season energetics, body size and nest cover (Pitelka et al. 1974, Ashkenazie and Safriel 1979, Myers 1981, R. Lanctot and P. Weatherhead, unpublished data).

Leks generally occur when either females or the resources they require cannot be economically defended by males (Emlen and Oring 1977, Davies 1991). Current lekking theory suggests that females may prefer to mate with males in groups or that males may benefit from displaying together (Wiley 1991). Groups of males may be easier for females to locate, allow females to compare and select the best quality mate, and minimise disturbance at nest sites located away from leks (see e.g., Bradbury 1981, Phillips 1990). Males may benefit from aggregating if they can mate with more females by (1) displaying at local "hotspots" (hotspot hypothesis, Bradbury et al. 1986) or (2) clustering around more "attractive" or "dominant" individuals (attractiveness and hotshot hypotheses, respectively; Beehler and Foster 1988, Höglund and Robertson 1990). Clumping together may also lower the risk of predation to individual males (Wiley 1974).

Available information suggests that the hotspot and predation hypotheses, but not the attractiveness or hotshot hypotheses, may partially explain the evolution of lekking behaviour in buff-breasted sandpipers (Pruett-Jones 1988, chapter 2,3). The role of female habitat preferences in the evolution of leks is currently being investigated (R. Lanctot, unpublished data).

Pair bond. No pair bond established by lekking males. See mating system, above, for possible pair bond with solitary displaying males. At Prudhoe Bay, Alaska, females nested an average of 3.4 km (2.4 SD, $N = 3$) from leks where they were captured. Little opportunity for adults to re-pair in subsequent years because of low breeding site fidelity.

Courtship displays and mate guarding. Compared to that of most sandpipers, both more complicated and different. Waving of one or both wings appears to be most important for display (Figure 1-5; see description in Rowan 1927, Oring 1964, Myers 1979); under-wings are satiny white with dark carpal patches that give illusion of flashing when wing waved (Figure 1-5). Males also Flutter-jump (see threat displays) and run along ground with erected wing and tail revealing white underside. Pruett-Jones (1988) recognised 17 different courtship behaviours. Females that visit male territories are led to slight depressions called mating posts (usually one or two per territory) where precopulation behaviour occurs. Females fly or walk on to male territories primarily in groups of 2-5 during the first few days of display and solitarily in later days. Some birds in these group may be males (Prevett and Barr 1976, chapter 3). Courtship behaviour also seen during spring migration (Rowan 1927, Oring 1964), on wintering grounds (Myers 1980; see social and interspecific behaviour), and occasionally during fall migration (K. Karlson, personal communication.).

Males regularly disrupt courtship behaviour of other males by flying into a neighbour's territory, landing at a mating post, and causing females to leave (32.2% of 236 visits were disrupted, Pruett-Jones 1988). Alternatively, males sneak onto a neighbour's

territory by walking through the vegetation with body pressed to the ground. Intruder waits near mating post until resident male has attracted females and then either rushes into disrupt courtship, or mimics female behaviour so as to interrupt it when copulation seems imminent (Pruett-Jones 1988). The intruder rarely copulates in the territorial male's presence by placing himself between the resident male and visiting female; detected intruding males are chased out by the resident male (chapter 3).

Copulation; pre and postcopulatory displays. At the mating post, males begin precopulation display by opening wings in parabola shape several times. Females walk into this embrace and appear to inspect the white undersides of the wings (Figure 1-6). Males often interrupt this display to fly up and around their territory boundary before returning to resume courtship. With wings outstretched, males finally tip their bill upward, stand on out-stretched toes, shake their entire body so that their wings move up and down vertically, and produce a series of 'tick' notes. Copulation is imminent when females open both wings and then turn so their back faces the male (Oring 1964, Myers 1979). Females seem to compete with one another to be closest to the male because only the nearest is mounted. Many times, however, the courtship is broken off when the male either flies up or the female(s) simply walk away from the male. Males mount females for 5-15 sec and both preen after copulation. As the number of females visiting leks

Figure 1-5. Wing-up display of a buff-breasted sandpiper. Used mostly by males to attract females, but also by females to reunite their broods and by males toward intruding conspecifics and heterospecifics. The under-wings are satiny white with dark carpal patches, so when the wing is waved up and down in display, it appears at a distance to flash on and off. Drawing by D. Otte from photo by J.P. Myers/VIREO.

decreases, males increasingly sneak on to neighbouring male's territories and occasionally participate in a homosexual mounting. This usually results when one of the approaching males goes to the backside of the resident male and mounts him. As many as 4 known males have been seen mounting each other (J. P. Myers and F. Pitelka, personal communication; chapter 3).

Extra-pair copulations. Because no pair bond is formed, extra-pair terminology not pertinent. However, preliminary estimates from DNA fingerprinting indicate 40% (19/47) broods had multiple-paternity (chapter 4). These results are supported by observations of females visiting leks in middle of egg-laying (R. Montgomerie, personal communication). See Breeding: eggs (egg laying) for information on multiple-maternity.

Social And Interspecific Behaviour

Degree of sociality. Males aggregate together to display on breeding grounds (see above) and large roosts form at night on wintering grounds (see Self-maintenance, sleeping, roosting, and sunbathing, above). On rare but regular occasions, groups of 10-50 birds congregate in small (0.01 ha) areas on wintering grounds where they display toward one another (Myers 1980). Similar behaviour seen in Oklahoma (Oring 1964) and in Alberta (Rowan 1927).

Play. No information.

Interactions with members of other species. Species are often associated with American golden plovers on wintering (Myers and Myers 1979; Blanco et al. 1993) and

Figure 1-6. Double-wing courtship embrace of a male buff-breasted sandpiper with approaching females -- part of the elaborate lek mating behaviour of this species. With wings outstretched, such males tip their bill upward, stand on outstretched toes, shake their entire body so that their wings move up and down vertically, and produce a series of 'tick' notes. Females move in close and appear to inspect the undersides of the male's wings. Drawing by M. Whalen.

breeding grounds (R. Lanctot, personal observation), and with upland sandpipers (Haverschmidt 1972) and white-rumped sandpipers (*Calidris fuscicollis*) during migration and on wintering grounds (C. Laredo, personal observation). May nest near black-bellied plovers (Paulson and Erckmann 1985) and American golden plovers (R. Lanctot, personal observation), perhaps taking advantage of their warning calls for protection.

Predation

Kinds of predators. Potential predators in Argentina include cinereous harrier (*Circus cinereus*), long-winged harrier (*C. buffoni*), crested caracara (*Polyborus plancus*), short-eared owl (*Asio flammeus*), Swainson's hawk (*Buteo swainsoni*), peregrine falcon (*Falco peregrinus*), aplomado falcon (*F. femoralis*), barn owls (*Tyto alba*), great-horned owls (*Bubo virginianus*), canid (*Dusicyon* sp.), felid (*Felis colocolo*) and humans (Myers 1980, Laredo 1992). Peregrine falcon killed one bird in dense flock of 100 and merlin (*Falco columbarius*) found feeding on one during migration in Alberta (Dekker 1980, 1988). Unsuccessful attacks on adults at lek by parasitic (*Stercorarius parasiticus*) and long-tailed jaegers (*S. longicaudus*) (Pruett-Jones 1988).

Potential predators during nesting and brood-rearing include arctic fox (*Alopex lagopus*) and red fox (*Vulpes vulpes*), short-tailed weasel (*Mustela erminea*), arctic ground squirrel (*Citellus parryi*), wolverine (*Gulo luscus*), common raven (*Corvus corax*), gulls (*Larus* spp.), snowy owl (*Nyctea scandiaca*), short-eared owl, jaegers (*Stercorarius* spp.), peregrine falcon, and sandhill crane (*Grus canadensis*).

Predation accounted for 50-65% of nest loss in northern Alaska in 1992 and 1993 (R. Lanctot, unpublished data). Pruett-Jones (1988) reported 61% nest depredation in same location from 1977 to 1980. Partial clutch loss from 2 of 11 nests from 1977 to 1980 (Pruett-Jones 1988) and from 4 of 24 nests in 1993; in latter case suspected predator was short-tailed weasel (R. Lanctot, unpublished data).

Manner of predation. Arctic and red foxes take entire contents of nest; bowl often destroyed and urine and scat common in or near nest. Short-tailed weasel suspected (based on mesh size of nest enclosures) of taking one egg at a time from nests until female finally abandons (R. Lanctot, personal observation). Jaegers observed diving on adult males at leks (Pruett-Jones 1988). One flying juvenile swooped on by long-tailed jaeger and hit to the ground, but juvenile escaped (R. Lanctot, personal observation). Peregrine falcons predominately use low surprise attack on foraging adults during migration (Dekker 1980).

Response to predators. Territorial adults foraging on wintering grounds flock in response to avian predators and then re-establish territories after predator leaves (some individuals remain crouched on ground). Flocking thought to lower predation risk but not to increase detection of predators (Myers 1980). Similar flocking observed in Alberta; birds that flush in front of peregrine falcon drop to ground or water and take off in different direction (Dekker 1980). Migratory birds are extremely tame; when approached by humans, nearest members of flock either funnel around on the ground or fly up and land on other side of flock (Sutton 1960).

Breeding adults on leks crouch or make short jumps in response to swooping jaegers (R. Lanctot, personal observation). Nesting females craned necks, turned heads, and exhibited alertness when avian predators are at a distance, but sit low and immobile when predators flew overhead or nearby (D. McDonald, personal communication). Response of incubating females to approaching humans varies from sneaking off nests when humans are 100-300 m away to flushing when humans <1 m. Females commonly fly out of sight and then return and land 30-50 m from the nest, occasionally flying circles around nesting territories and giving quiet calls. During brood-rearing, females are more secretive and do not flush from the ground unless approached directly. When a female's chicks are approached, she often flies within several meters, circles, and gives shrill, high calls. Females also exhibit typical Rodent Run behaviour, spreading wing and tail feathers, ruffling back feathers, while crouched low to the ground. When pursued, females perform short Lead Away flights and run along the ground. Females never seen chasing away predators that approach nest or brood. If chicks captured, females occasionally raise both wings and Flutter-jump (see courtship displays, above). Newly hatched chicks respond to female's alarm calls by freezing on ground, pre-fledglings run from approaching humans, and volant chicks walk in the open and only fly when approached (R. Lanctot, personal observation).

BREEDING

Phenology

Pair formation. Pairs unlikely to form (but see Cartar and Lyon 1988). Males and females simultaneously arrive on breeding grounds during late May through first week of June (Figure 1-3; Parmelee et al. 1967, Prevett and Barr 1976, Dorogoi 1983, Pruett-Jones 1988). Within 3-10 days of arrival, most males display together on leks, but some males display in solitary locations. Leks may remain active for 2-3 weeks but most last several days. Females may visit several males on a lek, several different leks, and repeatedly visit leks during egg-laying. Females rarely seen copulating with solitary males. Males leave breeding grounds in mid-June to early July, after females initiate nests, and only females incubate eggs (Pitelka et al. 1974, Sutton 1967).

First/only brood per season. Single brood per year. First eggs laid 6-8 days after male display initiated (Pruett-Jones 1988). Eggs laid considerably later than most other sandpipers and over protracted time (Figure 1-3). Median date of nest completion was 22 June 1992 (range 12-30 June, $\bar{N}$ = 7) and 17 June 1993 (range 10-21 June, $\bar{N}$ = 15) at Prudhoe Bay, Alaska (R. Lanctot, unpublished data). Single nests also found on 10 June at Firth River, Yukon Territories (Prevett and Barr 1976), and Wrangel Island (Dorogoi 1983); 24 June on Jenny Lind Island (Parmelee et al. 1967), and 28 June on Devon Island (Hussel and Holroyd 1974). Only one confirmed renest documented during three year study at Prudhoe Bay, Alaska (chapter 2).

Earliest hatch on 5 July 1992 and 4 July 1993 at Prudhoe Bay, Alaska (Figure 1-3), after 23-25 days of incubation. Peak hatch in second and third week of July; few chicks fledge at 16 days and majority fledge at 18-20 days (R. Lanctot, personal observation). Effect of rainy and windy weather on nesting chronology unknown.

Second brood per season. Renesting possible but second clutch in one season never documented.

Nest Site

Selection process. Females select site.

Microhabitat. Nest frequently in flattened moss hummock, surrounded on several sides by *Carex* spp. Ground cover within 1 m quadrat centred over nests at Prudhoe Bay, Alaska ($N = 78$), consisted primarily of moss, *Carex* spp., and litter, and smaller amounts of *Eriophorum* spp., *Dryas* spp., *Salix* spp., lichens, and *Equisetum* spp. Vegetation height in quadrat averaged 157 ± 90 mm (mean $\pm$ SD, range 0-400, $N = 44$) and height from lowest to highest point in quadrat was 126 ± 44 (range 60-235, $N = 43$; R. Lanctot, unpublished data).

Site characteristics. Nests in moist or wet sedge-graminoid meadows, occasionally in exposed dry, prostrate scrub habitats. Landform around nests is primarily non-patterned or strangmoor and occasionally on reticulate-patterned ground. Nests usually close to streams; distance to open water averaged 115 ± 66 m (range 17-400, $N = 44$) and to wetland interface 32 ± 33 m (0-125 m, $N = 44$; R. Lanctot, unpublished data).

Nest

Construction process. Only female builds nest; digs scrape by tossing vegetation over back with bill and pressing breast against ground. Nest lining added during egg-laying. Scrapes constructed during day and sunlit Arctic nights (R. Lanctot, personal observation). Length of time to build unknown.

Structure and composition matter. Nest cup is shallow scrape lined with lichens (e.g., *Thamnolia vermicularis*), dead willow leaves (*Salix arctica*, *S. lanata*), *Spaghnum* moss, dead *Equisetum* spp., dead *Dryas* spp. leaves, and sedges (*Carex rupestris* and *C. misandra*) (Parmelee et al. 1967, Sutton 1967, Dorogoi 1983).

Dimensions. Little information. Five nests in Wrangel Island were 8-10 cm wide (average 9.2) and 4-5 cm deep (average 4.5) (Dorogoi 1983).

Microclimate. No information.

Maintenance or re-use of nests, alternate nests. No information. Low breeding site fidelity by females limits possibility of nest reuse.

Nonbreeding nests. No information.

Eggs

Shape. Pyriform to oval (Harrison 1984).

Size. Eggs from Prudhoe Bay, Alaska: $N = 23$ clutches (87 eggs), length 38.13 ± 0.80 mm, breadth 26.98 ± 0.59 mm, calculated volume ($\text{length} \times \text{width}^2$) $27,768.74 \pm 1,392.68$ (R. Lanctot, unpublished data); Western Foundation of Vertebrate Zoology.

(WFVZ): 16 clutches ($N = 64$), length 38.09 mm (35.21-40.12), breadth 26.66 mm (25.70-27.67); Wrangel Island: $N = 20$, 5 clutches, average 38.1 x 26.6 (Dorogoi 1983). Significant variation in width and length among clutches at Prudhoe Bay, Alaska (R. Lanctot, unpublished data).

Mass. Fresh eggs weighed 11.8-18.8 g (average 13.0, $N = 20$ from 5 nests) on Wrangel Island (Dorogoi 1983). Mass of an egg 23% of average female mass (based on weights of Alaska females); therefore weight of 4-egg clutch equivalent to 92% of female's weight.

Eggshell thickness/weight. No evidence of DDE-induced eggshell thinning; mean empty egg shell weight of 16 clutches (64 eggs) was 0.615 g (0.503-0.685; WFVZ).

Colour. 'Cartridge buff' to dull white ground colours; some eggs darker: 'olive-buff,' 'chamois,' or 'cream buff.' Heavily marked, primarily at larger end, with slightly spiral and longitudinal blotches; small spots and blotches scattered over entire egg (Bent 1927, Harrison 1984). Ground colour and intensity of markings usually similar within clutches (R. Lanctot, personal observation).

Surface texture. Smooth and slightly glossy (Harrison 1984).

Egg laying. Interval between nest completion and laying not known. One female took minimum of 5-6 days to lay 4 eggs, single egg present for first 3 days. Two nests located with 3 eggs had fourth egg next day. Both events indicate shorter interval between later eggs than earlier eggs. One female collected while courting a territorial male at a lek had ovarian scars indicating one egg had been laid (R. Montgomerie,

personal communication); this suggests females may copulate during egg-laying. Unclear why date of nest initiation so variable, but it may be related to weather. Females continue incubating after losing 1 or 2 eggs, but abandon nest when 3 eggs lost to predation. Egg dumping found in 2 of 32 nests via DNA fingerprinting. Replacement of eggs not reported.

Incubation

Onset of broodiness and incubation in relation to laying. Females flushed from nests with 2 and 3 eggs, but probably no full-time incubation until 3 or 4 eggs (R. Lanctot, personal observation).

Incubation patches. Several females found with well-defined brood patches (Parmelee et al. 1967).

Incubation period. Twenty-three to 25 days in Prudhoe Bay, Alaska ($N = 4$; T. Walker, personal communication). One female incubated non-fertile eggs placed in nest for at least 30 days (R. Lanctot, unpublished data).

Parental behaviour. Displaying males near nests sometimes pursue females that leave the nest for a break in incubation. Males not known to incubate. Late incubating females attend nest 85.6% of day ($N = 2$); attendance spell less during daytime (06:00-18:00: 28.7 ± 13 min, range = 10-58, $N = 17$) than nighttime (00:00-06:00 and 18:00-24:00: 97 ± 37 min, range = 54-146, $N = 7$); perhaps because of higher ambient temperature (D. McDonald, personal communication). Non-attendant females primarily

foraged. Females on incubation breaks generally forage within 250 m of nest. Females foraging near nest return in zigzag fashion before running last few meters. Birds foraging long distances from nest fly back to within 15 m and then walk remaining distance (D McDonald, personal communication, R. Lanctot, personal observation).

Hardiness of eggs. No information.

Hatching

Preliminary events and vocalisations. Chicks begin peeping when egg pips. Incubation breaks more frequent but of shorter duration near hatch (R. Lanctot, unpublished data).

Shell breaking and emergence. Stars appear on large end of egg 1-3 days prior to hatch and a single pipped hole appears usually 1 day before hatch (but may occur as many as 3 days earlier). Chicks hatch within 6-8 hr of each other ($N = 2$ nests); older chicks may move ≤ 0.5 m from nest cup until all hatch. Chicks known to hatch morning through afternoon; no information on night. Females abandon non-fertile eggs and chicks not able to break out of shell (R. Lanctot, personal observation).

Parental assistance and disposal of eggshells. Parental assistance in emergence not reported; egg shells removed by female but when and how unknown.

