

HIGH PATERNITY WITHOUT PATERNITY-ASSURANCE BEHAVIOR IN THE PURPLE SANDPIPER, A SPECIES WITH HIGH PATERNAL INVESTMENT

ELIN P. PIERCE¹ AND JAN T. LIFJELD

Zoological Museum, University of Oslo, Sars gate 1, N-0562 Oslo, Norway

ABSTRACT.—Among birds, males investing highly in paternal care should be under particularly strong selection pressure to prevent extrapair paternity in their broods. Current literature implies that to obtain a high certainty of paternity, males should invest in paternity-assurance behaviors, and this makes them more likely to increase their investment in reproduction. The Purple Sandpiper (*Calidris maritima*) is a relatively long-lived arctic shorebird with a socially monogamous pair bond and strong mate and territory fidelity by both sexes. Paternal investment is high because males alone perform all of the brood care from hatching to fledging. We investigated the mating strategies of male and female Purple Sandpipers through genetic analysis and examined the possibility that this species exhibits paternity-assurance behaviors. We found no evidence that males exhibited behaviors such as frequent copulation or mate guarding during their mate's fertile period. Furthermore, high rates of copulation were not necessary for pairs to achieve complete fertility of the clutch. Multilocus DNA fingerprinting revealed little evidence for extrapair fertilizations: only 1 of 82 offspring was sired by an extrapair male. These results suggest that male and female Purple Sandpipers rarely seek extrapair copulations (EPCs). In contrast to several recent studies with similar findings, we believe that the apparent rarity of EPCs results because females have few genetic or other benefits to gain from seeking them. Thus, paternity-assurance behaviors by male Purple Sandpipers were not necessary for achieving full paternity of the clutch, and such behaviors cannot be said to have led to the observed high level of paternal investment in reproduction. Uniparental brood care, however, is associated with a high certainty of paternity in this species. Received 3 June 1997, accepted 13 November 1997.

STUDIES OF SPECIES that combine paternity data with information on the social and ecological factors that may affect paternity are essential for understanding the adaptive value of parental investment and thus the evolution of mating systems. Knowledge of the extent of extrapair reproductive activities can shape our evaluation of the costs and benefits of parental care (Reyer et al. 1997). Pairs in socially monogamous avian species were previously assumed to mate exclusively with each other, but recent studies have shown that in many species, individuals engage in extrapair reproductive activities (Westneat et al. 1990, Birkhead and Møller 1992). Although the number of such studies is increasing, most of them focus on passerines (Møller and Briskie 1995). One group of nonpasserines, the shorebirds, exhibit the greatest variation among birds in mating systems and in the relative amount of parental investment by the sexes (Oring 1982); the latter is one of the most important factors determin-

ing the intensity of sexual selection (Trivers 1972). For monogamous shorebirds in particular, few studies have presented behavioral data (e.g. Nol 1985, Ens 1991), and fewer still have presented both behavioral and genetic data on aspects of mating strategies (e.g. sperm competition; Heg et al. 1993), although such studies recently have been conducted on some non-monogamous shorebirds (e.g. Oring et al. 1994, Lank et al. 1995, Owens et al. 1995, Lanctot et al. 1997).

Our goals in this study were to: (1) investigate the possibility that Purple Sandpipers (*Calidris maritima*) exhibit paternity-assurance behaviors; and (2) examine parentage, the result of male and female mating strategies, through genetic analysis (minisatellite DNA fingerprinting). The Purple Sandpiper is a relatively long-lived shorebird (commonly >7 years) in which males and females form socially monogamous pair bonds and show strong annual fidelity to nesting territories and mates (Pierce unpubl. data). Males exhibit typical sex roles in that they defend large territories on the

¹ E-mail: elin.pierce@toyen.uio.no

tundra and court females (Pierce 1997). Purple Sandpipers in Svalbard were found to make only one nesting attempt per season, during which the sexes shared incubation equally overall (Pierce 1997). At hatching, however, the sex roles are atypical because females leave the nest, and males assume all brood-care duties alone until the chicks reach independence about 24 to 34 days later (Pierce 1997). Males thus invest highly in parental care. In the Purple Sandpiper, as in other species with extensive paternal care, males potentially have much to lose from extrapair paternity (EPP) within their brood because their investment in parental care presumably is costly, and it may occur at the expense of seeking additional mating opportunities (Emlen and Oring 1977, Clutton-Brock and Parker 1993, Owens et al. 1995). Males of avian species with sex-role reversed parental care should, therefore, be under especially strong selection pressure to prevent their mates from copulating with other males, i.e. males that care for extrapair young should be selected against (Oring 1982, 1986; Oring et al. 1994). In most social systems, females have the opportunity to mate with several males (Oring et al. 1994), and male behaviors that increase the likelihood of paternity, such as mate guarding, should be favored by natural selection (e.g. Trivers 1972, Westneat et al. 1990, Birkhead and Møller 1992).

In general, mate-guarding behaviors commonly are considered to be necessary prerequisites for achieving a high certainty of paternity, which, in turn, is considered to "predispose" males to parental care (Møller 1991, Birkhead and Møller 1992). Mate guarding is even proposed to be a key factor in the evolution of male parental care in birds (van Rhijn 1991, Birkhead and Møller 1992). In a comparative study, Møller (1991) concluded that investment by male birds in mate guarding "seems to lead to increased paternal investment in reproduction." Thus, species with a high level of paternal investment can be expected to exhibit intense mate guarding (cf. Morton 1987, Oring et al. 1994). Furthermore, males of some species may scale their parental effort directly to their likelihood of paternity (Mock and Fujioka 1990). Based on the above theories, the large investment in parental care by male Purple Sandpipers should be correlated with a high certainty of paternity that must

be achieved through some kind of paternity-assurance behavior. However, such predictions also should take into account species-specific ecological factors, which are considered below.

In the Purple Sandpiper, ground and flight chases involving two to four birds are common early in the season (Pierce 1997), which could be interpreted as mate guarding. Because of this and the high level of paternal investment, we expected to find that males exhibit strong mate-guarding behavior that intensified during the female's fertile period. Birkhead and Møller (1992) specifically predicted that mate-guarding behavior serves to prevent or reduce the occurrence of extrapair copulations (EPCs). If male Purple Sandpipers exhibit mate-guarding behavior, we would expect that during the female's fertile period, the male would: (1) spend a large proportion of time in close enough proximity to the female to be able to disrupt any possible EPC attempt; and (2) initiate moves less frequently than the female, and follow her initiated moves more often than vice versa (Birkhead and Møller 1992).

The level of paternity gained by male Purple Sandpipers can be predicted to be either low or high, depending on the factors examined. Opportunities for EPCs are proposed to be greater in species that are migratory and territorial (Westneat et al. 1990), like the Purple Sandpiper (Pierce 1997). Thus, we would predict a low level of paternity in this species. Furthermore, males have been observed to be mostly absent from the nest during the first few days of incubation and thus have the opportunity to seek EPCs while the female incubates (Pierce 1997). However, a high paternity level would be predicted in this and other species in which male parental care and the breeding territory are critical to reproductive success. Recent comparative evidence has indicated a positive correlation between EPP and divorce rates (Cezilly and Nager 1995). The divorce rate of Purple Sandpipers is very low (7.7%), and mate changes usually occur only between seasons when a pair member fails to return (Pierce unpubl. data). In addition, the effectiveness of mate guarding is thought to be enhanced if the species occupies a habitat that is not visually occluded, such as arctic tundra (cf. Sherman and Morton 1988).