Young Birds

Condition at hatching. Mass of chicks at day-of-hatch in Alaska ranged from 7.5-10.5 g (8.8 ± 0.6 , $N = 48$); tarsus ranged from 22.8-26.8 mm (25.1 ± 0.9 , $N = 52$); one day old chick wing length 27-28 mm ($N = 2$) (R. Lanctot, unpublished data).

Precocial and completely covered with down at birth. Down whitish below and brownish-gray above; back mottled blackish-brown with tips of down white; eye-strip dark to nape with grayish-buff stripes above bordering dark crown patch (Harrison 1984). Legs light green, eyes open, and egg tooth retained first few hours after hatch. Most chicks leave nest within 12 hr, but based on weight changes probably attain little food for first few days (Lanctot 1994).

Growth and development. Age-dependent weight gain described by Linear regression. $\text{weight} = 8.68 + 2.26(\text{age})$ (age measured in days, $R^2 = 0.92$, based on repeated measures of 18 broods). Five day chicks ($N = 4$): tarsus 29.0-31.2 mm, wing 35-42 mm, culmen 12.2-14.0 mm; 11 day chicks ($N = 4$): tarsus 28.7-32.3, wing 69-73, culmen 14.5-15.6. Twenty-day-old chick still had down along temples to back of neck and on tail; primaries and secondaries fully developed (R. Lanctot, personal observation).

Hatch-day chicks remain within 1-2 m of each other but spread out after several days. Chicks usually within 50 m of nest 1 day after hatch, but may move 400 m or more. Brood movements of 0.5 km or more in a day are common; see also behaviour, predation. No evidence of intersibling rivalry.

Parental Care

Brooding. Females brood young for about 4 days, longer if weather inclement. Young defended for 2-3 weeks and occasionally attended by conspecific parent. Unclear if adoption results from female desertion or intermixing of broods during disturbances.

Feeding. Chicks feed themselves; walk and peck at food on ground, and usually stay near female.

Cooperative breeding

Not known to occur.

Brood Parasitism

DNA fingerprinting indicated 1 of 47 nests had eggs dumped (not laid by resident female). Females will also incubate conspecific eggs placed into nest by researchers (R. Lanctot, personal observation).

Fledgling Stage

Chicks leave nest within 12 hours of hatching. Weak flight at 16 days, sustained flight by 20 days. No information on minimum age young can survive without parent. Attended by female for 2-3 weeks (see Parental care: brooding). Regularly seen near American golden plover broods, although significant positive association not confirmed.

Young are precocial; they leave the nest within 12 hr and feed independently.

Immature Stage

Juveniles may migrate several weeks later than adults; juveniles seen on breeding grounds in August and occasionally in September (Campbell and Gregory 1976).

Juveniles seen more frequently on Atlantic and Pacific coasts than adults (see Migration: timing and routes of migratory movements). Juvenile plumage retained until young reach wintering range (Palmer 1967; see Appearance: molts and plumages). Absence of birds on wintering grounds during austral summer suggest first year birds migrate north (Myers and Myers 1979).

DEMOGRAPHY AND POPULATIONS

Measures Of Breeding Activity

Age of first breeding; intervals between breeding. Presumably 1 year, although lack of natal philopatry prevents accurate determination. Some females return second or third year after banding at Prudhoe Bay, Alaska, but not known if these individuals breed elsewhere or forfeit breeding in off-years (D.M. Troy, personal communication).

Clutch: size and number per season. Nearly always 4 eggs; 4 eggs in each of 86 nests at Prudhoe Bay, Alaska (Pruett-Jones 1988, R. Lanctot, unpublished data). Four nests with 2 or 3 eggs found, but loss from predation in two instances (R. Lanctot, personal observation). Murdoch reports one 5-egg nest (*in* Bent 1927). All other

accounts report 4 egg clutches (Bent 1927, Parmelee et al. 1967, Sutton 1967, Dorogoi 1983).

Annual and lifetime reproductive success. In Alaska (Prudhoe Bay), hatching success was 41.7% (31 hatched/72 eggs laid) in 1992 and 43.1% (45/108 eggs) in 1993. Minimum fledging success was 18.1 and 7.4% (no. fledged/no. eggs) in these years, and nesting success was 44.4% in both years (8/18 and 12/27 nests; percentage of total nests to hatch at least one young) (R. Lanctot, unpublished data). Pruett-Jones (1988) had 27.8% (5/18 nests) nesting success in same area during 1977-1980. No estimate of lifetime reproductive success because of low breeding site-fidelity. One brood per season.

Life Span And Survivorship

See above for survival of eggs through fledging. Information on survivorship beyond fledging and lifespan not reported. See Range (below) for minimum estimate of lifespan based on breeding site fidelity.

Disease And Body Parasites. No information.

Causes Of Mortality

Predation. See Behaviour: predation.

Human/research impacts. See Conservation and Management: effects of human activity on populations.

Range

Natal philopatry. None reported. None of 13 chicks seen up to 2 years after banding and none of 8 chicks seen 3 years after banding (K. Moitoret, personal communication). None of 33 chicks (8 known to fledge) seen the next year (R. Lanctot, unpublished data).

Fidelity to breeding site and winter home range. 16.7% (1/6) and 9.1% (2/22) of males banded were resighted next year; one male seen in three consecutive years. Resighted males displayed at same spot (within 100 m) from year-to-year, but duration of display varied from 1 to 14 days in given year. Thirteen percent (3/24) of banded females resighted the next year; 1 female nested in same area both years, other two nested first year and seen only 1 day next year (R. Lanctot, unpublished data). K. Moitoret (personal communication) reported no breeding fidelity by females (0 of 12 females one year later, and 0 of 7 two years later). D. Troy (personal communication) had 1 of 6 banded females resighted 3 years later and 1 of 21 females banded resighted 2 years later. No information on fidelity to winter home range.

Dispersal from breeding site or colony. No natal philopatry and low adult breeding fidelity indicated most breeders immigrate from elsewhere. Single day resightings of males and females on breeding grounds suggested both sexes visit several breeding sites in given year. This is supported by large variation between years in local population density (see Population status).

Home range. On breeding grounds, females nest as many as 6.2 km from lek where they were captured (3.4 ± 2.4 , $N = 3$). Early arriving males disperse over large area (radio-equipped males could not be located by airplane in 10 km wide area). Males also commonly display at one location for 1 day, disappear, and return 1-2 weeks later. These facts suggest males and females occupy a large range when they first arrive on the breeding grounds. Incubating females seen within 1 km of nest site, and females and their broods seen within 1-3 km² area.

Population Status

Estimates or counts of density. Number of adults seen during surveys on breeding grounds vary dramatically on an annual basis; breeding density (no./km²) in Alaska varied from 0 to 10 during 1971-1974 (Bergman et al. 1977) and 0.5-14.0 from 1981 to 1989 (average = 5.7; Troy and Wickliffe 1990). Densities vary from 1 to 19 birds/km² on Wrangel Island and 0-14 on Chukotka (M. Stishov, personal communication). Nesting densities also vary along Alaska Arctic coast (range from 0 to 3.3 nests/km²; Troy and Wickliffe 1990).

Densities on Estancia Medaland (Buenos Aires Province of Argentina) ranged from 5 to 18 birds/ha in October and November 1973 (Myers and Myers 1979), and from 0.25 to 2.7 birds/ha in November 1992 to January 1993 (M. Martinez, personal communication). Densities in northwest Argentina averaged 1.8 birds/ha (± 1 SD, range 0.3-4.3) between November 1992 and February 1993 (Laredo 1993). During 11,534 km

of surveys (mostly from cars on roads), 899 buff-breasted sandpipers were seen in Argentina and Uruguay from August 1992 to March 1993 (Blanco et al. 1993).

An estimated 2,000 adult breeding birds present on Banks Island (63,960 km²; Manning et al. 1956). Morrison (1993/94) estimated 5,000-10,000+ individuals present in Canada. Dorogoi (1983) believed breeding population on Wrangel Island "not to exceed several tens of nesting birds." See Migration: timing and routes of migration, for peak numbers of birds seen during migration and on wintering grounds.

Geographic and temporal trends. Population probably numbered in the hundreds of thousands to millions at turn of 20th century (Forbush 1916, Hudson 1920). Human activities brought the species near extinction in early 1920s (Wetmore 1927). Based on historical sightings of birds (listed in *Audubon Field Notes and American Birds*), J. Strauch (personal communication) estimated "no more than a few 10s of thousands" exist today. Recent rise in sightings in many places (e.g., Europe, Africa, Australia) suggests species may be recovering (Pringle 1987), although Rappole et al. (1983) listed this species as one "likely to show serious declines within next decade" because of its small population size, restricted range, and the staging of large segments of its population at vulnerable locations. Long-term shorebird surveys in central and eastern Canada also indicate this species is declining (Morrison 1993/94). Comparisons of density estimates at Estancia Medaland, Argentina, between 1973 and 1992, however, suggests species may no longer be declining, although differences in survey methods and potential problems of

inter-year variability in population densities require surveys for several years (M. Martinez, personal communication).

Population Regulation

Needs study. Predation on eggs and chicks significant, but overall effect on population unknown. Hunting and pesticides and other contaminants on habitats along migration route and on wintering grounds may be also important (see Conservation and management).

CONSERVATION AND MANAGEMENT

Effects Of Human Activity

Sensitivity to disturbance at nest and roost sites. Banding and human visits of nests may cause nest abandonment (in Alaska 12.5% in 1992 and 4.5% of nests in 1993) and increase predation. Construction of roads and availability of garbage may boost fox and common raven populations around arctic communities, resulting in predation of nearby nests and juveniles. However, vast majority of breeding grounds are in remote areas. No information from roost sites.

Shooting and trapping. Large numbers killed in late 1800s and early 1900s by commercial hunters in central United States and to lesser degree on wintering grounds (McIlheney 1943; Myers 1980; D.E. Blanco, personal communication). Their extreme tameness and tendency to return to a wounded flock member made these birds vulnerable

to hunting (Rowan 1927). Passage of the Migratory Bird Treaty Act in 1918 reduced market hunting in United States and Canada (Senner and Howe 1984). Legislation passed in 1920s protecting birds on wintering grounds (Wetmore 1927); hunting thought to be minimal or non-existent at present (D.E. Blanco, personal communication, C. Laredo, personal observation).

Pesticides and other contaminants/toxins. Habitats (e.g., agricultural fields, golf courses) in United States and Canada visited regularly during migration often have applications of organochlorines (e.g., pesticides/herbicides); 3 adults died from feeding on planted rice seed treated illegally with Furadan 4F in Texas in 1983 (Flickinger et al. 1986). Pesticide exposure implicated in decline of other upland species (e.g., upland sandpipers; White 1988) in South America. Expansion of agriculture into wintering grounds may threaten population in future (Senner and Howe 1984, Blanco et al. 1993); more information needed.

Degradation of habitat. Large decline in buff-breasted sandpipers, and species such as eskimo curlew (*Numenius borealis*), upland sandpiper, and hudsonian godwit (*Limosa haemastica*) occurred concurrently with settlement (i.e., agriculture) of the United States plains and Argentine/Paraguay pampas, beginning in the 1870s (Wetmore 1927). Cattle ranching on wintering grounds has changed grassland communities from taller tussock grasses to shorter grasses and dicots, possibly resulting in range extension, although much of this pastureland was converted to agriculture (plowed) during the 1900s (Soriano et al. 1991, Blanco et al. 1993). Other loss of key habitat in the Altiplano of

northwestern Argentina and southwestern Bolivia has been caused by overgrazing by sheep, goats, and donkeys, and fire on shrub- and grass-covered areas adjacent to wetlands (C. Laredo, personal observation). Flooded pampas region of eastern Argentina, which is too wet for agriculture, is major wintering area today (Blanco et al. 1993).

No direct threat to breeding grounds, aside from potential effects of oil development in limited areas (e.g., road construction often occurs in drier, upland areas).

Management

Measures proposed and taken. Listed as Category 3 of Red Book of the Russian Republic and protected by State Nature Preserve on Wrangel Island (Kondratev 1989). Recommended that species is listed as endangered in U.S.S.R. red book (Dorogoi 1983).

The United States and Canada should join the Convention on the Conservation of Migratory Species of Wild Animals (Bonn or Migratory Species Convention). The participation of these two countries, along with present members Argentina and Uruguay (the wintering area of the species), would allow negotiations of regional agreement on all aspects of the conservation of buff-breasted sandpipers and other migratory species (D.E. Blanco, personal communication).

Wetlands for the Americas made the following recommendations for protection of key habitat on the wintering grounds (Blanco et al. 1993): (1) establish refuges to protect key grasslands (such as Estancia Medaland in Buenos Aires Province of Argentina), (2) continue monitoring populations and documenting regional distributions, and (3) study the

relation between American golden plovers and buff-breasted sandpipers, and the effects of different cattle management on habitat use by these species. Land management in wintering areas and historic migration staging sites might include restricting organochlorine applications in agricultural areas and maintaining pasturelands and associated cattle grazing to yield suitable grass height.

Research on breeding grounds is underway to determine habitat requirements and potential effects of oil development.

Effectiveness of measures: the species' response. Little action to date. See Demography and Populations: population status, geographic and temporal trends.

APPEARANCE

Molts And Plumages

Timing and extent of molt not studied in detail.

Hatchlings. See Breeding: young birds.

Juvenal plumage. Prejuvenal molt complete; timing unknown. Head and underparts as adult, except broader, paler fringes to buff feathers. Mantle and scapular feathers as adult but fringes are a wider, paler, whiter buff, with dark feather centres more rounded giving more scaly appearance. Undersides of primary and secondary flight feathers are finely speckled grey as opposed to larger, blackish spots in adults (see Definitive Alternate plumage).

Basic I plumage. Prebasic I molt begins upon arrival on winter grounds and completes before start of spring migration in April. Molt almost complete; includes head, body, wing, and tail. Some juvenal feathers on upperparts may remain (Cramp and Simmons 1983).

Head and underparts buff, brown spotting or streaking on crown, hindneck, and sides of breast. Lesser under secondary coverts deep buff; greater under primary coverts strongly mottled dark brown with a bold brown subterminal bar; median and lesser under primary coverts, and median and greater under secondary coverts silky-white; undersides of primary and secondary flight feathers mottled distally with dark brown vermiculation on a whitish background. Vermiculation becomes more distinct as birds mature from juveniles to adults, and adult females less bold than males but more bold than juveniles (Campbell and Gregory 1976, Cramp and Simmons 1983, Hayman et al. 1986). Back, scapular, upper tail and upper wing coverts show buffish-brown feather edgings and narrow, lanceolate, dark-brown feather centres. Upper secondaries, greater upper secondary and primary coverts, and allula show buffish-white fringe, a dark subterminal spot or bar, and dark-brown mottling on the proximal part of each feather (Hayman et al. 1986).

Alternate I plumage. Prealternate I molt unknown.

Definitive Basic plumage. Definitive Prebasic molt begins on breeding grounds in early July with head, mantle, scapulars, underparts, back, and upper tail coverts. Molt suspended in late July or August and completed on winter grounds beginning in October

with body, tail, tertials, wing coverts, and remiges. Flight feathers are molted last, sometimes as late as late February through March (Wetmore 1926, Bent 1927, Cramp and Simmons 1983). Plumage same as Basic I but without some retained Juvenal feathers on upperparts

Definitive Alternate plumage. Definitive Prealternate molt occurs March - April on winter grounds; includes head and much of body (Cramp and Simmons 1983, C. Laredo, personal observation).

Plumage identical to Basic plumage except upper-body and wing feathers tend to have narrower and lighter brown edgings (Hayman et al. 1986).

Bare Parts

Same for adult and juveniles.

Bill. Short, straight, black with tinge of yellow to green at base of mandible.

Iris. Dark brown.

Legs and feet. Dull olive-yellow to bright yellow-ochre (Cramp and Simmons 1983, Hayman et al. 1986).

MEASUREMENTS

Linear

See Table 1-2. Slight variation among geographic regions may be result of birds measured alive versus dead; differences are not consistent across all morphological measurements. In Alaska, adult males significantly larger than females in dimensions of culmen, tarsus, wing, tail, and headbill. In British Columbia, hatch-year males also significantly larger than females in dimensions of wing, culmen, and tarsus (Campbell and Gregory 1976). Despite dichotomy in size between sexes, some overlap in dimensions exists.

Mass

Males average larger than females throughout annual cycle but overlap occurs (Table 1-1). Adults are heaviest during spring migration.

Table 1-2 Morphological measurements (mm) of adult and juvenile buff-breasted sandpipers

ALASKA - ADULTS ¹					MANITOBA - ADULTS ²				
	SEX	MEAN	SD	RANGE	N	MEAN	SD	RANGE	N
Culmen	M	19.7	0.7	18.1-21.1	68	19.6	0.5	19.0-20.3	7
	F	17.9	0.9	15.4-20.4	132	18.3	0.5	17.6-19.1	7
Tarsus	M	32.9	1.1	29.6-36.6	67	31.7	1.4	29.2-33.2	7
	F	29.5	1.3	23.0-34.0	122	29.0	1.0	27.2-30.3	7
Wing	M	135.5	3.0	129.0-142.0	69	131.3	2.4	128.0-156.0	7
	F	128.9	2.6	122.0-136.0	132	125.6	1.6	123.0-128.0	7
Tail	M	--	--	--	--	59.0	1.0	58.0-60.0	7
	F	--	--	--	--	53.8	1.5	52.0-56.0	6
Longest Toe	M	--	--	--	--	26.2	0.8	25.1-27.3	6
	F	24.3	0.8	23.7-24.8	2	24.5	0.9	22.9-25.4	7
Head-bill	M	48.5	1.2	44.7-51.5	66	47.7	1.6	45.4-49.9	6
	F	44.6	1.1	38.5-46.4	77	44.2	0.8	42.9-45.6	7

Table 1-2 Continued

		QUEBEC, ONTARIO, NEW YORK - ADULTS ³				NORTHWEST TERRITORIES - ADULTS ⁴			
	SEX	MEAN	SD	RANGE	N	MEAN	SD	RANGE	N
Culmen	M	19.3	0.7	18.4-19.9	4	19.5	0.4	19.0-20.0	6
	F	18.6	1.5	17.5-20.3	3	18.3	0.5	17.4-18.8	6
Tarsus	M	31.6	0.9	30.6-32.5	4	32.3	1.1	30.8-34.0	7
	F	28.7	0.3	28.5-29.1	3	29.2	1.0	27.3-30.3	6
Wing	M	130.5	2.6	127.0-133.0	4	134.0	2.9	131.0-140.0	7
	F	126.0	4.6	122.0-131.0	2	125.7	2.2	123.0-128.0	6
Tail	M	--	--	--	--	58.3	1.3	57.0-60.0	7
	F	--	--	--	--	55.8	1.5	54.0-58.0	6
Longest Toe	M	--	--	--	--	25.8	0.9	24.9-27.5	7
	F	--	--	--	--	24.8	0.9	22.9-25.7	6
Head-bill	M	48.6	0.8	47.2-49.7	4	47.6	0.7	46.5-48.4	6
	F	45.2	2.0	43.8-47.5	3	43.3	1.4	42.2-46.0	6

2

PM-1 3 1/2"x4" PHOTOGRAPHIC MICROCOPY TARGET
NBS 1010a ANSI/ISO #2 EQUIVALENT

PRECISION^{SM} RESOLUTION TARGETS

Table 1-2. Continued.