METHODS

Study site and species.—Purple Sandpipers breed from the mid-Canadian arctic islands to central and eastern Siberia. We conducted parentage and behavioral studies on one of the most northerly breeding populations of this species, which occurs in the Svalbard archipelago in the Norwegian High Arctic. The study was conducted during the summers of 1994 and 1995 on Spitsbergen Island, Adventdalen Valley, near the mining community of Longyearbyen (78°13'N, 15°35'E). Summers in Svalbard are short, usually eight weeks during June and July, when there is continual daylight. The open, arctic tundra landscape and vegetation in the Adventdalen study area, and some of the species' breeding behaviors have been described elsewhere (Pierce 1993, 1997). Birds were captured while foraging or incubating and were banded with a unique color code if they were unmarked. We searched for nests in pairs by dragging a rope between us systematically throughout 11 chosen sites. A 1:5,000 map was used to plot and estimate the area (in km²) of each searched site, and to plot the location of nests. The clutch completion date of a nest is the day the last egg was laid. For clutches where this was unknown, it was estimated either by backdating from the hatching date, assuming a 21.5-day incubation period (Pierce 1997), or by floating the eggs to estimate their age (Pierce 1997). For broods captured in the field that had hatched from unknown nests, clutch completion dates were obtained by backdating from their estimated ages. Brood ages were estimated twice by comparing the brood's average mass and bill length to growth curves of known-aged chicks (Pierce 1993), and taking the average of the two estimates. The fertile period of female Purple Sandpipers is unknown; the fertile period is defined as beginning three days before the day first egg is laid in some passerines (Björklund and Westman 1983, Carlson et al. 1985, Krokene et al. 1996) and seven days before the first egg in some nonpasserines (Lawless et al. 1997). With an average egg-laying interval of 32 h, Purple Sandpipers require about five days to complete their four-egg clutch (Pierce 1993). One pair, whose clutch was found and clutch completion date estimated, was also seen copulating about four days before the first egg was laid. The fertile period was thus defined as a 9-day period starting five days before the egg-laying period and ending the day the penultimate egg was laid. The calculation of a breeding-synchrony index (Kempnaers 1993) was based on this fertile period length and the completion dates of all clutches located.

Behavioral study methods.—To determine the extent of paternity-assurance behaviors prior to the onset of full incubation, time budgets were taken of banded pairs when they were located on the tundra during June of each year. For each 2-min interval, we noted

distance between mates (<1, 1 to 5, 6 to 10, 11 to 20, or >20 m), and if any site change occurred, which sex initiated it and whether the mate followed. A site change was defined as any definitive movement (walk, run, or fly) away from the mate or mate's direction of movement. The open tundra allowed unobstructed vision for possible mate guarding, and thus the recorded times that pairs spent <1 m apart and 1 to 5 m apart were combined. Because time-budget data were related to clutch completion date, data on pairs whose nests were not located were discarded. Data from several time budgets of a pair recorded on the same day were combined into one time budget. Thus, a total of 16 and 11 time budgets (762 min total) was taken of five and six pairs in 1994 and 1995, respectively. All time budgets ($n = 27$) lasted 22 to 60 min, except for two (6 and 16 min) of two pairs that also were observed during other time budgets. Data recorded during the female's prefertile and fertile periods were compared using two-group tests, because we sampled too small a number of pairs during both periods to allow paired-sample tests. For each of the two periods, data from several time budgets of individual pairs (one to three per pair, each lasting 22 to 168 min, $\bar{x} = 54$ min) were combined such that each pair was represented only once. All tests were two-tailed.

DNA fingerprinting methods.—Blood samples were collected from 12 nuclear Purple Sandpiper families (i.e. comprising male, female, and chicks) in 1994 and from 15 nuclear families in 1995. About 50 μ L of blood were collected from the brachial vein of adults, all of which were captured on the nest during incubation. Pair members were seldom caught on the same day. Because females are larger than males, sex was determined from biometrical measurements and confirmed with behavioral observations (cf. Pierce 1997). From chicks, 15 to 25 μ L of blood were collected from the brachial vein or, if taken on the hatching day, from a femoral vein. Chicks were allowed to rest for at least 10 min in a warm environment before being released in the field with the attending parent. All blood samples were immediately dispensed into a lysis buffer. No bird deserted a nest, nor did any individual suffer mortality or apparent injury as a result of capture or blood sampling (see Colwell et al. 1988). In an attempt to avoid nest predation in 1994, most clutches were replaced upon discovery with dummy eggs, and the original eggs were stored in an incubator until hatching. Because the dummy eggs were inadequate replacements, some birds in 1994 deserted their nests three to seven days after clutch replacement. Subsequently, some eggs ($n = 5$, in three clutches) were transferred to a freezer two to seven days before hatching. From each frozen egg (offspring), tissue samples were extracted and pulverized in liquid nitrogen, after which they were treated according to the protocol for blood samples (see below).