OVERALL - ADULTS					JUVENILES ⁵				
	SEX	MEAN	SD	RANGE	N	MEAN	SD	RANGE	N
Culmen	M	19.7	0.7	18.1-21.1	92	19.4	0.3	19.0-19.9	8
	F	18.0	0.9	15.4-20.4	154	18.1	1.1	16.9-20.7	10
Tarsus	M	32.7	1.2	29.2-36.6	92	31.2	1.3	29.9-33.3	9
	F	29.5	1.3	23.0-34.0	144	28.9	1.4	26.7-31.3	10
Wing	M	134.6	3.4	126.0-142.0	94	131.9	3.1	127.0-136.0	9
	F	128.4	3.0	117.0-136.0	154	125.4	4.9	121.0-138.0	10
Tail	M	58.6	1.2	57.0-60.0	16	57.0	1.7	55.0-60.0	8
	F	54.9	1.6	52.0-58.0	14	55.0	2.8	52.0-61.0	9
Longest Toe	M	26.0	0.8	24.9-27.5	15	24.9	0.9	23.8-26.6	8
	F	24.5	0.9	22.9-25.7	15	23.9	1.1	22.4-26.1	9
Head-bill	M	48.4	1.2	44.7-51.5	89	47.6	0.9	46.5-49.3	8
	F	44.6	1.2	38.5-48.2	99	44.2	2.5	40.5-49.8	10

Table 1-2 Continued.

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- ¹ R. Lanctot, D. Troy, P. Martin, unpublished data.
- ² Canadian Museum of Nature (CMN) study skins measured by L. Slater and R. Lanctot.
- ³ CMN and Denver Museum of Natural History (DMNH) study skins
- ⁴ CMN study skins.
- ⁵ CMN and DMNH study skins from Alberta, Alaska, British Columbia, Colorado, Manitoba, Ontario, and Quebec. See also Campbell and Gregory (1976) for measurements of juveniles from British Columbia.

Chapter 2.

Ephemeral lekking behaviour in the buff-breasted sandpiper, *Tryngites subruficollis*

This chapter formed the basis of a paper of the same title published in *Behavioral Ecology* and co-authored with Patrick J. Weatherhead.

ABSTRACT

I studied male reproductive behaviour of the buff-breasted sandpiper for three years on a 16-km² study site in northern Alaska to document variation in male lekking behaviour and to explore the causes of that variation. Over the breeding season, about 75% of males on the study area displayed on leks, with the remainder displaying solitarily. Leks averaged between 2.3 and 3.0 males each (maximum size = 20). Most leks (69%) were present in only one year and about one-tenth were active all three years. Half of the leks were active for only one survey (maximum of 3-4 days) in a given year. Individual male behaviour varied substantially, from remaining at a single lek for most of the breeding season or attending multiple leks over the season, to displaying solitarily or displaying both on leks and solitarily. Some males (30% or less) displayed near nests during the later part of the breeding season, perhaps attempting to copulate with females during egg-laying. The proportion of males that displayed on leks remained consistently high throughout the breeding season despite changes in the operational sex ratio and in the

intensity of male-male competition. However, the absolute number of males (lekking and solitary) in the study area was positively correlated with the number of fertile females over both breeding seasons. I suggest that buff-breasted sandpipers may be unusual among lek-breeding birds in that males have the option of leaving areas when the number of fertile females becomes depressed and flying to new areas where breeding opportunities are still available. Breeding opportunities may be especially variable in the high arctic due to uneven snow accumulation and differential melt-off that can delay breeding by two or more weeks. This interpretation suggests that the mating system of the buff-breasted sandpiper must be viewed at a much larger scale than what has typically been used in mating system studies.

INTRODUCTION

Leks are aggregations of males which are thought to occur when either females or the resources they depend upon can no longer be defended economically by males (Bradbury 1977, Emlen and Oring 1977, Davies 1991). Such a situation may arise when females use widely dispersed resources, resulting in large, undefendable ranges, or when females share a common range and local density is high, resulting in intense male-male competition for females (Davies 1991). However, even within lek-breeding species, not all males behave similarly. For example, males may employ a variety of alternative reproductive tactics or strategies besides lekking, such as solitary display (Pruett-Jones and Pruett-Jones 1990, Apollonio et al. 1992, Westcott and Smith 1994), satellite or sneaky behaviour (Trail 1990, Westcott and Smith 1994, Lank et al. 1995) and pursuit of

females off leks (Gibson and Bradbury 1987, Lank and Smith 1987). Whereas considerable research has explored the extent and reason for variation in male mating behaviour in lek-breeding mammals (Leuthold 1966, Montfort-Braham 1975, Jarman 1974, Schuster 1976, Clutton-Brock et al. 1988, Apollonio 1989, Clutton-Brock 1989, Gosling and Petrie 1990, Apollonio et al. 1992, Balmford et al. 1993), studies designed to understand this phenomenon in lek-breeding birds are limited (but see Bradbury et al. 1986, Gibson and Bradbury 1987, Lank and Smith 1987, Pruett-Jones and Pruett-Jones 1990). This study investigated male mating behaviour in the buff-breasted sandpiper, a lek-breeding shorebird in which male display tactics appears to be extremely variable.

Although traditionally described as an "exploded" lekking species (Parmelee et al. 1967, Pitelka et al. 1974, Prevett and Barr 1976, Myers 1979, Dorogoy 1983), male buff-breasted sandpipers in some populations have been reported to defend resource territories (Cartar and Lyon 1988) or switch from lekking to solitary display (Pruett-Jones 1988). Although previous work on this species is suggestive of a variable mating system, studies conducted to date have been limited in duration and covered relatively small areas. My first aim in this study was to document the variation in male mating behaviour, and my second aim was to try to explain that variation by investigating the social context of various behaviours. I conducted this study over an extensive area so that I could monitor males simultaneously on and away from leks.

Emlen and Oring (1977) suggested that male aggregations were most likely to occur when the operational sex ratio was highly skewed towards males (i.e., few fertile females relative to the number of sexually active males). In this situation, intrasexual

competition was predicted to be too intense for males to defend resource territories economically, and male success then becomes based on dominance or position effects on leks. An opposite prediction might be made, however, if stable dominance relationships are difficult to establish among males. This may be especially true in species where male tenure on leks is short and male site fidelity to leks across years is low. Here, intense levels of intrasexual competition, especially when female visits to leks are few, may result in males abandoning leks and displaying solitarily. Other competing forces, such as female preferences for aggregated males, male tendencies to clump around 'hotshot males' (Beehler and Foster 1988) or to display in areas with high female densities (i.e., hotspots, Bradbury et al. 1986), may cause some males to continue displaying on lek territories. Thus, the predicted relationship between the operational sex ratio (OSR), intrasexual competition and the tendency for males to display on leks is not straight forward. Here, I tested the prediction that the OSR influences the level of intrasexual competition on leks and that male mating behaviour varies with the OSR.

Additional insight into how the OSR may influence male mating behaviour can be gained by following individual males through time. If the OSR influences all males similarly, I predict that all individual males should exhibit the same mating tactics (e.g., all males display on leks and then all males switch to solitary display as female visits to leks decrease; see Pruett-Jones 1988). However, if individual males behave differently, factors besides variation in the OSR, must be found to explain this variation. These could include unequal male competitive abilities (Matalo et al. 1992) or variation in lek "quality" which results in males on high quality leks maintaining territories while males on low quality leks

abandon territories. To test the hypothesis that males exhibit similar mating behaviour in response to changes in the OSR, I documented the mating behaviour of individually marked males through time during three breeding seasons.

In a previous study, Pruett-Jones' (1988) reported that male buff-breasted sandpipers switched from lekking to solitary display as the breeding season progressed. He suggested this strategy increased males' opportunities for mating with reneesting females. If males initially display on leks to fertilise first clutches and then display solitarily near nests to fertilise replacement clutches, I predict a temporal shift in male display from leks to solitary sites late in the nest initiation period (i.e., when the chance of fertilising a replacement clutch is greater than the chance of fertilising a first clutch).

METHODS

Survey procedures and lek definitions described in the general methods were used to document the location of leks throughout the breeding season. As mentioned earlier, I considered a male to be part of a "lek" if he was located within 200 m of another displaying male. To determine how sensitive my results were to using 200 m to define leks, I repeated my analyses using both 100 m and 300 m as my criterion. In neither case did this alter my results qualitatively, so I only present results based on the criterion of 200 m. Displaying males that I classified as being on leks typically were separated from other groups of males by several kilometres or more (Pruett-Jones 1988; this study).

For comparisons of male display behaviour among years, I considered males detected alone to be part of a lek if a previous or subsequent survey detected multiple

males in the same area. This allowed me to calculate the minimum number of leks, the maximum and mean lek size, and to categorise leks according to their stability. I classified leks as "stable" if males were present in the same area for at least two surveys within a year and as "unstable" if males were present only during a single survey. To calculate the percentage of males that displayed on leks and in solitary locations during each survey within a year, I used the status (i.e., solitary display or lek display) of each male on the day of the survey. To calculate the density of males on the study area each year, I assumed unmarked males seen in the same location during subsequent surveys were the same individuals. This yielded a minimum estimate because observations of marked males indicated that some movement occurred.

Factors influencing male mating behaviour

To estimate the OSR, I first tallied the number of males present during each strip transect survey conducted in 1993 and 1994. I assumed all males detected during surveys were sexually active because males do not provide parental care and are consequently free to mate whenever a partner is located. Second, I determined the number of females sexually available using the phenology of nests located throughout the breeding season. I did not use survey counts to estimate the number of fertile females available because not all females may have been sexually active (e.g., females incubating a clutch but on a feeding break). I considered females sexually available six days prior to egg laying until the third egg of a four egg clutch was laid (i.e., -6 to +2 days where day 0 = date the first egg was laid). I used -6 days as the cut-off point for when pre-laying females were

receptive to males because peak copulation frequency for lekking species has been reported to be -5.06 ± 1.08 ($\bar{x} \pm \text{SE}$) days (Birkhead and Møller 1993). Two females captured on leks and later located at nests also indicated this pre-fertilisation period was reasonable (egg-laying occurred 4 and 7 days after females visited males on a lek). I assumed that females laid an egg every 24 hrs once clutches were initiated. Although I could not differentiate between females initiating first and replacement nests, this does not affect my OSR calculations because females in both stages were sexually active. Next, I calculated the OSR by dividing the number of sexually active females by the total number of males detected during surveys for each survey date. Because the methods used to estimate the number of males and females differ, my OSR estimates can only be used as relative, rather than absolute, values.

I used male behaviour on leks to derive an independent measure of intrasexual competition. During each focal observation (see general methods) I recorded four easily recognised behaviours used by male buff-breasted sandpipers to defend their territories or mates (see Myers 1979; Pruett-Jones 1988, chapter 1). These included aerial chases (AC), ground chases (GC), vertical flights (VF) and fights (FI). Aerial and ground chases occurred when a resident male chased an intruder out of his territory. Such chases occurred regularly throughout the lekking period. Vertical flights occurred less frequently, and consisted of two males flying upward together above their respective territory boundaries. Males typically participated in several of these flights before returning to their territories or resorting to fighting. Fights occurred very rarely (typically when a male tried to reclaim his territory after returning from a feeding break) and

involved bill pecking and foot grappling. I also recorded when males sneaked on to another male's territory and disrupted (DI) the resident male's courtship behaviour. I considered DI more aggressive than AC or GC because it involved a male leaving the safety of his own territory. Based on the location and context of these behaviours, I scored each behaviour in order of increasing intensity of competition, where AC and GC = 1, DI = 2, VF = 3, and FI = 4. The intensity of competition for each focal-sampled male was calculated by summing the number of occurrences of each behaviour, weighted by their score, and dividing by the minutes sampled. These values were then averaged across all focal males sampled over 3 days with the middle day of each 3-day period coinciding with the date of each survey.

To determine if and when males displayed near nests, I calculated the percentage of males that displayed near active nests during each survey. Males were considered to be associated with a nest if they displayed to the attending female or were located within 150 m of an active nest site. The large display area of males and observations of males following females as they approached and left their nests indicated males were generally "aware" of nests within this area. Males were not considered to be near nests in cases where females initiated nests near previously active lek sites because my goal was to determine when males moved to be near females. I further subdivided males located near nests into those detected with other males (i.e., within 200 m of each other but both within 150 m of the nest) and those seen alone. To test the hypothesis that males switch their display to the vicinity of nests to increase their opportunities to mate with renesting females, I determined the proportion of nests that had displaying males nearby when

females were fertile (-6 to +2 days) and post-fertile (+3 to +27 days) [see above for numbering sequence]

RESULTS

Buff-breasted sandpipers arrived at Prudhoe Bay alone or in flocks of 2 to 4 birds during late May each year. Early migrants usually foraged in snow-free areas along river bluffs and ridges, occasionally displayed, but generally moved on after several hours. The first sandpipers were encountered on the 27, 28, and 24 of May in 1992 through 1994, respectively (Figure 2-1). Typically, the number of birds increased slowly, reached a maximum around 6-7 June, and then gradually decreased as females began nesting and males departed the area. In 1994, however, a sharp decline in temperatures and an accumulation of snow resulted in most birds postponing arrival until conditions had improved. In that year, birds arrived in large numbers on the evening of 7 June. During the 10-14 day interval between first detection and peak counts, the average maximum temperature rose to above 0°C and snow cover declined from an average of 58% to 5% (R. Lanctot, unpublished data).

Marked birds seldom returned to the study area in subsequent years. Of 59 males and 76 females captured in 1992 and 1993, only five males and five females were observed in more than one year (an additional 56 males and 33 females were captured in 1994). Of the males that returned, four were observed in two years and one was observed in three years. Three males visited the same lek in subsequent years and two males displayed at different leks. All five females that returned were observed in two years. A

Figure 2-1 The number of buff-breasted sandpipers counted during surveys, 1992-1994. Males are indicated by solid bars and females by open bars. Data are based on variable circular plot surveys in 1992 and complete coverage strip transect surveys in 1993 and 1994. An "*" indicates that only snow-free portions of the study area were surveyed.

Number of sandpipers counted

Date (May - June)

comparison of return dates for marked males and females indicated both sexes arrived on the breeding grounds at similar times (males: 31 May, and 1, 4, 5, 9 and 16 June; females: 28 May, and 2, 4, 10 and 21 June).

Male Mating Behaviour

Males began displaying on the study area 2-11 days after first arriving at Prudhoe Bay; aerial and ground displays were observed between 30 May - 27 June 1992, 30 May - 8 July 1993, and 4 June - 9 July 1994. An average of 39, 57 and 59% of the birds detected during all surveys in 1992-1994, respectively, were males (Figure 2-1).

Of the males detected, the number that displayed on leks remained relatively stable through time (Figure 2-2, E,I). An average of 77.1 and 75.6% were detected on leks across all survey periods in 1993 and 1994, respectively. Lekking males were most common during the second, fourth and seventh survey periods in 1994 ($\chi^2 = 14.6$, $df = 6$, $P = 0.02$) but did not vary across survey dates in 1993 ($P = 0.32$).

The number and location of leks detected within a year varied considerably. During a single survey, the number of leks recorded ranged from 5 to 15 in 1993 ($\bar{x} \pm SD$, 9.4 ± 4.1) and from 2 to 16 in 1994 (7.9 ± 4.8 ; Figure 2-3). Summed across all survey periods, lek densities were similar between 1993 and 1994 (ca. 1.65 leks/km²; Table 2-1). Stable leks were initiated significantly more frequently during early survey periods than unstable leks in 1994 but not in 1993 (1993: log-likelihood ratio $\chi^2 = 9.2$, $df = 5$, $P = 0.10$; 1994: $\chi^2 = 18.6$, $df = 5$, $P = 0.002$ [one of the seven surveys were excluded from the analyses in each year because no new leks were initiated]). The number of stable leks

Figure 2-2. Seasonal chronology at Prudhoe Bay, Alaska, in 1993 (A-E) and 1994 (F-I).

A: Mean male competition scores ($\pm$ SE; number of individual males that contributing to the mean are listed above the error bars); **B,F:** number of fertile females present on date of surveys; **C,G:** total males counted during surveys; **D,H:** OSR (operational sex ratio) defined as the number of fertile females divided by the total number of males; **E,I:** percentage of the total number of males counted on surveys that displayed on leks. See text for description of when females are sexually available and for definition of a lek.

Figure 2-3. Size and distribution of buff-breasted sandpiper leks on surveys in 1994.

4 June

7 June

10 June

13 June

- Solitary Male
- 2-5 Males
- 5-10 Males
- >10 Males

17 June

21 June

0 1 2 Km

Table 2-1. Lek stability and abundance of male buff-breasted sandpipers based on seven ground surveys conducted each year on a 16-km² study area in northern Alaska, 1993-1994.

	1993	1994
Number of leks ^a		
Active		
Stable	15	11
Unstable	12	14
Additional	--	13
Active previous year	--	10
Number of displaying males/lek ^a		
Stable		
$\bar{x}$ (SD) ^b	2.3 (1.3)	3.0 (1.8)
Range	1 - 11	1 - 20
Unstable		
$\bar{x}$ (SD) ^b	2.9 (1.0)	2.6 (1.4)
Range	2 - 5	2 - 7

Table 2-1. Continued.

Lek density (leks/km ²)	1.7	1.6
Number and percentage (%)		
of solitary males ^c	13 (13)	19 (17)
Total number of males	103	114
Male Density (males/km ²) ^d	6.4	7.1

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^a Calculations assume males were part of a lek if they were located within 200 meters of another male and if a previous or subsequent survey detected multiple males in the same area.

^b Values represent the average number (and SD) of males present at the lek during all observations.

^c Includes only males seen in areas that were not previously lek sites or did not become lek sites subsequently. Unmarked males seen in the same location during subsequent surveys were assumed conservatively to be the same individuals.