In conducting DNA fingerprinting analyses, we followed standardized lab procedures described in previous papers from our lab (e.g. Krokene et al. 1996, Bjørnstad and Liffield 1997). In brief, DNA was cut by the *Hinf*I enzyme and electrophoresed on 40-cm long gels of 0.8% agarose with TBE buffer. DNA of the young was loaded in the center lanes and those of the putative parents on either sides. DNA was transferred by Southern blotting onto Hybond Nfp nylon membranes (Amersham), which were hybridized with the multilocus minisatellite probe *per* (Shin et al. 1985) according to the manufacturer's protocol. The probe was radioactively labeled with P^{32} dCTP (Amersham) by random priming using the Prime-a-Gene labeling system (Promega). Autoradiographs were made by exposing the membranes to Kodak BioMax MS-1 film with one intensifying screen at -80°C for one to three days.

To determine parentage, we scored autoradiographs independently using procedures outlined by Krokene et al. (1996). Both scorers obtained identical conclusions with regard to parentage assignment and exclusion, and thus only the scoring results of JTL are presented here. The proportion of bands shared between any two individuals was determined using the coefficient *D*, defined by Wetton et al. (1987). The proportion of bands shared by unrelated individuals, the background band-sharing in the population, was determined using the profiles of mated adult pairs run on the same gel. Bands found in the profile of an offspring, but not in those of either putative parent, were considered to be novel fragments.

RESULTS

Courtship phase.—In theory (Birkhead and Møller 1992), a male exhibiting mate-guarding behavior should stay closer to his mate, and follow her (i.e. her site changes) more often, during her fertile period than otherwise. Male and female Purple Sandpipers associated from at least 16 days before their first egg was laid. The proportion of time pairs stayed within 5 m of each other was highly variable but did not change significantly from the pair female's pre-fertile period (>5 days before egg laying; $\bar{x} = 48.6 \pm \text{SD of } 33.9\%$, $n = 7$) to her fertile period (0 to 5 days before egg laying; $\bar{x} = 35.2 \pm 33.1\%$, $n = 8$; Mann-Whitney $U = 22.0$, $P = 0.49$; Fig. 1). Furthermore, some paired individuals (banded, $n = 3$) were observed during the female's fertile period to spend time foraging in the vicinity of other individuals of the opposite sex when their mates were nowhere nearby. These comprised separate incidences: two

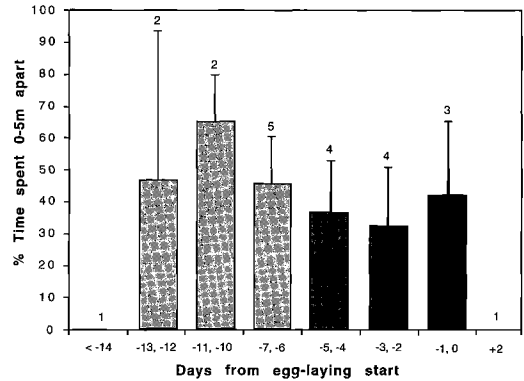


FIG. 1. Mean percentage (\pm SE) of time Purple Sandpiper pairs were observed within 5 m of each other during time budgets taken in Svalbard, 1994 to 1995. Percentages are plotted in relation to the day the pair female laid the penultimate egg of her clutch (day 0). Darker bars indicate the female's fertile period. Numerals denote the number of pairs used to calculate means.

paired females, each seen foraging off their territory (two and four days before the first egg was laid), and one paired male seen near another female foraging on his territory the day after he was observed copulating with his mate (time budgets lasted 22, 6, and 42 min, respectively).

The following behavior analyses include two types of data on movements by pair members: (1) the proportion of all site changes initiated, and (2) the proportion of site changes initiated by one pair member that was followed by the other. Of all site changes, females did not initiate a significantly greater proportion during their fertile period than did males (Wilcoxon matched-pairs signed-ranks test, $z = -0.94$, $n_1 = 6$, $n_2 = 6$, $P = 0.35$), and neither sex initiated significantly more site changes during the female's fertile period than during the nonfertile period (converse proportions for the sexes; $U = 24.0$, $n = 12$, $P = 0.34$). However, for both periods combined, males initiated significantly more site changes ($\bar{x} = 69.2 \pm 26.7\%$) than did females ($\bar{x} = 30.8 \pm 26.7\%$; $z = -2.0$, $n = 12$ pairs, $P = 0.04$).