^d Includes solitary and lekking males, and uses maximum counts of males seen at individual leks.

detected always exceeded the number of unstable leks during each survey, but the relative proportions of each type remained the same throughout both breeding seasons (1993: $\chi^2 = 7.4$, $P = 0.28$; 1994: $\chi^2 = 9.2$, $P = 0.17$, $df = 6$ for both years).

Across years, leks seldom occurred in the same location. Of the 49 lek sites documented during 1992-94, only five (10.2%) were active all three years, ten (20.4%) for two years, and 34 (69.4%) for one year. Five of 17 leks (29%) detected in 1992 were observed during all three years, although surveys were not conducted over the entire study area in that year. Stable leks were no more likely to be present than unstable leks in succeeding years (1993 to 1994: Fisher's exact test, $P = 0.43$), and leks present in both 1993 and 1994 were just as likely to change lek types as to stay the same (Fisher's exact test, $P = 0.63$).

The average size of leks (regardless of type) detected during surveys was 2.6 males (± 1.2 , $N = 27$) and 2.7 males (± 1.6 , $N = 25$) in 1993 and 1994, respectively. The most common lek size was two, but leks with as many as 20 males were present (Table 2-1). The average number of males displaying at stable and unstable leks at one time ranged between 2.3 and 3.0 (total number of males that used a lek was much higher due to male turnover, see later). The highest numbers of males were recorded at stable leks, although stable leks were not consistently larger. Daily visits to stable leks during each year of the study indicated the number of males detected on a given day was quite variable (e.g., the number of males at one lek ranged from 2 to 12). For all leks, however, counts generally peaked during the second week of June.

Seasonal Variation In Sexually Active Females And The OSR

Nest initiation was relatively synchronous in 1993 but more prolonged in 1994 (Figure 2-4). Median clutch initiation dates occurred on 14 June 1993 and 15 June 1994. Nests initiated late in the season were probably from either late arriving or renesting females. Only one renest was documented.

The number of females sexually available peaked during the second week of June in both 1993 and 1994 (Figure 2-2 B,F). Females were available for a slightly longer period in 1994, reflecting the prolonged nesting season of that year. However, the delayed arrival of birds in 1994 had little effect on when fertile females first became available. The OSR was highly correlated to the number of fertile females in 1993 ($r_s = 0.99$, $P < 0.0025$, $N = 7$) but not in 1994 ($r_s = -0.09$, $P > 0.25$, $N = 7$). The primary difference in 1994 occurred on 4 June when only three males were detected during surveys (Figure 2-2).

Intrasexual Competition

Although male competition scores did not vary significantly among survey dates (Kruskal-Wallis test: $X^2_5 = 6.29$, $P = 0.28$), the most intense and variable competition occurred during the first week of June (Figure 2-2, A). This variation did not appear to be related to whether males had female visitors during focal observations although previous studies have shown elevated male interactions coincide with female visits to leks (Avery 1984). Male competition scores derived from focal observations restricted to when females were present were highly correlated with scores derived from all focal

Figure 2-4. Percentage of males that displayed near and away from active nests during each survey relative to nest phenology, 1993-1994. Total number of males monitored during each period are listed above the bars in the upper panels. Initiation dates were unknown for nine nests in 1993 and one nest in 1994. Median nest initiation dates are marked with asterisks. R = known renesting attempt. See text for definition of what constituted male display near a nest.

1993

1994

Males
Detected

0 13 18 39 44 40 21 14

0 3 46 48 48 25 13 9

observations regardless of female presence ($r_s = 0.93$, $P < 0.0005$, $N = 23$). Focal observations of males without females often had high competition scores because these males would frequently disrupt the courtship of neighbouring males. The intensity of intrasexual competition also did not vary significantly with the OSR ($r_s = 0.09$, $P > 0.25$, $N = 6$). This suggests that the intensity of intrasexual competition on my leks is not simply a reflection of the OSR but is an independent measure of the competitive environment experienced by lekking males.

Lekking Relative To Variation In The OSR And Intrasexual Competition

Contrary to my predictions, the OSR and the proportion of males on leks were not correlated (1993: $r_s = 0.43$, $P > 0.10$, $N = 7$; 1994: $r_s = -0.25$, $P > 0.25$, $N = 7$, Figure 2-2). However, the number of males, irrespective of display location, was correlated strongly with the number of sexually available females on the study area across surveys in both years (1993: $r_s = 0.98$, $P < 0.0025$, $N = 7$; 1994: $r_s = 0.98$, $P < 0.0025$, $N = 7$, Figure 2-2). This suggests males were tracking the presence of sexually available females and visiting and leaving the study area accordingly. The intensity of intrasexual competition was not significantly correlated with the proportion of males on leks (1993: $r_s = 0.09$, $P > 0.25$, $N = 6$, Figure 2-2).

Individual Male Mating Behaviour

Despite the consistent proportion of males on leks throughout the breeding season, individual males exhibited substantial variation in their mating behaviour. Daily visits to

stable leks in each year of the study indicated most males stayed at a lek for a day or less (57%, $N = 56$) and that only 16% stayed for >8 days (Figure 2-5). Typically, one to three long-term (9-22 days), one to four intermediate (2-7 days), and four to ten short-term (1 day) males were resident at each stable lek throughout the breeding season. The number of short-term males was actually even higher, because birds present for only one day were almost certainly less likely to be captured, and the above values do not include males at unstable leks, which usually were active for only one day.

Resightings of marked and radio-equipped males on my study area indicated most males displayed at a single lek (Table 2-2). However, 57% ($N = 73$) of these birds were present for only one day before presumably leaving the study area to display at new locations. Seven of the 11 males equipped with radio transmitters in 1992 were not located the day after capture despite daily ground tracking and one aerial survey that extended ten kilometres from the study area. The remaining four males displayed at one or more leks for 2, 3, 4, and 15 days, respectively, before disappearing. One banded male was sighted on a lek 23 km away from my study area two days after disappearing (L. Payne, personal communication). Males that were banded but not equipped with radios were resighted on the study area at similar rates as radio-equipped males (males present 1 day versus >1 day: Fisher's exact test, $P = 1.0$) and birds marked in previous years also exhibited large variation in lek tenure (e.g., five returning males were sighted for 1, 1, 2, 4, 7, and 9 days [one male returned in two different years]). This high turnover rate of males on my study area was also apparent in my surveys (Figure 2-1). Most of the males resighted on the study area were seen at 2-3 leks. One male visited three different leks in

Figure 2-5. Residency times for individually identifiable males at "stable" leks on the Prudhoe Bay Oil Field, Alaska, 1992-94. Males from the same lek within a year are similarly shaded. All leks were active for a minimum of nine days and had at least nine males banded. Estimates of lek attendance may be conservative because males may have been present prior to banding.

Table 2-2. Mating behaviour and movement of individual male buff-breasted sandpipers on a 16-km² study area in northern Alaska, 1993-94.

	1993 (<u>N</u> = 39)	1994 (<u>N</u> = 59)
Percentage of males		
that displayed at:		
one lek	74	75
two leks	23	14
≥ three leks	0	7
only solitary sites	3	7
solitary sites and leks	13	9
only nests	0	2
nests and leks	23	36
Days to move between leks		
mean (SD)	3.0 (2.1)	2.6 (1.5)
range	1-6	1-5
Distance moved between leks (Km)		
mean (SD)	2.2 (2.1)	1.2 (0.6)
range	0.5 - 6.4	0.4 - 2.3
<u>N</u>	6	7 ^a

Table 2-2. Continued.

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* Excludes one male seen displaying 23 km outside the study area two days after being banded.

a 7-day period, and males occasionally abandoned a lek, disappeared, and then returned several days later (range = 3-8 days, $N = 4$). For males present on more than one lek, the average time between sightings on different leks was 2-3 days and the average distance moved between leks was 1-2 km (Table 2-2). From 3-7% of males were detected displaying solitarily, and 9-13% of males were detected displaying both solitarily and with other males in 1993 and 1994 (Table 2-2).

Male Display Near Nests

As reported by Pruett-Jones (1988), some males appeared to shift their display locations toward nest sites as the breeding season progressed (Figure 2-4). The majority of males (generally >70%), however, continued to display at sites away from nests. Few females initiated nests near active lek sites (four nests in 1993, one in 1994). Male movements to nest sites did not begin late in the nest initiation period as I had predicted, but rather occurred as soon as the first nests were initiated. Nests were more likely to have males nearby when females were fertile as opposed to post-fertile in 1994 but not in 1993 (1993: Fisher's exact test, $P = 0.57$; 1994: Fisher's exact test, $P = 0.02$). This difference may be attributed to the prolonged nesting period in 1994 (Figure 2-4). In that year, males may have been able to visit more nests during the fertile period because females completed clutches over a longer period of time. These results are contrary to Pruett-Jones' (1988) suggestion that males display near nests to increase their opportunity to mate with renesting females. Most males appeared to display near nests so as to fertilise eggs in the female's first clutch rather than to fertilise eggs in a second nest. Also

in contrast to Pruett-Jones' (1988) observations, males frequently displayed near nests with other males (i.e., on unstable leks) as opposed to being alone. Indeed, on several occasions I documented up to four marked males near a single nest.

Between 23% and 38% of marked males were seen near nest sites in each year (Table 2-2). Of the 31 males detected near nests, two were present at three nests, nine at two nests, and 20 at one nest. (Six males were able to display at two nests simultaneously because the nests were near each other). On four occasions, males left a nest and then returned several days later. Males displayed near nests for one to 12 days, but the majority (74%, $N = 38$ male/nest combinations) was present for only one day ($\bar{x} \pm SD = 1.7 \pm 1.9$). All occasions when males were located near nests for longer than two days occurred because females had nested near male display sites.

Males observed near nests primarily foraged and only occasionally exhibited courtship behaviour. Females generally did not respond to these displays. Males rarely succeeded in copulating with egg-laying females. I observed only five (of 33) copulations away from leks and paternity analyses indicated only two of 47 families were sired by males captured near nests (chapter 4). Males also followed incubating females as they flew to and from nests during foraging breaks. On no occasion, however, did I observe a female soliciting courtship from males at this time. Similar behavioural interactions between males and incubating females were reported by Pruett-Jones (1988).

DISCUSSION

Variation In Male Mating Behaviour

Lekking by male buff-breasted sandpipers was ephemeral on several time scales. Buff-breasted sandpiper leks were seldom traditional among years. Most leks lasted for only a few days within a year, and males regularly displayed on solitary sites, as well as leks, throughout the breeding season. The low incidence of traditional lek sites was also documented by Pruett-Jones (1988) in his study of buff-breasted sandpipers at Prudhoe Bay. This trait is unusual among lek-breeding species (Wiley 1991, Höglund and Alatalo 1995), and is typically associated with marked increases or decreases in population size, the size of individual leks (smaller leks are more likely to disappear), and unstable habitat conditions (Wiley 1991). The first two factors do not appear to explain the lack of traditional lek sites in buff-breasted sandpipers. Male density was relatively constant throughout the study, and stable leks, which are typically larger, were just as likely as unstable leks to disappear in succeeding years. It seems more likely that the lack of traditional lek sites may be related to local habitat availability, the species migratory habits, and its low breeding site fidelity. The paucity of returning males to display at and "initiate" traditional lek sites may reduce the likelihood of a lek site being used repeatedly. Traditional leks may simply result from some areas being regularly free of snow early in the spring or being located near travel corridors such as rivers (Pruett-Jones 1988, Lanctot 1995). Ruff also exhibit lower levels of site faithfulness in less stable arctic regions relative to temperate areas that are intensely managed (e.g., agriculture, bird reserves) by humans (D. Lank, personal communication).

Short-term use of lek sites within years has been reported in a number of other lek-breeding species (see e.g., Koivisto 1965, Lemnell 1978, Gibson and Bradbury 1987, Bradbury et al. 1989a), but in most cases, adults returned to traditional areas once habitat conditions improved (e.g., snow melted). Male buff-breasted sandpipers that abandoned leks, in contrast, typically established leks at new sites or left the study area and were not seen again. This was especially true during the latter part of the breeding season when unstable leks were most common. Similar mobile leks were documented for ruff on the Indigirka Delta, Russia (Kistchinski and Flint 1973 in Cramp and Simmons 1983) and in central Finland (Lank and Smith 1987).

The consistently high proportion of males present on leks appears to contrast sharply with Pruett-Jones' (1988) observations of males switching from lekking to solitary display and Cartar and Lyon's (1988) observations of males defending resource territories. Although observed differences may be a result of variation in population density or habitat homogeneity (see Cartar and Lyon 1988), most of the discrepancies probably are due to the scale at which the studies were conducted. My study area was substantially larger (16 km² versus 1-2 km²) and encompassed a larger number of leks than the other two studies. I also had more people (6-8) who banded and followed a larger number of birds over a three year period. This contrasts with a limited number of banded birds and 1-2 people working during one field season in the other two studies. (Pruett-Jones' [1988: 1741] observations were collected over four years but the majority of his data was from one lek that he observed from 8 to 19 June, 1980). Consequently, I offer alternative explanations for the data reported in the two previous studies. Cartar and

Lyon (1988) interpreted males displaying and fighting near nests as evidence of resource defence territoriality. However, I know from my observations of marked birds that individual males seldom remained near nests for more than a day, but that the same nest could have different males nearby on successive days. Because Cartar and Lyon (1988) did not have marked birds in their study, they too may have been seeing a succession of males at a nest, and not a single territorial male. Their observations are consistent with my data that indicate some males do display solitarily. Similarly, Pruett-Jones' (1988) observation that males switched from lekking to solitary display may simply reflect that the lek he observed did break up, leaving only solitary males in his study area, while simultaneously, new leks were formed outside the study area.

Factors Influencing Male Use Of Leks

I did not find support for Emlen and Oring's (1977) prediction that male aggregations occur when the OSR is skewed toward males. Indeed, despite large variations in the OSR through both breeding seasons, about 75% of males consistently displayed at leks. These results are consistent with a reanalysis of Lank and Smith's (1987) data on ruff, insofar as neither species exhibited the predicted negative relation between the proportion of males on leks and the OSR. Male ruff were less likely to be on leks when the number of females visiting leks was low relative to the number of sexually active males (correlation between 'lek ratio' and OSR defined as the mean number of females visiting leks divided by the total number of males counted during censuses: May: $r_s = 0.60$, $P < 0.05$, $N = 15$; June: $r_s = 0.81$, $P < 0.001$, $N = 14$).

A possible explanation for my failure to support Emlen and Oring's prediction might be related to the scale at which I calculated my OSR value. Indeed, if males abandon leks to establish new leks where breeding opportunities are higher (potentially outside of my study area), than these males would in effect be shifting to new lek sites where OSR levels are higher. This scenario would support Emlen and Oring's (1977) predictions of how OSR should affect male display on leks, but only when viewed at a very large scale. Alternatively, consistent display by males on leks, regardless of changes in the OSR, may be explained by differential predation risks on and off leks (Wittenberger 1978, Wrangham 1980, Phillips 1990, Balmford and Turyaho 1992, Deutsch and Weeks 1992), the importance of leks in providing females a choice of mates (Bradbury 1981), and consequently, the relative mating success of lekking and solitary males.

I also failed to find any relationship between the intensity of interactions among males on leks, the proportion of males on leks or the OSR. Interactions appeared more intense when leks were forming. The total number of males on the study area (lekking and solitary males combined) did vary in both years of the study with the number of fertile females that was present. This apparent tracking of females by males, also observed by Pruett-Jones (1988) and in other lek-breeding species (Lank and Smith 1987, Bradbury et al. 1989b) suggests males may respond to changes in OSR by moving to areas with more fertile females, as opposed to switching from lekking to solitary display. This option may not be available to non-migratory lek-breeding species.

I found no support for Pruett-Jones' (1988) observations that males switched to displaying near nests to fertilise replacement clutches. Rather, my observations suggested

males displaying near nests were attempting to fertilise first clutches rather than replacement clutches. Observations of multiple males near these nests suggest males may compete for access to these females. The large number of males that continued to display away from nests suggests that some females prefer to mate with males away from their nesting area, perhaps to minimise male display near nests which might attract predators (Wrangham 1980).

Individual Differences In Male Mating Behaviour

Individual males appeared to use several tactics for acquiring mates, including displaying: (1) at a single lek for most of the breeding season, (2) at multiple leks for a short period of time each, (3) at solitary sites, and (4) at both leks and solitary sites. These findings suggest that theoretical predictions of how the OSR should influence male display on leks may be too simplistic. Indeed, recent studies on a variety of species have revealed that individuals respond differently to inter- and intrasexual conflicts, producing a variety of mating patterns within populations (see e.g., Alatalo et al. 1981, Davies 1989, 1992, Davies et al. 1995, Kempenaers 1995).

The large variation in male attendance at leks and the high level of male movement among leks in buff-breasted sandpipers has rarely been reported in other lek-breeding species. Notable exceptions include populations of ruff (Lank and Smith 1987 and references therein) and great snipe (Lemnell 1978, Höglund and Robertson 1990). In both species, a high proportion of non-resident males visit leks and numbers of males at leks change daily. Non-resident males have been reported in many other lek-breeding species

but generally they are considered to be few in number (see e.g. Stiles and Wolf 1979, Pruett-Jones 1985; Théry 1990, Petrie et al. 1991, Schroeder and Braun 1992). Explanations for variation in male tenure at leks generally include differences in the competitive ability, attractiveness, or energetic limitations of males (Vehrencamp et al. 1989, Höglund and Robertson 1990, Höglund et al. 1992, Alatalo et al. 1992, Westcott and Smith 1994, Widemo and Owens 1995). These factors probably do not adequately explain the high mobility and low breeding site fidelity of male buff-breasted sandpipers. I suspect the answer may relate to the short arctic breeding season, the species' migratory abilities and the variable breeding opportunities available at a regional level (see discussion in Pruett-Jones 1988). For example, males appeared to have only 1-2 weeks in which to establish territories, attract females and copulate successfully on my study area (80% of nests were completed within 10 days in 1993 and 1994). At a regional level, however, males may gain an additional week during which to search for mates by simply travelling 10-50 km northward (due to a coastal gradient of snow melt; Walker et al. 1980). Over a wider area of the arctic (e.g., Western Canada vs. Alaska), appropriate breeding conditions may vary by two or more weeks (Foster 1989). The species' ability to migrate large distances (individuals annually migrate 13,000 km one-way to their wintering grounds) would make it easy for a male to travel 500 km or more to an area that only recently became available for breeding.