Of site changes by one pair member that were followed by the other pair member, the proportion initiated by females did not change significantly from the pre-fertile period to the fertile period, but was highly variable (pre-fertile period, $\bar{x} = 55.6 \pm 46.6\%$, $n = 7$; fertile pe-

riod, $\bar{x} = 60.5 \pm 38.4\%$, $n = 6$; $U = 18.5$, $P = 0.72$). The same was true of the proportion of male-initiated movements in which the female followed (prefertile period, $\bar{x} = 46.7 \pm 42.1\%$, $n = 6$; fertile period, $\bar{x} = 45.5 \pm 32.7\%$, $n = 6$; $U = 18.0$, $P = 0.67$). For both periods combined, males followed their female mates when they initiated site changes about as often as females followed males ($z = -1.29$, $n = 12$ pairs, $P = 0.23$). The data on both distances between mates and site changes initiated by males and females thus provided no evidence that Purple Sandpipers exhibit mate-guarding behaviors. Rather, many pair movements seemed coordinated and cooperative, as three independent observers noted. When a pair foraged on its territory, the female often followed the male's search patterns and sometimes could overtake his foraging area, while the male moved on. If the pair flew, it often took place by the male first lifting both wings, the female taking flight, and the male following.

Copulation frequency of Purple Sandpipers was quite low. We observed copulations or copulation attempts five times during a total of 145 observation days, and four times during previous years (1986 to 1988; Pierce 1993). Copulation behaviors mainly took place on the territory ($n = 7$), but some observed attempts occurred on the foraging grounds ($n = 2$). Copulations occurred mostly in the afternoon (eight of nine), and a successful one observed in its entirety lasted 25 s. We never observed an attempt to force or interrupt a copulation.

DNA fingerprinting.—Samples, collected during two summers, comprised a total of 82 offspring and 54 adults in 27 families. Between the study years 1994 ($n = 12$) and 1995 ($n = 15$), sampled families did not differ significantly in clutch size ($U = 66.0$, $P = 0.24$) or clutch completion dates ($U = 78.5$, $P = 0.57$), so the data were pooled. The mean clutch completion date was 20 June (± 8.8 days, range 3 June to 9 July, $n = 27$). On average, sampled clutches comprised 3.8 ± 0.4 eggs (range 3 to 4), and a mean of 3.0 ± 1.2 offspring were sampled from each nest (range 1 to 4). An average of 25.6 ± 6.8 bands (range 9 to 42, $n = 82$) were scored in the profiles of offspring and 25.8 ± 6.0 bands (range 15 to 40, $n = 54$) in those of adults.

The fingerprints revealed a high degree of band-sharing between offspring and their putative parents. Of the 82 offspring, 66 had pro-

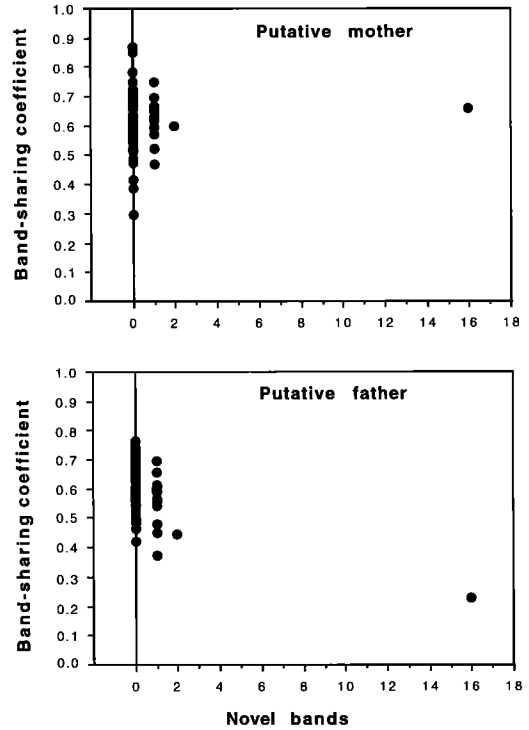


FIG. 2. Relationship between the coefficient D , the proportion of bands in profiles of Purple Sandpiper offspring ($n = 82$) shared with those of their putative mother (upper panel) and father (lower panel), and the number of novel fragments in the offspring's profile ($n = 27$ families).