The unpredictable breeding conditions on the Arctic Coast also offer an explanation for the low breeding site fidelity exhibited by males among years. For example, a male returning in late May to my study area would have found suitable

breeding conditions in 1992 and 1993 but only snow in 1994. Thus, migrating males might benefit by attempting to mate at the first suitable site they encounter rather than risk returning to a site in which they previously bred. This interpretation suggests that the mating system of the buff-breasted sandpiper, and possibly some populations of ruff and great snipe, can be understood fully only when viewed at a very large scale. This contrasts sharply with the majority of studies of other lek-breeding species in which the focus of research and subsequent interpretations has been at the level of individual leks (Wiley 1991, Höglund and Alatalo 1995). However, the fact that males of most lek-breeding species are far more sedentary during the breeding season than male buff-breasted sandpipers, suggests that regional variation in breeding opportunities may affect lekking only in species or populations where individuals can move large distances in a short time. In some ways, this regional view might be considered as a large scale version of the hotspot model of lek evolution (Bradbury et al. 1986), whereby males form leks in areas with an abundance of reproductive females. However, recall that within my study area, the total population of males, not just those on leks, changed in concert with female abundance. Thus, my regional model may explain the ephemeral nature of lekking in this species, but it does not explain why males use leks, nor why some males do not.

CHAPTER 3.

MALE TRAITS, MATING TACTICS AND REPRODUCTIVE SUCCESS IN THE BUFF-BREASTED SANDPIPER

INTRODUCTION

Males in a wide variety of taxa use alternative tactics to breed (Rubenstein 1980, Dunbar 1982, Arak 1984, Lott 1991). This use of alternative mating tactics is typically attributed to phenotypic or competitive differences amongst males, environmental conditions that favour the use of one mating tactic over another by certain individuals, or more rarely, genetic differences that predispose males to use a particular tactic. In this chapter, I explore the basis for alternative male mating tactics in the buff-breasted sandpiper.

Alternative male mating tactics have been documented in most avian lek-breeding species. Besides defending territories at leks, males display in solitary locations (e.g., Pruett-Jones and Pruett-Jones 1990), share courts with territorial resident males (Hogan-Warburg 1966, McDonald 1989b), mimic female behaviour and sneak copulations from other territorial males (Trail 1990, Westcott and Smith 1994) or pursue females off leks (Gibson and Bradbury 1987, Lank and Smith 1987). A limited number of long-term studies have identified differences between males that use alternative tactics. For example, solitary males in black grouse (*Lyrurus tetrix*) and yellow-whiskered greenbul (*Andropadus latirostris*) are typically juveniles or subordinates (Kruyt and 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 1989b, McDonald and 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 are fixed for life, depending on the male's genetically derived plumage and behaviour (Hogan-Warburg 1966, Lank and Smith 1987, Höglund and Lundberg 1989, Lank et al. 1995).

Little information is available on males that change mating tactics within years. 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 maximise their mating chances (see e.g., Alatalo et al. 1992, Höglund et al. 1993, Widemo and Owens 1995). Despite this assumption, early studies of lek behaviour have focused exclusively on long-term resident males at one or a few leks (e.g., Höglund and Lundberg 1987, McDonald 1989b, Gibson et al. 1991, Hill 1991, Petrie et al. 1991). Non- and short-term resident males were generally dismissed as being juveniles or non-breeders.

In chapter 2, I reported that male buff-breasted sandpipers use several alternative mating tactics. About 75% of males display on leks at any one time, while the remainder display in 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 between one to three long-term (>9 days), one to four intermediate term (2-7 days), and four to ten short-term (1 day) males resident throughout the breeding season. A small proportion males that display solitarily and on leks are found near nests. In addition to these tactics, males mimic female behaviour, and either disrupt or steal copulations from territorial males on leks (Myers 1979, chapter 4).

The first objective of this chapter was to document within and among year changes in male mating tactics, and to determine if individual differences among males could explain variation in their use of alternative mating tactics. I also investigated how mating tactics affected male mating success. Here, reproductive success was determined by combining observations of copulations obtained during focal behaviour observations with paternity results from a DNA fingerprinting study (chapter 4). Second, I investigated the prevailing social conditions when males altered tactics. Male use of particular tactics may be mediated by such factors as their competitive ability, their attractiveness, or their energy levels relative to other males on the lek (see e.g., Vehrencamp et al. 1989, Höglund and Robertson 1990, Alatalo et al. 1992, Höglund et al. 1992, Westcott and Smith 1994, Widemo and Owens 1995). To determine this, I compared the behaviour and morphology of males that abandoned and maintained territories at leks on a daily basis. I also followed individual males through time and compared the social conditions experienced by these males in previous and new display locations.

I identified the following male traits as potential variables that may influence a male's mating tactics and mating success. Body size and condition may effect a male's ability to establish long-term territories on leks or to mimic female behaviour. Larger, better conditioned individuals are likely to be able to displace other territorial males and withstand territorial challenges and disruptions by neighbouring males. In contrast, smaller males are likely to be more successful at joining female groups, mimicking female behaviour, and ultimately stealing copulations from resident males (females are smaller than males in this species, chapter 1). Other studies have shown male display to be an important component in female choice (e.g., Gibson and Bradbury 1985, Pruett-Jones and Pruett-Jones 1990). Inferior males may be forced to adopt alternative

tactics to acquire mates which rely less on female choice based on male display. 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 (chapter 1). 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 (Höglund et al. 1990) and peafowl (*Pavo cristatus*; Petrie and Halliday 1994), and to increase the dominance status of European starlings (*Sturnus vulgaris*; Swaddle and Witter 1995). 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 and Walsh 1993). Experimental and correlational studies have shown that males with low levels of fluctuating asymmetry are preferred by females (see e.g., Møller 1992, Swaddle and Cuthill 1994) and are dominant over asymmetrical individuals (Thornhill and Sauer 1992, Liggett et al. 1993, Manning and Chamberlain 1993). The location of a male's territory, i.e., whether centrally or peripherally located on a lek, may also influence a male's mating success and ultimately his ability to maintain a territory on a lek. Males on central territories have relatively higher mating success in many lek-breeding species (Höglund and Alatalo 1995). Finally, the length of time males attend leks has also been shown to influence male mating success (Höglund and Alatalo 1995, Mackenzie et al. 1995). This variable was used to separate males into different mating tactics (see below) and as a predictor variable in male mating

success analyses.

METHODS

Male sandpipers were surveyed, captured, and marked as described in the general methods. The number, identity and behaviour of males was also recorded daily on two to three intensively studied leks during each year of the study. Focal behavioural observations were conducted on males in 1992 and 1993, and on females in 1994. Consequently, all analyses involving male behaviour are restricted to 1992 and 1993.

Male Mating Tactics

Based on male display location, tenure at leks and overall movement patterns, I categorised males as exhibiting one or more alternative mating tactics. First, I separated males based on resightings of individuals throughout the study area (i.e., on and off of leks). Males were considered to be "solitary" if they were observed displaying alone (>200 m from an adjacent male; see chapter 1) and on "leks" if they were with other males. Similarly, I considered males to be near "nests" if they were observed displaying within 150 m of an active nest site (chapter 2). I did not consider males to be near nests if those nests were initiated by females after the male had begun displaying in the area. This approach allowed me to compare males that chose to display near nests with those males that were away from nests or simply occurred near nests by chance (i.e., because females chose to nest near displaying males). Incomplete surveys on the study area in 1992 did not allow me to classify males as having displayed in solitary locations or near nests, or to follow them to document changes in mating status.

Second, I separated marked males that visited my intensively studied leks into "long-" and "short-term" resident males based on lek tenure. Tenure was scored as the proportion of visits to a lek on which a male was observed, beginning with the day the male was banded. In all cases, leks were active for at least three additional days after a male was banded ($\bar{x} \pm SD = 13.8 \pm 4.4$ days). This fact prevented late arriving males from being assigned an artificially high score. For males banded in previous years, I considered all days a lek was visited as possible days a male could be sighted. A score of 25% was used to separate long- and short-term males (Figure 3-1), with approximately one third of all ($N = 61$) males being classified as long-term. I also 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.

Male Traits

To identify whether individual differences among males explained variation in their use of alternative mating tactics, I recorded several morphological and behavioural traits for each male.

Male morphology

I 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 (tip of bill to back of head). I also calculated an index of body condition for each male by regressing the first principal

Figure 3-1. Lek tenure of males marked on 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, I considered all days a lek was visited as possible days a male could be sighted. These values represent minimum estimates because males may have been present at the lek prior to capture.

component score with body weight. Residuals from this regression were used as an index of condition, 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, standardised among and combined across years, indicated capture date did not affect the weight of males and therefore body condition estimates (ANOVA, 1, 114 df, $F = 1.05$, $P = 0.31$). All body size and condition calculations used averages when left and right sides 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 chapter 1). This spotting becomes more bold as birds mature from juveniles to adults, with adult females being less boldly spotted than adult males, but more boldly spotted than juveniles. The number of spots and the proportion of the wing that is darkly coloured decrease as juveniles mature. However, it is not known whether wing spotting and coloration continues to change as adults age. To determine the extent and variation of this spotting amongst males, I photographed both the right and left underwing of each male against a plywood board covered with graph paper. This allowed the size of wings to be standardised in subsequent image analyses. Photographs were taken in a shaded location using a 35 mm camera and flash, converted to CD-ROM images, and digitised and measured using an image analysis system (National Institutes of Health's IMAGE vers. 1.56). The number of spots per unit area and proportion of black area to white on both the left and right tenth primary feathers were measured on each male. Analyses were restricted to a rectangular area approximately 100 mm² (4 mm x 25 mm) centred on the inner web 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.

I 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. I used a two-way, mixed-model analysis of variance [sides (fixed) x individuals (random)] with repeated measurements to test for whether the between-sides variation was significantly larger than the measurement error (Palmer and Strobeck 1986, Palmer 1994). This analysis indicated all four variables were suitable for fluctuating asymmetry analysis (i.e., between-sides variation was significantly larger than the measurement error). The mixed-model ANOVA also detected directional asymmetry in wing length and spot density variables (Table 3-1). To control for this, I subtracted the $(\text{mean}[R - L])/2$ 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 Inc. 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 dependence of fluctuating asymmetry within males for wing spottiness ($F = 5.04$, $df = 1, 75$, $P = 0.03$) and wing darkness ($F = 8.29$, $df = 1, 74$, $P = 0.005$). I did not correct for this, however, because scaling these variables 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,

Table 3-1. Size and fluctuating asymmetry scores for four morphological characters measured on male buff-breasted sandpipers "R" and "L" refer to the right and left side of each trait, respectively. N refers to the number of males in the sample.

Trait ¹	[(R + L) / 2]				(R - L)				R - L				Non-directional asymmetry			Directional asymmetry		
	N	$\bar{x}$	SE	Mean	SE	Skew	Kurtosis	$\bar{x}$	SE	F	df	P	F	df	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			

Table 3-1. Continued.

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¹ Wing and tarsus length are measured in mm. Wing darkness is the proportion of black to white in a 100 mm² area located on the tenth primary of each bird, and wing spottiness is the number of spots/mm² in this same 100 mm² area. Wing length and wing spottiness have been corrected to a mean of zero to remove directional asymmetry.

Palmer 1994: 354). My 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, I 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 (Table 3-2). I 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 vs. nonmated; see below). Spearman correlation analysis indicated all three behaviour scores were independent of each other ($P > 0.10$).

To determine if female presence affected male behaviour (see e.g., Wiley 1973, Avery 1984, Ellison and Bradbury 1985), I used a paired Wilcoxon signed rank test to compare male behaviour scores when females were and were not present. Where significant differences existed, I used only that portion of each focal observation when females were present (Table 3-2). 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 ($F = 4.98$, $df = 1,32$, $P = 0.03$). 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

Table 3-2. Behaviour categories of male buff-breasted sandpipers.

Category ²	Behavioural components	Focal Duration ¹	
		1992	1993
Attraction	single and double wing-waves, flutter-jumps	entire	female
Solicitation	wing-raises with tail flash or tail flashes alone while male proceeds to mating post, embraces, female pursuit, attempted and successful copulations	female	female
Aggression	vertical flights, fights, aerial and ground chases, aerial and ground disruptions	entire	entire

¹ Proportion of each focal used to generate scores for each behaviour category.

Observations were limited to time periods when females were present for those cases where female presence was shown to significantly influence male behaviour scores.

² Correlation analysis indicated each category was an independent measure of male display ($P > 0.05$ for all pair-wise comparisons within years).

insignificant or weak seasonal effects, I did not restrict the dates of focal observations used in subsequent analyses.

For each male, I also determined the percentage of female groups visiting each male that were disrupted by other males, and the rate 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, I simply recorded males as having either exhibited these behaviours or not.

Vocalisations

In contrast to most lekking birds (e.g., sage grouse, *Centrocercus urophasianus*, Gibson 1989), buff-breasted sandpiper leks are very quiet. Male precopulatory displays are typically accompanied by a series of soft "tick" notes that are barely audible from 10-20 m (chapter 1). Although these tick notes are associated with courtship, they probably play a minor role in female choice because the vocalisation varies little between males (R. Lanctot, personal observation) and similar vocalisations are made by males at territorial boundaries and during spring migration when females are absent (Oring 1964, chapter 1). Consequently I did not measure this variable.

Territory location

The position of each male's territory on a lek was determined by measuring the distance from the centre of a male's territory to the centre of the lek on a daily basis.

These measures were then standardised 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, an average score was determined for each male by averaging standardised values over all days a male was present at a lek. I used the centre of male territories, as opposed to territory boundaries, because the size of territories fluctuated daily, and sometimes hourly, as males initiated and deserted territories at the lek (Pruett-Jones 1988, R. Lanctot, unpublished data). In contrast, territory centres were relatively stable (see Pruett-Jones 1988) and easy to locate because they corresponded with copulation posts located at the centre of male territories (Myers 1979). The centre of each lek was determined by enclosing individual male territory centres located within 200 m of each other (see chapter 2) with a circle or rectangle. I then used the centre of each circle or rectangle (determined by drawing diagonals through the corners) as the lek centre.

Male Mating Success

Male mating success was determined in two ways. First, I categorised males as having mated if they copulated with at least one female during behavioural observations or if paternity analyses (chapter 4) indicated they had successfully sired offspring. Second, I calculated male mating success based on the number of female visits to a male's territory. I assumed all visits by unmarked females were by different individuals because females marked prior to nesting were never seen twice at the same lek. To generate a male's visitation score, I determined a female visit rate for each focal observation and averaged these values across all observation periods. I 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: $r_s = 0.45$, $P = 0.1087$, $N = 14$; 1993: $r_s = 0.78$, $P = 0.0001$, $N = 18$; data combined across years: $r_s = 0.60$, $P = 0.0003$, $N = 32$). 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 and Pruett-Jones 1990). The relative measure of mating success (i.e., female visits) was limited to 1992 and 1993 when intensive behavioural observations of males were collected.

Data Analysis

The combined time individual males were observed (mean = 93 min, SD = 103.3, range = 11 - 417, $N = 32$) varied with their tenure on the study area. To determine how observation time affected male mating success and behaviour scores, I related each male's observation time with whether he mated or not using logistical regression, and his female visitation rate and behaviour scores using Spearman correlation analysis. No significant relationship for any pair-wise comparison was detected when 1992 and 1993 data were analysed separately ($P > 0.05$). When data from 1992 and 1993 were combined, however, the probability of being classified as having mated and a male's solicitation score increased significantly with observation time (male mating status: maximum likelihood estimate = 0.009, Wald $\chi^2 = 4.94$, $P = 0.026$; solicitation: $r_s = 0.38$, $P = 0.044$, $N = 28$). These analyses indicated it was acceptable to use observational data for each male (regardless of sampling time) as long as information from both years was not pooled.

For some analyses, I 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. I analysed data from different years separately because female choice and values of fluctuating asymmetry may differ between years within populations (Zhakarov 1981, Zuk et al. 1990, Møller 1993).

RESULTS

Male Traits

Information on male morphology and/or behaviour was collected on 23, 36, and 57 males in 1992-1994, respectively. Focal behavioural observations were collected on 14 and 16 of these males in 1992 and 1993, respectively, for an average of 3.5 days in each year ($SD = 4.3$ and 3.0 , respectively). Across years, male morphological and behavioural scores were very similar (Table 3-3). Traits with the highest variation included behavioural measures and lek tenure. Aside from maintenance behaviours, males spent most of their time soliciting females, followed by attracting females and interacting with other males. A relatively high percentage of female groups that visited focal males were disrupted by other males, but the rate at which individual males performed disruptions was rather low. Lek tenure was extremely variable among males, with scores ranging from four to 100%.

Table 3-3. Summary of the morphological and behavioural scores of male buff-breasted sandpipers in 1992-1994.

Trait ¹	N ²	$\bar{x}$	SD	CV ³	Min	Max
body size ⁴						
1992	23	0.42	1.38	--	-2.72	3.32
1993	35	-0.49	1.51	--	-3.97	2.44
1994	57	0.06	1.57	--	-4.27	3.73
weight						
1992	23	70.1	3.1	4.4	64.5	77.5
1993	36	68.3	4.1	5.9	57.5	76.5
1994	57	68.1	3.3	4.9	60.0	82.5
body condition						
1992	23	1.37	3.0	--	-4.28	9.16
1993	35	0.12	3.7	--	-8.59	7.80
1994	57	-0.35	3.3	--	-8.63	14.72
aggression						
1992	14	0.04	0.08	211.18	0	0.28
1993	16	0.04	0.06	153.12	0	0.22
attraction						
1992	14	0.07	0.06	88.61	0	0.22
1993	15	0.11	0.14	129.60	0	0.47
solicitation						
1992	10	0.15	0.11	73.40	0	0.30
1993	15	0.26	0.19	73.73	0	0.71
% female groups disrupted						
1992	11	0.14	0.20	140.57	0	0.5
1993	13	0.41	0.40	97.90	0	1.0

Table 3-3. Continued.

Trait ¹	<u>N</u> ²	$\bar{x}$	SD	CV ³	Min	Max
rate of disruptions toward other males						
1992	14	0.01	0.02	184.06	0	0.06
1993	16	0.02	0.03	168.65	0	0.09
distance from lek centre						
1992	18	3.74	1.04	27.83	2.04	5.60
1993	25	3.91	1.39	35.64	1.61	5.87
1994	19	3.47	1.60	46.13	0.0	5.80
lek tenure						
1992	18	0.21	0.29	141.04	0.05	1.00
1993	25	0.28	0.24	85.79	0.04	0.77
1994	19	0.26	0.24	90.78	0.08	0.88

¹ See text for definition of each trait.

² N = sample size. This value varied depending upon whether the trait was morphological or behavioural (i.e., only a portion of the males had behavioural data) and whether females visited males (e.g., a measure of disruption rate could not be determined unless females were present).

³ CV = coefficient of variation = (SD/mean) x 100. The CV for body size is not meaningful because principal component analyses corrected scores to a mean of zero (i.e., SD divided by a value close to zero yields extremely large CV values). Similarly, the CV for body condition is not meaningful because these were the residual scores from the linear regression of body weight on body size.

⁴ Males from all years were combined in a principal component analysis to generate these scores.

Male Mating Tactics

Patterns within and among years

Individual males varied in the number and type of mating tactics used within a year (Figure 3-2). 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 chapter 2). A few males were observed strictly at solitary sites, although many of these males may have displayed at lek sites prior to being banded. The greater number of mating tactics used by individual males in 1994 relative to 1993 coincided with a longer breeding season in that year (23 days in 1994 relative to 13 days in 1993, see chapter 2). The number of males that displayed at a second, third, or fourth lek decreased substantially in both years (Figure 3-2). Occasionally, males abandoned a lek, displayed at a solitary site, and then displayed at one or more leks again (1 of 39 males in 1993 and 5 of 59 males in 1994). Roughly 25% of marked males were seen near nests each year (9 of 39 in 1993, and 22 of 59 in 1994).

The number of days males spent at their first, second, or third lek did not change significantly (Wilcoxon paired-sample test, $T_+ = 30$, $T_- = 61$, $P > 0.20$; analysis involved 18 males seen at more than one lek). Male tenure at solitary sites was much shorter than at leks, and generally lasted only 1 day before males moved to new locations to display 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 3-4). Similarly, the number of males that displayed on leks for one day always exceeded the number of males that returned on subsequent days.

Figure 3-2. Inter-display 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 a male displayed at while displaying at 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. These values were based on study-wide ground surveys conducted every 3-5 days and daily visits to 2-3 leks per year. As such, they represent only rough estimates of lek attendance. "Gone" refers to males that were not subsequently seen during that field season.

1993

1994

Table 3-4. Number of male buff-breasted sandpipers observed in different mating tactics.

Category ¹	Year		
	1992	1993	1994
Lek tenure			
short-term	15	14	14
long-term	3	11	4
Site fidelity to lek			
failed to return	12	13	10
returned	6	12	9

¹ 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 two different days were classified as having "returned", whereas males observed on only one day were classified as having "failed to return". Information is only presented for males captured on my intensively studied lek sites.

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 two and three years, respectively, and a third male was a short-term lek resident in two years (1992 and 1994). The remaining two males were long-term lek residents in one or two 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 $P > 0.10$). Males observed near nests differed significantly in body size from males never seen near nests in both 1993 (Wilcoxon 2-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 (Figure 3-3). In both years, males that displayed near nests were much more variable in size than males not observed near nests. No other morphological or behavioural trait distinguished males that displayed near nests from those that did not.

Short-term lek males had a significantly higher percentage of female groups visiting their territories disrupted than long-term lek males. This was true in 1993 ($Z = 2.61$, $P = 0.005$) but not in 1992 ($Z = 0.31$, $P = 0.76$ [behavioural data were not collected on males in 1994]). In 1993, I also found that males that visited leks for only one day had more symmetrical wing coloration ($Z = -2.83$, $P = 0.005$, $N = 6$ for both categories) and were more likely to have female visitors to their territories disrupted ($Z = 2.12$, $P = 0.03$,

Figure 3-3. Body size of males observed near nests relative to males not seen near nests in 1993 and 1994. Males were categorised as being near nests if they were observed displaying within 150 m of an active nest site at least once during the breeding season. I did not consider males to be near nests if those nests were initiated by females after the male had begun displaying in the area. 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

returnees $N = 10$, fail to return $N = 2$) than males seen on two or more days. Low sample sizes, however, made these relationships difficult to interpret.

Male abandonment of leks

To determine what characterises males that abandon leks, I compared the morphology and behaviour of males that returned on successive days with those that failed to return. I predicted males that remained on leks should be bigger, be in better condition, have lower fluctuating asymmetry scores, and be located in the central portion of the lek (based on mating success correlations in previous studies, Höglund and Alatalo 1995). Appropriate data were collected for 23 days over three years of the study (i.e., when leks were visited on consecutive days and a portion of the marked males left and returned on subsequent days). Contrary to predictions, there were no differences in body size, condition, fluctuating asymmetry scores, or territory location of males that returned to leks and those that failed to return (Wilcoxon-paired sample one-tailed tests, all $P > 0.10$). Nor did I find a significant difference in wing spotting or darkness, although no *a priori* predictions were made for these variables. There were only seven occasions where I had focal behavioural data to compare males that left and returned to a lek. These data indicated that returning males had similar aggression, attraction, solicitation, and disruption scores as non-returning males.

Males that move to new leks may be expected to move to leks where they are more competitive (e.g., larger) or can attract females more easily (Alatalo et al. 1992). To test this prediction, I compared the morphology of other resident males located at a

"moving" males first lek to the morphology of residents located at a lek the moving male subsequently visited. Contrary to my prediction, the average size of males on second and third leks was larger than males located on first leks (9 of 10 comparisons, $P = 0.02$). No other variables differed significantly in this analysis. I 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, $T_1 = 93.5$, $T_2 = 77.5$, $P > 0.5$).

Male disruptions and female mimicry

Males also used courtship disruption and female mimicry to enhance their reproductive success. Courtship disruption 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, and then either disrupting visiting female groups prior to copulation, or mimicking female behaviour and attempting to steal copulations by placing themselves between the resident male and approaching females.

Disruptions were very effective at preventing males from mating. Forty-three percent of the 95 female visits to males documented during behavioural observations in 1993 and 1994 were disrupted. Almost half of these involved repeated intrusions by one or more males, and only 12 female visits resulted in copulations (seven of these occurred despite disruptions by other 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

(2.7%). Whether intruders disrupted males by flying in or sneaking did not significantly affect the response of females (likelihood ratio $\chi^2 = 7.09$, $df = 3$, $P = 0.07$), 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 females were present ($N = 52$) and when other intruding males were already 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. The latter observations are more puzzling. Here, the intruding males entered the double-wing precopulatory embrace of the resident male (despite the absence of females) before flying back to their original territories. Very rarely, intruding males mounted the resident male after running behind the resident male. On at least three occasions, four or more different males tried to mount each other simultaneously.

Behavioural observations of marked males on leks in 1993 indicated 58% of males were disrupted by neighbouring males and 42% disrupted neighbours themselves ($N = 19$ males). About 40% 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 $\chi^2 = 1.69$, $df = 2$, $P = 0.43$). Males with the longest lek tenure were disrupted by more males than any other males. Two of the stolen copulations were by long-term males and the third was by a short-term lek male.

Data from 1992 and 1994 are less reliable because only one observer recorded behaviour on each male in 1992 and the focus of observations was on females in 1994.

Male Mating Success and Mating Tactics

I 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 (in four tactic by year comparisons all P values were > 0.08). Short-term lek males, however, had significantly higher female visitation rates than long-term lek males (data available for 1993 only: $Z = 2.80$, $P = 0.005$, long-term $N = 9$, short-term $N = 5$). Short-term lek males were also more likely to be disrupted by other males on the lek (see above).

Paternity analyses and behavioural observations indicated both solitary and lek (both short- and long-term) males successfully mated, although the number of successful males on leks was always higher within each year (Table 3-5). This relationship was only significant in 1994 (behavioural and genetic data combined when possible; 1992: likelihood ratio $X^2 = 0.52$, $df = 1$, $P = 0.47$; 1993: $X^2 = 1.21$, $df = 1$, $P = 0.27$; 1994: $X^2 = 9.49$, $df = 1$, $P = 0.002$). 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 three years were combined, short- and long-term lek males had relatively equal mating success and solitary males were the least successful. Long-term lek males appeared to have sired additional young by mating more frequently with multiple females and siring a higher number of full clutches than short-term lek males (Table 3-6),

Table 3-5. Number of male buff-breasted sandpipers that successfully mated at least once relative to mating tactic. Number of males that mated with multiple females is enclosed in parentheses. Males were either observed copulating with females during focal behavioural watches or were determined to have sired offspring via single locus minisatellite DNA fingerprinting.

Year and Measure ¹	Lek			
	Solitary	Short-term	Long-term	Unknown ²
<u>1992</u>				
Behaviour	3	1	2 (1)	3
<u>1993</u>				
Behaviour	1 (1)	1	3	1 (1)
Genetic	2	1 (1)	3	0
<u>1994</u>				
Behaviour	0	1	1 (1)	1 (1)
Genetic	0	6	2 (2)	0
<u>Subtotal</u>				
Behaviour	4 (1)	3	6 (2)	5 (2)
Genetic	2	7 (1)	5 (2)	0
<u>Total</u>	6 (1)	10 (1)	10 (4) ³	5 (2)

Table 3-5. Continued.

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¹ Paternity analyses were not conducted in 1992.

² These numbers represent matings by unmarked males. I could not be certain of the mating tactic of these males because they could not be reliably identified from day-to-day.

³ The total number of males 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.

Table 3-6. Full and partial paternity of clutches relative to male mating tactic as revealed by single-locus minisatellite DNA fingerprinting.

Paternity ¹	Solitary	Lek	
		Short-term	Long-term
<u>1993</u>			
Full	1	2	2
Partial	1	1	1
<u>1994</u>			
Full	0	0	5
Partial	0	6	2
<u>Total</u>			
Full	1	2	7
Partial	1	7	3

¹ Three males are included more than once because they successfully sired young in more than one nest. This includes one short-term male in 1993 who fertilised two full and one partial clutches, and two long-term males in 1994 who fertilised three full and two partial clutches, and two full clutches, respectively.

although neither of these relationships were significant when compared across mating tactics (multiple mating: $P = 0.51$; clutches: $P = 0.10$). These results must be viewed with caution, however, because the small number of males and associated low power of my statistical tests may have prevented significant relationships from being detected. A comparison of the mating success of males that returned to leks and those that failed to return indicated returning males were significantly more likely to have mated (Sign test, 16 of 20 comparisons, $P < 0.05$). Males who displayed near nests were never observed to copulate with females but DNA fingerprinting indicated they successfully fertilised eggs in two of 47 clutches analysed (chapter 4).

Comparisons of this nature were potentially confounded by uneven sampling of males. For example, the majority of my behavioural data were collected on males at leks. This may have resulted in artificially low number of matings observed at solitary sites. Similarly, my genetic analysis may have unevenly identified long-term lek males as sires because they were more likely to be captured (due to their longer tenure) and subsequently identified as fathers. This is consistent with my inability to identify the sires of 25 and 12 clutches for paternity in 1993 and 1994, respectively (see chapter 4). It seems likely that many of these unidentified fathers were solitary or short-term lek males.

Due to the large number of males that switched tactics within years and my inability to identify a mating tactic that was disproportionately successful, I combined males together within years and investigated the effect of 13 predictor variables on male mating success. These analyses indicated only two variables, male attraction behaviour and lek attendance, that significantly predicted a male's mating status (Table 3-7).

Table 3-7. Morphological and behavioural traits of successful and unsuccessful male buff-breasted sandpipers during 1992 - 1994.

Variable	Year	No matings			Matings			Wilcoxon 2- sample test ¹			Combined probability
		Median	Range	N	Median	Range	N	Z	P		
<u>Male morphology</u>											
body size	1992	0.434	-2.715 - 3.322	20	1.133	0.116 - 1.212	3	0.59	0.55	ns	
	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		
body condition	1992	1.81	-4.28 - 9.16	20	0.48	-0.20 - 1.75	3	-0.68	0.49	ns	
	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	0.27s		
wing spot density	1993	0.201	0.160 - 0.335	15	0.187	0.154 - 0.244	6	-1.25	0.21	P < 0.05	
	1994	0.197	0.125 - 0.294	47	0.178	0.125 - 0.285	8	-1.22	0.22		
wing darkness	1993	0.22	0.12 - 0.37	15	0.25	0.167 - 0.362	6	0.90	0.37	ns	
	1994	0.22	0.11 - 0.35	47	0.21	0.132 - 0.380	8	0.0	1.00		
wing asymmetry	1993	1.16	0.16 - 3.66	28	1.34	0.16 - 3.34	8	0.0	1.00	ns	
	1994	0.66	0.16 - 3.84	48	0.66	0.34 - 2.16	9	0.39	0.70		
tarsus asymmetry	1993	0.30	0 - 1.05	26	0.15	0.10 - 1.25	9	-0.51	0.61	ns	
	1994	0.35	0 - 1.25	48	0.25	0.05 - 0.65	9	-1.28	0.20		

Table 3-7. Continued.

Variable	Year	No matings			Matings			Wilcoxon 2- sample test ¹			Combined probability
		Median	Range	N	Median	Range	N	Z	P		
wing spot asymmetry	1993	0.030	0.008 - 0.128	15	0.028	0.009 - 0.039	6	-0.51	0.61	ns	
	1994	0.029	0 - 0.127	47	0.043	0.010 - 0.068	8	1.47	0.14		
wing darkness asymmetry	1993	0.022	0.003 - 0.087	15	0.035	0.005 - 0.246	6	1.09	0.27	ns	
	1994	0.029	0 - 0.196	47	0.045	0.007 - 0.126	8	0.64	0.52		
<u>Male behaviour</u>											
Attraction	1992	0.048	0 - 0.221	11	0.078	0.047 - 0.090	3	0.62	0.53	P < 0.05	
	1993	0.122	0 - 0.467	10	0.000	0 - 0.185	5	-1.93	0.05		
Solicitation	1992	0.124	0.002 - 0.271	8	0.154	0.084 - 0.297	3	0.68	0.49	ns	
	1993	0.228	0.043 - 0.442	10	0.292	0 - 0.707	5	0.55	0.58		
Aggression	1992	0.007	0 - 0.282	11	0.009	0.002 - 0.014	3	0.0	1.00	ns	
	1993	0.013	0 - 0.221	11	0.020	0 - 0.111	5	0.06	0.95		
Distance from lek centre	1992	3.404	2.04 - 5.60	15	3.838	3.46 - 4.81	3	0.83	0.41	ns	
	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		

Table 3-7. Continued.

Variable	Year	No matings			Matings			Wilcoxon 2-sample test ¹			Combined probability
		Median	Range	N	Median	Range	N	Z	P		
Lek attendance	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	P < 0.05	

¹ Normal approximation with continuity correction of 0.5.

Because data from different years were collected on different males (only five males were resighted among years), I 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 and Rohlf 1981). This process indicated males that attended leks for longer periods of time and had fewer wing spots were significantly more likely to mate (Table 3-7, Figure 3-4). 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). Combining probabilities across years like this, however, has the potential problem of obtaining significant values simply by chance (Rice 1989). To correct for this I applied the sequential Bonferroni technique to the combined probability tests to obtain a new p-value of 0.0017 (0.05/30 tests). With this as the critical value, none of the variables was statistically significant.

Interestingly, my two measures of male mating success (i.e., female visitation rate, and number of matings observed and inferred from paternity analyses) were not correlated 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 actually mated with a male. Thus a male's ability to attract females may not reflect his ability to copulate successfully with females.

DISCUSSION

The social organisation of the buff-breasted sandpiper appears to be more complex

Figure 3-4. Number of wing spots per mm² on male outer primary feathers relative to mating status (mated = yes, unmated = no) in 1993 and 1994. See text for description of how spots were counted. Figure illustrations are the same as those listed in Figure 3

than most other lekking species. Males employed several reproductive tactics that included displaying at one or more leks, displaying solitarily, or displaying both on leks and solitarily. A proportion of males occasionally displayed near nests, and lekking males exhibited a high level of courtship disruption that frequently involved female mimicry. Resightings of marked males indicated males frequently switched between tactics within years and occasionally among years. This contrasts with most lek-breeding species where the majority of males maintain stable display locations, either at leks or solitary sites, that may last for several months or more (Wiley 1991, Höglund and Alatalo 1995). Male switching between mating tactics has also been reported in a northern population of the closely related ruff (Lank and Smith 1987). Here, individual males switched among three conditional tactics that included "following" females off leks, "intercepting" females at resource rich sites, and "true lekking". Lank and Smith also reported a high turnover of males at leks, with many short-term and few long-term residents (p. 142). They suggested that male use of different tactics may be dependent on male phenotype (e.g., stable lek residents appeared older and followers appeared younger), although further study was needed to substantiate their interpretation.

In this study, I found few morphological traits that differentiated between males that displayed at solitary locations, near nests, or on leks. Body size was the only variable that successfully predicted male display near nests, although the pattern was inconsistent across years. The large variation in body size of males seen at nests suggests that displaying near nests may be a tactic available to a larger number of males than displaying at leks. Similarly I was unable to identify any morphological trait that consistently

distinguished short-term lek residents from long-term residents, or males that abandoned leks after one day versus those that returned to leks. The lack of distinguishing characteristics may not be that surprising, however, if some males unknowingly switched among tactics within a given breeding season. Typically, males in other species are restricted in their use of mating tactics because they are limited by some factor, e.g., delayed plumage maturation (Kruijt and Hogan 1967, McDonald 1993) or genetically controlled plumage and behaviour (in regard to resident versus satellite male ruff, Lank et al. 1995).

The use of alternative mating tactics by male buff-breasted sandpipers appears to be partially controlled by local social conditions. For example, short-term males were significantly more likely to be disrupted and had lower mating success than long-term males, despite having higher numbers of female visitors. Male-male interference was proposed as an explanation for 50% of Ochre-bellied flycatcher (Mionectes oleagineus) males failing to establish display territories (Westcott and Smith 1994). Surprisingly, male buff-breasted sandpipers that returned to leks were not larger or in better condition than males that abandoned leks. Indeed, males that abandon leks were more likely to join leks with larger males than the males present on the lek they abandoned. Apparently, larger body size offers few advantages to males. It is also possible that males with small bodies can more easily mimic female behaviour and disrupt the courtship of other males.

Regional variation in breeding opportunities may also influence a male's decision to abandon leks. Uneven snow accumulation and differential melt-off in the high arctic may result in suitable breeding conditions varying by two or more weeks. Males may,

therefore, benefit reproductively by abandoning local areas (irrespective of the males in the local area) when female numbers decrease and moving to new locations where breeding opportunities remain (see chapter 2).

Male Mating Success and Mating Tactics

Where alternative mating tactics have been described previously for male birds, observations of mating frequency suggest that the relative payoffs of different tactics may differ considerably (Lank and Smith 1987, Kruyt and de Vos 1988, Fiske et al 1994, McDonald and Potts 1994) or be very similar (e.g., Pruett-Jones and Pruett-Jones 1990, Westcott and Smith 1994). Here, using behavioural observations and DNA fingerprinting, I was able to show that there was little difference between short- and long-term lek males in terms of reproductive success. Males that displayed at solitary sites also successfully mated but less frequently, and males located near nests only rarely fertilised eggs in the nest near which they displayed. Male assignment of paternity indicated that long-term lek males may do slightly better reproductively than short-term lek males by mating with multiple females and fertilising eggs from entire clutches more frequently. These results must be viewed with caution, however, because sample sizes were low, sampling effort was biased toward long-term lek males and it was impossible to determine the mating success of males once they left the study area.

An analysis that combined males across mating tactics within a year indicated that male lek attendance, wing spottiness, and attraction behaviour significantly influenced male mating success. Numerous studies have found that male mating success correlates

significantly with male lek attendance (e.g., Höglund and Robertson 1990, Hill 1991, Gibson and Bradbury 1985, Fiske et al. 1994, Höglund and Alatalo 1995). This relationship may result from females visiting leks repeatedly and using a male's attendance to ascertain his quality (Hill 1991). This seems unlikely in buff-breasted sandpipers given that females have never been observed visiting the same lek multiple times. Alternatively, the higher mating success of long tenured males may reflect their ability to maintain territories on leks for long periods. Territory maintenance may be especially difficult in arctic lek-breeding species because of the potentially high energetic costs of maintaining territories throughout the day and arctic sunlit nights (matings may occur at any time of day, R. Lanctot, personal observation). Lek attendance has also been shown to be energetically expensive in the subarctic breeding great snipe (Höglund et al. 1992). There was little support for this hypothesis, however, as body condition did not significantly predict male mating tactic, although a more detailed study involving more sophisticated techniques (e.g., double-labeled water) is warranted. Perhaps, a more likely explanation is that long-term lek males received higher mating success scores because they were observed for longer periods of time (i.e., females selected males randomly and thus males that remained longer were more likely to be considered successful). Unfortunately, this hypothesis is impossible to evaluate until the complete mating history of males, particularly those that leave the study area, are available.

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. Differences in the number of spots

between juveniles and adults, and between adult females and males (chapter 1) suggests that successful males (i.e., males with few spots) may be older males. More data are needed to document how wing spotting changes with age to test this hypothesis adequately (only three males were recaptured in this study). 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. Spotting on the tail feathers of great snipe and peafowl have also been shown to significantly influence male mating success (Höglund et al. 1990, Petrie and Halliday 1994). In both of these species, increased mating success by males was thought to be mediated through female choice as opposed to male-male competition. Female buff-breasted sandpipers have ample opportunity to evaluate a male's wing spotting during pre-copulation display (Myers 1979, Pruett-Jones 1988). On many occasions females 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 limited number of males observed during the study and the limited amount of observation time collected on some males. Further research is needed to investigate how male behaviour influences mating success.

Male Disruptions, Female Mimicry, and Sexual Monomorphism

Male disruption and female mimicry appears to be an additional tactic used by most if not all males in the population. Every lek male observed during this study either disrupted others, was disrupted themselves, or did both. This included both short- and long-term lek males, as well as males that visited leks for only one day. Such behaviour is possible because male and female buff-breasted sandpipers resemble each other, although males are slightly larger (chapter 1). Differences between the sexes in wing spotting is only apparent when males open their wings. Males appear to use disruption and female mimicry to increase their own mating opportunities. Over one-tenth of the disruptions documented resulted in the visiting female abandoning the territory of the resident male and joining the disrupter. Intruding males were also successful at sneaking copulations three times. This represented one-fourth of the total copulations observed at my intensively studied leks.

Trail (1990) presented three hypotheses to explain plumage monomorphism in lek-breeding birds, including phylogenetic constraints, behavioural transference, and social selection hypotheses. The first hypothesis, which suggests that sexual dimorphic characters are lacking because the species only recently evolved lek behaviour, seems unlikely given that the closely-related lek-breeding ruff (Sibley and Ahlquist 1990) shows extreme size and plumage dimorphism. The behavioural transference hypothesis, which suggests that other characteristics besides plumage have developed as a result of sexual selection, may be more plausible given the elaborate courtship displays of males (but see discussion above on wing spotting). A modification of the social selection hypothesis,

which suggests that males and females share similar plumages as a result of balanced selective forces acting on each sex, seems the most likely explanation for plumage monomorphism in buff-breasted sandpipers. Males appear to be under balanced selection pressures to retain their female like plumage. On the one hand, intense male-male competition, which occurs during territory establishment and disruptions, may favour the evolution of larger bodies, while on the other hand, benefits associated with female mimicry may favour the maintenance of female-like plumages. In contrast to Trail's (1990) social selection hypothesis, females appear to be under little direct selection. Additional information on body-size effects on disruption and female mimicry is needed to substantiate this hypothesis. The evolution of wing spotting is consistent with this hypothesis as it can be easily hidden by males when attempting to mimic female behaviour.

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. In only one instance, however, was a male observed to take over another male's territory after mounting the resident (the resident male left with a female that was visiting him at the time). This hypothesis is weakened further by the fact that resident males appeared to be unable to identify the sex of visiting birds. Males frequently courted males from adjacent territories despite having participated in fights and territorial flights with these same males numerous times. Male intrusions or homosexual mounting has also been documented in ochre-bellied flycatchers (Westcott and Smith 1994) and Guianan cock-of-the-rock (*Rupicola rupicola*, Trail and Koutnik

1986). Intruding males in both species were primarily inexperienced males that appeared to be either observing (or practising) courtship or evaluating the vigour of the territorial male. Buff-breasted sandpiper homosexual behaviour, in contrast, occurs between mature adults and occasionally includes several males at a time. The evolution of such behaviour, while at first puzzling, may be related to the potentially high reproductive rewards associated with stealing copulations (especially by low ranking males who rarely copulate on leks) and the negligible costs associated with homosexual mounting.

In contrast to 'classic' lekking species, buff-breasted sandpiper males used a variety of tactics besides lekking to acquire mates. My analyses suggests that male use of these tactics is unlikely to be dependent on the phenotype of a male. Indeed, males using different tactics could not be separated based on a series of morphological and behavioural traits. Although other variables not measured in this study may have been important, it seems unlikely given the extensive tactic switching that occurred within and among years. Changes in the number of males using different tactics across years indicates local ecological conditions may have a stronger influence on the mating tactics used. Such ecological conditions may include unpredictable snow conditions which may require males to be flexible in their breeding behaviour. The fact that males continue to display on leks, despite observations and genetic analyses that indicate solitary males are also reproductively successful, suggests female preference to mate on leks may also be an important factor.

CHAPTER 4.
LEKKING WITHOUT A PARADOX
IN THE BUFF-BREASTED SANDPIPER

This chapter formed the basis of a paper of the same title published in *The American Naturalist* and co-authored with Kim T. Scribner, Bart Kempenaers, and P J Weatherhead.

ABSTRACT

Females in lek-breeding species appear to copulate with a small subset of the available males. Such strong directional selection is predicted to decrease additive genetic variance in the preferred male traits, yet females continue to mate selectively, thus generating the "lek paradox". In a study of buff-breasted sandpipers, I combine detailed behavioural observations with paternity analyses using single locus minisatellite DNA probes to provide the first evidence from a lek-breeding species that the variance in male reproductive success is much lower than expected. In 17 and 30 broods sampled in two consecutive years, a minimum of 20 and 39 males, respectively, sired offspring. This low variance in male reproductive success resulted from an effective use of alternative reproductive tactics by males, females mating with solitary males off leks, and multiple mating by females. Thus, the results of this study suggests that sexual selection through female choice is weak in buff-breasted sandpipers. The behaviour of other lek-breeding birds is sufficiently similar to that of buff-breasted sandpipers, that the need is suggested

for paternity studies of those species to determine whether leks generally are less paradoxical than they appear.

INTRODUCTION

Lekking species have traditionally been favoured in studies designed to identify the adaptive significance of female mate choice because males in these species provide no parental care or territorial resources to females, and females appear to be able to choose their mates freely (Bradbury 1981). The female receives only sperm from the male (but see Reynolds and Gross 1990). Despite the male's minimal contribution to the reproductive effort, only a small subset of males within a lek usually obtain most of the matings (Wiley 1991, Höglund and Alatalo 1995). Such strong directional selection is predicted to decrease additive genetic variance in the preferred male traits. Understanding why females continue to select mates despite the predicted absence of genetic variation in male traits is commonly called the "lek paradox" (Borgia 1979, Taylor and Williams 1982, Reynolds and Gross 1990, Kirkpatrick and Ryan 1991). Lekking behaviour would be substantially less paradoxical if true male mating success was less skewed than suggested based on direct observations alone. Discrepancies between apparent and true reproductive success have been reported in monogamous (Kempnaers et al. 1992, Pinxten et al. 1993), polygynous (Gibbs et al. 1990, Hartley et al. 1993), polyandrous (Oring et al. 1992) and cooperative breeding species (Haig et al. 1994, Quinn et al. 1994). To date only one study has been published in which paternity was determined for a lek-breeding bird (Höglund and Alatalo 1995). Although strong concordance between apparent and

true male mating success was found in that study, the generality of that relation in lek-breeding birds is unknown

Here, I combine detailed behavioural observations with paternity analyses using single locus minisatellite DNA probes to investigate whether differences exist between apparent and true mating success in the buff-breasted sandpiper, a lek-breeding shorebird. I identify several behavioural mechanisms, common to many lek-breeding species, that may lead to lower than expected variance in male reproductive success. Finally I examine the implications of these results on sexual selection theory and in particular the lek paradox.

METHODS

This chapter focuses on data collected in 1993 and 1994; two years when I had both behavioural and genetic data. I surveyed birds using variable circular plot and strip transect surveys and classified males as being on leks as described in the general methods. About one-half of all leks encountered were active over several survey periods ("stable" leks), whereas the remainder had males present for only one survey period ("unstable" leks, see chapter 2).

Behavioural Observations

Males ($N = 97$ over both years) and females ($N = 89$ over both years) were captured and colour-banded at most leks and in solitary locations throughout the study area. Twenty-four females were equipped with radio transmitters to monitor female

sampling of males at leks and to locate nests. Observers recorded mating activity daily on 2-3 leks each year as described in the general methods. All female visits, solicitations, and copulations were recorded. I assumed all visits by unmarked females were by different individuals because females marked prior to nesting were never seen twice at the same lek. Multiple copulations by a male with the same female during a single visit to a lek were counted as one mating.

DNA Fingerprinting and Determination of Paternity

I sampled blood from captured adults and newly hatched chicks, and collected eggs to obtain embryonic tissue. Genotypic data over four variable minisatellite loci were used to assign genetic paternity. DNA (5 µg) from each individual was run on 1.0% agarose gels and transferred to nylon membranes (Hybond-Nfp, Amersham) using standard techniques (Sambrook et al. 1991; Bruford et al. 1992). Filters were sequentially hybridised with four single-locus probes (cPpuMS3, cPpuMS4, cPpuMS8, and cPpuMS11 developed for ruffs, *Philomachus pugnax*; Lank et al. 1995), labelled with [α - ^{32} P]-dCTP, and then probed with ^{32} P-labelled internal marker DNA (1 Kb standard; BRL) to facilitate fragment size determination within and across gels. More details on the fingerprinting techniques used in this study are described in Sambrook et al. (1991), Bruford et al. (1992), and Verheyen et al. (1994).

Allele sizes for each locus were determined empirically following alignment of the 1.6 kb marker bands on the test and marker autoradiographs. Paternity analysis was restricted to adults and chicks where allele sizes were identified on at least three loci. In

all cases DNA from the putative female (i.e., the female incubating a nest or tending recently hatched young) was available. Females were run adjacent to their offspring in all cases, allowing maternal and paternal alleles to be identified. A sizing error for each probe was used to 'bin' alleles together for all adult males and to calculate probabilities of identity and false inclusion (Galbraith et al. 1991, Table 4-1). For each chick, I identified potential fathers by searching for paternally-derived alleles among the genotypes of males captured on the study area. I excluded males as potential sires if the size of their alleles did not match (within a sizing error) the size of a chick's paternally-derived alleles for any loci. I assumed sires were correctly identified if a male and chick's alleles matched on at least three loci. Using this approach, I was able to identify a single father for 62 of 65 chicks (the three exceptions had 2 to 4 potential fathers). For families where fathers were not identified for all or a portion of the brood, I parsimoniously combined paternally-derived alleles from the remaining offspring to determine the minimum number and genotype(s) of males that fathered offspring within each brood. I then compared paternal genotypes among all families to estimate the minimum number of males that fathered offspring within each year.

RESULTS

Behavioural Observations

Systematic surveys throughout the study area located 15 and 11 different stable (i.e., present for more than one survey) leks in 1993-1994 (Figure 4-1). Daily observations at several stable leks in each year indicated the distribution of female visits,

Table 4-1 Characteristics of four minisatellite single-loci in the buff-breasted sandpiper

locus	allele size		N*	alleles ^b	sizing error ^c	H _{obs}	H _{exp} ^d	P _d ^e	P _s ^f
	range (kb)								
cPpuMS3	2.8-4.4		91	21	49 (138)	0.8681	0.9308	0.0092	0.1334
cPpuMS4	1.8-7.5		79	38	54 (61)	0.9710	0.9507	0.0047	0.0961
cPpuMS8	4.7-7.0		75	15	107 (53)	0.9178	0.9133	0.0143	0.1658
cPpuMS11	1.8-4.3		92	25	53 (125)	0.8587	0.9115	0.0150	0.1691
combined									
probabilities ^g									
2 probes								$\leq 2.1 \times 10^{-4}$	$\leq 2.8 \times 10^{-2}$
3 probes								$\leq 2.0 \times 10^{-6}$	$\leq 3.7 \times 10^{-3}$
4 probes								$\leq 9.3 \times 10^{-9}$	$\leq 3.6 \times 10^{-4}$

* Number of breeding males from study area used to assess allelic variation and heterozygosity.

Table 4-1. Continued.

- ^b Number of distinguishable alleles observed based on binning criteria defined in the text.
- ^c 3 SD of the differences in allele size (base pairs) determined for all individuals (sample size in parentheses) run on at least two gels (Galbraith et. al. 1991).
- ^d H_{exp} = expected heterozygosity calculated with the formula $1 - (\sum_{i=1}^N p_i^2)$ assuming Hardy-Weinberg equilibrium where p_i represents the frequency of the i th allele and N = the total number of alleles (Verheyen et. al. 1994).
- ^e P_{id} = probability of identity: probability that two unrelated individuals share the same genotype, calculated using the mean allele frequency $q = 1 - H_{exp}$ in the formula $P_{id} = q^2(2-q)$ (Wong et. al. 1987)
- ^f P_{fi} = probability of false inclusion probability that an offspring's paternal allele is also present in an unrelated individual, calculated by $P_{fi} = 2q - q^2$ (Wong et al. 1987). I assumed correct maternity in all broods except one where a maternal mismatch occurred, presumably due to egg dumping
- ^g Combined probabilities were calculated by multiplying the lowest probability values together first Paternities were ascertained with three or four probes for all chicks

Figure 4-1 Location of stable leks (i.e. present for more than one survey) and nests in the study area in 1993-94. An additional 10 and 14 unstable leks (i.e. present during one survey) were found in 1993 and 1994, respectively. Filled circles represent lek sites, filled squares represent nests or sites where chicks were sampled for blood or eggs were collected, and the open squares represent depredated nests. One sampled nest located south of the study area is not shown.

OF / DE

3

PRECISION^{SM} RESOLUTION TARGETS

Figure 4-2. Female visits, solicitations and matings at one lek observed daily in both 1993 and 1994. Similar distributions of male mating success were seen on other intensively studied leks in each year. Unbanded males are not included in the figure because their individual mating success could not be determined due to difficulties in reliably identifying individuals across days. Nevertheless, only one unbanded male in each year received any matings (two matings on the same day for each male) and on average only 4.5 (SD = 2.3, range = 1 to 10) males were unmarked each day over all days of observation for the lek shown. The number of days males attended leks are listed above the bars in the first panel. Only males present on dates when females visited leks are included (1993: 31 May-13 June; 1994: 6-10 June). A total of 91 and 36.5 observation hours were conducted at this lek in 1993 and 1994, respectively.

1993

1994

solicitations, and matings were skewed toward a few males (Figure 4-2). Although I saw very few copulations at my leks, the large number of female visits and solicitations, which generally correlated with the number of matings, also indicated the presence of a mating skew. In a previous study of this same population, Pruett-Jones (1988) also reported a highly skewed distribution of copulations among lek males, so the mating patterns on leks in buff-breasted sandpipers seem typical of lekking species generally (Wiley 1991, Höglund and Alatalo 1995). Observations at unstable leks indicated males at these leks received few female visitors and rarely, if ever, successfully copulated with females.

Paternity Analyses

To determine whether my observations of mating success predicted true mating success, I analysed paternity in 109 offspring from 30 broods in 1993 and 55 offspring from 17 broods in 1994 (Figure 4-3). These analyses (Table 4-1) revealed a much more even distribution of male mating success than predicted from behavioural observations (Figure 4-3). A minimum of 39 and 20 different males fertilised eggs in the 30 and 17 families analysed in 1993 and 1994, respectively, so among these broods there were actually more fathers than mothers. At least eleven and eight broods (40% overall) in 1993 and 1994, respectively, were multiply sired. Among the males that sired young in the families I sampled, only four individuals overall (6.8%) sired more than four young (i.e., the modal clutch size), with the most successful male siring 10 young. Because most clutches were sired by a single male, and most sires were represented in only one

Figure 4-3 Distribution of paternity in 30 and 17 families of buff-breasted sandpipers sampled in 1993 and 1994, respectively, based on assignment of male genotypes. In six and twelve broods, genetic information was available for only two and three young, respectively (i.e., hence the large number of males that sired only 2 and 3 young).

Number of offspring

family, genetically this mating system would best be described as monogamy, an unexpected outcome for a lek-breeding species

Observed mating success was a poor predictor of true mating success for males for which both behavioural and genetic data were available. For example, two of three males determined genetically to have sired young were never observed copulating on my intensively studied leks. Conversely, only one of the five males observed copulating on my leks was genetically linked to any offspring. That male was observed copulating with four different females but only fertilised a single egg in the families I sampled. Limited behavioural data were available for the 19 remaining males identified as fathers: nine displayed on less studied leks, two were captured late in the season near nests (see below), and eight were captured in 1994 but sired young from broods sampled in 1993 (i.e., I failed to capture these males in 1993 and hence no behavioural information was available). Of the seven males that sired one or more clutches, four displayed on the same leks for a minimum of seven days, one displayed at a lek for a single day, one displayed solitarily, and one had no behavioural data (male was captured in subsequent year).

I could not identify the males that sired many of the broods, including 24 and 12 males who sired partial and single clutches, respectively. It is unlikely that these males had been long-term residents on any lek in my study area because intensive mist-netting would probably have resulted in their capture. Eighty-two ($N = 34$) and 70% ($N = 54$) of the males captured and scored for allele sizes in 1993 and 1994, respectively, were not identified as sires in the nests that I sampled. However, they may have fertilised eggs in the many nests lost to predators that I was unable to sample.

Behavioural and Genetic Discrepancies

The discrepancy between apparent and true measures of mating success may have arisen several ways. First, multiple mating by females at different leks may devalue the mating success of males at any one lek through sperm competition. Of the 19 broods identified to have multiple-sires, five had a minimum of three sires and 14 had a minimum of two sires. No females, however, were ever observed to multiply mate. Using radio telemetry, I determined that a minimum of 7% ($N=15$) of females visited multiple leks. Most of the remaining radio-equipped females travelled sufficient distance to have visited several leks.

Second, females may copulate with males away from leks. Solitary males comprised about 24% of the males detected during surveys (1993: $\bar{x} \pm SD = 22.9 \pm 10.2$, $N = 7$; 1994: 24.4 ± 15.8 , $N = 7$), although most males continued to display on leks throughout the breeding season (chapter 2). Behavioural observations indicated that at least two solitary males copulated with females in this study and genetic analyses indicated two additional solitary males sired offspring in nests near which they displayed. Further, at 62% of 66 nests I observed one or more males displaying within 150 m at least once during egg-laying, including 31 of 98 banded males that I had also observed displaying on leks.

Third, my estimate of a male's mating success based on data from one lek may be inaccurate if unsuccessful males occasionally become successful by changing leks (Alatalo et. al. 1992). Banded males spent an average of only 4.7 days (range = 1-22, $SD = 6.2$, $N = 56$) on a given lek, and 20 males ($N = 98$) were seen at two or more leks. Indeed, one

male displayed 23 km away at a second lek two days after he was captured on a lek in my study area. No males were observed copulating at multiple leks, however

Fourth, males may disrupt matings on leks and sneak copulations (Foster 1983)

This may be especially important in monomorphic species such as buff-breasted sandpipers. Intensive observations of banded territorial males revealed that males routinely sneaked onto adjacent territories, and by mimicking female behaviour, were able to join and then disrupt females visiting neighbouring males. Of the 95 visits by females to lekking males observed in 1993 and 1994, 43% were disrupted by other males. On only three occasions, however, was I able to document an intruder stealing a copulation by placing himself between the territorial male and the visiting female(s).

Another possible explanation for the discrepancy between the patterns of apparent and true male reproductive success is that females nesting in my study area collectively may have copulated with the preferred males on many different leks outside the study area. However, the isolated nature of my study area, both in terms of habitat suitability and location, make this unlikely. Variable circular plot surveys conducted throughout the oil field indicated buff-breasted sandpiper densities on my study area were about 2.8 times higher than elsewhere (R. Lanctot, unpublished results). Also, resightings of banded ($N = 11$) and radio-equipped ($N = 11$) females captured on leks within my study area indicated that at least 23% of them nested within the study area. The high rate of nest predation (>62% in each of the three years) suggests that many of the other marked females may also have nested locally but were not resighted because of early nest failure. Also, of 20 females for which a mate was identified, all nested on average 0.9 km (SD = 1.1, range =

11–48) away from the male's display site. Thus, it is unlikely that the 27 remaining females whose broods I sampled all copulated with different, but preferred males elsewhere.

DISCUSSION

This study suggests that sexual selection through female choice is weak in buff-breasted sandpipers, and as a result, offers a solution to the lek paradox, at least in this species (i.e., females were not as choosy as behavioural observations suggest). Indeed, despite my observations that a limited number of males were involved in mating at any one lek (see also Pruett-Jones 1988) and previous reports indicating that variation in male mating success in buff-breasted sandpipers is similar to that in other lekking species (Mackenzie et al. 1995), my genetic results indicated monogamy was the most common form of mating. Only rarely was a male able to fertilise the eggs of more than one female in my population.

The lack of congruence between patterns of apparent and true male reproductive success may be more pronounced in buff-breasted sandpipers than in other lekking species. The low rate of copulation I observed on leks, and the short tenure of males on leks may contribute substantially to the low skew in male reproductive success. Also, the male tactic of mimicking females on leks is unavailable to males of sexually dimorphic species. However, a review of the literature on other more "classic" lekking species indicates that there are also reasons to expect that the skew in male reproductive success in these species may be less pronounced than it appears. For example, in several species

females have been observed mating with multiple males, visiting multiple leks, and copulating with males at solitary display sites or foraging sites (Table 4-2). Males have also been observed displaying off-leks, displaying at different leks throughout the season, and attempting to steal copulations on leks (Table 4-2). Indeed, most lek-breeding species, where detailed behavioural work has been conducted, have one or more characteristics that may lower the skew in male reproductive success. I suspect that additional supporting data will emerge as biologists studying lek-breeding species focus more on female behaviour and expand their studies beyond the confines of a single lek. More generally, recent paternity analyses for a variety of species with different mating systems have revealed surprising discrepancies between apparent and true reproductive success. These discrepancies presumably arise because observers are unable to document all copulations or because some copulations are more likely to lead to paternity than others (Dunn and Lifjeld 1994). It is reasonable to expect similar problems when studying lek-breeding species.

Few other studies have used genetic techniques to document paternity in lekking species. Kellogg et al (1995) found that lek-breeding cichlid fishes had higher than suspected levels of polyandry (85% of 13 broods) using microsatellite DNA analyses as compared to estimates based on field observations. A similarly high level of polyandry

Table 4-2. Occurrence of copulations, visits, and display patterns of females and males in lek-breeding species. Percent and sample size of females and males involved in each behaviour are listed where possible, otherwise the probability of occurrence is listed in ascending order of frequency from unlikely, to likely, rarely, occasionally, and regularly. Traits of species that may substantially decrease the variance in male mating success are bolded.

species	female			male			references ¹
	multiple-male copulations	multiple lek visits	copulate off leks	display off leks	display at multiple leks	mimic female behaviour	
<i>Alcedo leucogaster</i>	unknown	regularly	occasionally	25% (102)	48% (102)	occasionally	1,2
<i>Phaethornis superciliosus</i>	unknown	9% (44)	likely	unknown	rarely ^a	rarely	3
<i>Phaethornis guy</i>	unknown	unknown	likely	occasionally ^b	likely	rarely	4
<i>Manacus manacus</i>	24% (42)	unlikely	rarely	rarely	unlikely	occasionally	5
<i>Pipra erythrocephala</i>	13% (48)	37% (49)	unlikely	unlikely	unlikely	occasionally	6
<i>Pipra pipra</i>	unknown	regularly	unknown	likely	regularly^a	unlikely ^c	7
<i>Chiroxiphia linearis</i>	unlikely	regularly	unlikely	unlikely	regularly^a	unlikely ^c	8-10
<i>Rupicola rupicola</i>	24% (88)	unknown	unlikely	rarely	unlikely	unlikely ^c	11,12
<i>Perisoreocephalus tricolor</i>	unlikely	unknown	unlikely	unlikely	unlikely	occasionally	13
<i>Parotia lawesii</i>	unlikely	regularly	regularly	31% (172)	rarely ^a	likely ^d	14,15

Table 4-2 Continued

species	female			male		
	multiple-male copulations	multiple lek visits	copulate off leks	display off leks	display at multiple leks	mimic female behaviour references ^a
<i>Pavo cristatus</i>	41% (87)	likely	unlikely	rarely	likely ^a	unlikely 16, 17
<i>Gallinago media</i>	12% (33)	30% (92); 65% (17)	unknown	rarely	likely ^c	rarely 18-23
<i>Phalomachus pugnax</i>	59% (32)¹	regularly	rarely ^a	occasionally ^b	regularly^a	unlikely 24-28
<i>Tryngites subruficollis</i>	40% (47)¹	7% (15)	occasionally ¹	22-23%	20% (98)	regularly This study
<i>Tetrao urogallus</i>	unlikely	6% (55)	unlikely	unlikely	occasionally ^a	rarely 29-32
<i>Tetrao tetrix</i>	14% (36)	regularly	rarely	occasionally	10% (42) adult 58% (31) juv.	unlikely 33-38
<i>Centrocercus urophasianus</i>	unlikely	regularly	10% (154)	occasionally	27% (11) adult 100% (17) juv.	2-3% 39-44
<i>Pedioecetes phasianellus</i>	unlikely	occasionally	rarely	occasionally	3% (110)	unlikely 45-47
<i>Tympanuchus cupido</i>	unlikely	85% (79)	unknown	5% (21) ¹	occasionally ^a	unlikely 48, 49

Table 4-2 Continued.

- ^a Interlek movements restricted primarily to yearling males or floater males.
- ^b Ten visits by males to nest sites; six cases of young males displaying away from leks (Snow 1974)
- ^c Immature males visit territorial male courts and display and disrupt courtship.
- ^d Immature males, which resemble females, travel in female groups to visit males; homosexual mounting by females also observed (Pruett-Jones 1985).
- ^e Five of 27 males switched leks between years, a percentage of males do not establish permanent territories and new males arrive at leks throughout the breeding period, presumably after displaying at other leks (Hoglund and Robertson 1990)
- ^f Occurrence based on genetic analyses
- ^g 0.02 copulations/male/hr occurred off-lek compared to 0.11 and 0.09 for lek sites (Lank and Smith 1987)
- ^h The frequency of off-lek display varies with study site. Lank and Smith (1987) saw only 12% of males attending leks each day and over 90% of social display occurred away from leks, whereas in other studies, male display is restricted more to lek sites
- ⁱ Two of 17 matings occurred off-lek, genetic analyses indicated 2 males sired offspring in nests near which they displayed
- ^j 5% of 286 observations of 21 radio-equipped males occurred away from leks (Schroeder and Braun 1992)
- ^k References 1, Westcott (1992), 2, Westcott and Smith (1994), 3, Stiles and Wolf (1979), 4, Snow (1974), 5, Lill (1974), 6, Lill (1976), 7, Théry (1990), 8-9, McDonald (1989a,b), 10, McDonald and Potts (1994), 11, Trail (1984), 12, Trail and Adams (1989), 13, Trail (1990), 14, Pruett-Jones (1985), 15, Pruett-Jones and Pruett-Jones (1990), 16, Petrie et al (1992), 17, Petrie et al (1991), 18, Lemnell (1978), 19, Hoglund and Lundberg (1987), 20, Hoglund and Robertsen (1990), 21, Fiske and Kálás (1995), 22, J. Hoglund, personal communication, 23, S. A. Sæther, personal communication, 24, Hogan-Warburg (1966), 25-26 Lank and Smith (1987, 1992), 27, Hoglund et al (1993), 28, D. B. Lank, O. Hanotte, T. Burke, C. M. Smith, unpublished results, 29, Larsen et al (1981), 30, Wegge and Rolstad (1986), 31, Wegge and Larsen (1987), 32, Milonoff (1995), 33, Sexton (1979), 34, Koivisto (1965), 35 Kruijt et al (1972), 36, Kruijt and de Vos (1988), 37, Alatalo et al (1992), 38, Hoglund and Alatalo (1995), 39, Scott (1942), 40, Wiley (1973), 41, Wallestad and Schlodweiler (1974), 42, Emmons and Braun (1984), 43-44, Bradbury et al (1989a,b), 45, Sexton (1979), 46, Moyles and Boag (1981), 47, Oring (1982), 48, Schroeder and Braun (1992), 49, Schroeder and Robb (1993)

was found in ruffs; 59% of 32 broods had multiple sires (D.B. Lank, O. Hanotte, T. Burke, and C.M. Smith, unpublished results) and only half of the sampled offspring could be assigned to particular males. The remaining young may have been sired by uncaptured males, males displaying away from leks or by males at leks not studied (D.B. Lank, personal communication). There was nonetheless, a positive correlation between observed matings and the number of young assigned to each male for those young where paternity was known. In contrast, no evidence of multiple paternity was found in eleven broods of black grouse, and males observed to copulate with females were found to have successfully sired young in those broods (Höglund and Alatalo 1995). It seems from these studies that the incidence of multiple paternity within a brood, and the relationship between behavioural observations of matings and true paternity can be quite variable. Clearly, more detailed genetic analyses of paternity in other lek-breeding species are required to determine the extent to which observed copulation patterns predict true male reproductive success.

If distributions of true male success proved to be more egalitarian than previously thought, leks would become less paradoxical and the need for alternative solutions to the paradox (Lande 1981, Hamilton and Zuk 1982, Reynolds and Gross 1990, Kirkpatrick and Ryan 1991, Wiley 1991) would be diminished. Inaccurate male mating success assignments would also throw into question previous studies focusing on female choice and the evolution of male secondary characteristics (e.g., Höglund and Lundberg 1987, McDonald 1989a, Alatalo et al. 1991, Gibson et al. 1991, Hill 1991, Petrie et al. 1991), and may explain the inability of researchers to identify consistent mate choice cues within

and across species (Gibson et al. 1991, Fiske et al. 1994). In addition, evolutionary explanations for lekking (e.g. Widemo and Owens 1995), and for why females choose to mate at particular-sized leks (Alatalo et al. 1992, Höglund et al. 1993, Deutsch 1994), which depend on copulation patterns at leks, may require reconsideration.

GENERAL CONCLUSIONS

Data collected during this study indicated that buff-breasted sandpipers have one of the most complex social organisations of any lek-breeding species. By marking a large number of males and repeatedly surveying a large area over several years, I discovered that most buff-breasted sandpiper leks were present in only one year and about one-tenth were active all three years. Half of the leks were active for only one survey (maximum of 3–4 days) in a given year. Individual males exhibited a variety of mating tactics including displaying at a single lek for most of the breeding season, attending multiple leks over the season, to displaying solitarily or displaying both on leks and solitarily. Some males (30% or less) also displayed near nests in an attempt to copulate with females during egg-laying. In addition, males mimicked female behaviour and either disrupted or stole copulations from territorial males on leks. Males also frequently switched between tactics within and among years.

This variation in male mating behaviour allowed me to test several predictions of lekking theory unavailable to researchers studying more “classic” lekking species. Contrary to predictions, male display on leks did not appear to be related to the local operational sex ratio or to the level of male-male competition on leks. Rather, the proportion of males that displayed on leks remained consistently high (about 75%) throughout the breeding season. However, the absolute number of males (both lekking and solitary) on the study area was positively correlated with the number of fertile females. I suggest that the buff-breasted sandpiper’s ability to move large distances in a short time

combined with the variable arctic conditions may give individual males the option of leaving areas when the number of fertile females becomes depressed and flying to new areas where the breeding opportunities are still available. Males, in effect, may be responding to "regional" changes in the operational sex ratio, and forming leks in areas with an abundance of reproductive females. The formation of leks in this species might be explained, therefore, by a large scale version of the hotspot model of lek evolution.

This regional model may explain the ephemeral nature of lekking in this species, but it does not explain why only a portion of the males display on leks. To determine this, I investigated whether a multitude of morphological and behavioural traits might differentiate males that use alternative mating tactics. Surprisingly, none of the traits studied consistently separated males based on their mating tactic. The lack of distinguishing characteristics may not be that unexpected, however, given the fact that many males switch tactics within years and that there was little difference in reproductive success amongst tactics. Indeed, both solitary and lekking (both short- and long-term) males copulated successfully during this study. When males that used different mating tactics were combined, I found that males with long lek tenure and fewer wing spots were more reproductively successful. Although data on how wing spotting changes with age are lacking, it seems likely that male mating success may be mediated by age, with older males mating more. Further research, possibly through experimental removals of males or modifications of wing colouration, is needed to confirm these findings.

My investigations of male mating success lead to one unexpected but very important finding. That is, the variance in male reproductive success based on DNA

fingerprinting was far lower than expected based on behavioural observations of males mating on leks. Indeed, paternity analyses that used single locus minisatellite DNA probes indicated only four males (6.8%) sired more than four offspring, the modal clutch size of this species. Additionally, 40% of the 47 families analysed were multiply sired. These patterns indicated the mating system of the buff-breasted sandpiper was more similar to monogamy than lekking. Previous studies on lek-breeding species had consistently shown that a small subset of males within a lek obtained most of the matings. In such a system, researchers had predicted that strong directional selection associated with such a skew would decrease the additive genetic variance in the preferred male traits (i.e., males should become genetically similar over time). Why females continued to select mates despite the predicted absence of genetic variation in male traits is commonly called the "lek paradox". The absence of a mating skew in this study provided a simple solution to the paradox, simply that females were less choosy than behavioural observations of males mating on leks would suggest.

Not only was a mating skew absent in this study, but I also found a poor correlation between a male's apparent and true mating success. I suggest that these discrepancies may have arisen by females mating with multiple males, females mating away from leks, and males effectively using alternative mating tactics (i.e., mating at multiple leks, sneaking copulations). These behaviours are also common in many other lek-breeding birds. Such inaccurate male mating success assignments throw into question previous sexual selection studies focusing on female choice and the evolution of male secondary characteristics. In addition, evolutionary explanations for lekking and for why

females choose to mate at particular-sized leks, which depend on copulation patterns at leks, may also require reconsideration.

The results of this thesis indicate further research is needed in two major areas. First, information on mating success which uses modern DNA fingerprinting techniques is needed for "classical" lekking species to confirm whether the mating discrepancies seen in this study are widespread. This task may be most easily accomplished in non-migratory species because females can be captured and equipped with radio transmitters prior to the breeding season, followed to leks to document male mating partners, and then tracked to their nests where their offspring could be sampled. Such a protocol can be used to determine whether a female's mating partners actually sire offspring. Detailed radio tracking will also confirm whether females mate with multiple males on additional leks or away from leks.

Additional research on males that fail to establish territories on leks is also needed. The role these males play in reproduction is unknown for many species at present but may be substantial based on recent studies on monogamous birds that suggest a high rate of paternity by non-territorial "floater" males. This study clearly indicated that males displaying either for a short time at leks or away from leks reproduced successfully. However, the objective of this research may be difficult to achieve given the problems associated with following non-territorial males in the field and identifying true fathers through genetic techniques. The advent of small satellite radio transmitters offers one possibility for tracking these individuals, although capturing them and observing their behaviour in the field will continue to be problematic. Future research on the buff-

breasted sandpiper might particularly benefit from these transmitters because individual males could be tracked across a vast area of the Arctic to determine their mating success over an entire breeding season.

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