files that did not contain any novel fragments (Fig. 2). Because 100% of the bands in their profiles were shared with those of the putative parents, it is extremely likely that these young were the offspring of the pair associated with the nest. Of the remaining offspring profiles, 14 of 16 had only one novel fragment not present in either parent's profile, one contained two novel fragments, and a single offspring's profile contained 16 novel fragments (Fig. 2). Novel fragments can arise either through mismatched parentage or through mutations, which are known to occur in minisatellite DNA at a rate of about one per 100 to 300 fragments per generation (Jeffreys et al. 1985b, Burke et al. 1989, Lifjeld et al. 1993, Westneat 1993). Thus, among the average 26 bands in an offspring's profile, it is highly unlikely that more than one or two novel fragments could have arisen through mutation. In contrast, mismatched parentage would be indicated if a profile con-

tained a relatively large number of novel fragments. We determined the expected number of novel fragments to occur, given mismatched parentage, by calculating the average allele frequency q from the equation of Jeffreys et al. (1985b):

$$D = 2q - q^2. \quad (1)$$

This equation expresses the average proportion of bands shared between unrelated individuals in our study population ($D = 0.26$, $SD = 0.08$, range 0.13 to 0.44, $n = 27$ mated pairs). In this case, $q = 0.14$. The expected proportion of bands shared between an offspring and a parent is given by:

$$(1 + q - q^2)/(2 - q) \quad (2)$$

(Jeffreys et al. 1985a), which is 0.60. Accordingly, an average of 60% of the bands in an offspring's profile (average 25.6 bands) will be shared with the offspring. If 15.4 bands are shared with the mother, then an offspring will have 10.2 bands remaining that are attributable only to the father. By subtracting the average proportion of bands shared by unrelated individuals (0.26), we can expect that in cases of mismatched paternity, an average of 7.6 fragments in the profiles of offspring will not be shared with those of the putative fathers.

Of the 16 offspring profiles containing novel bands, 15 had only one or two novel fragments, much lower than the expected number. Furthermore, they shared a high proportion of bands with the mother ($D = 0.63$, $SD = 0.07$, range 0.47 to 0.75) and with the father ($D = 0.56$, $SD = 0.09$, range 0.37 to 0.69), in similarity with the offspring profiles with no novel fragments ($n = 66$, average $D = 0.60$ with the mother, $SD = 0.10$, range 0.30 to 0.87; average $D = 0.62$ with the father, $SD = 0.08$, range 0.42 to 0.76). All of these band-sharing proportions are much higher than those found between unrelated adults (pair members, average $D = 0.26$, $SD = 0.08$). The data therefore indicate that all 81 young whose profiles had zero to two novel bands were the offspring of both putative parents. The average mutation rate was calculated from the sum of all novel bands (16) of the total number of bands (2,052) in the 81 profiles of legitimate offspring, or 0.008. This rate is the same or very similar to those at minisatellite loci in other species (see Decker et al. 1993, Lifjeld et al. 1993).

The remaining offspring's profile had 16 nov-

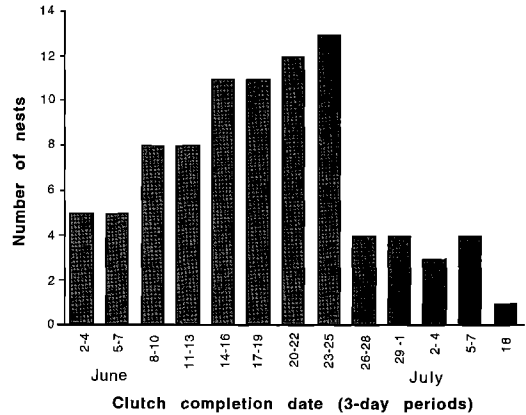


FIG. 3. Number of Purple Sandpiper clutches completed during three-day intervals in the 1994 and 1995 breeding seasons in Adventdalen Valley, Svalbard.

el bands out of a total of 40, and shared only 23% of all the bands with its putative father ($D = 0.66$ with the mother). Therefore, this individual most likely was unrelated to the putative father, i.e. it resulted from an extrapair fertilization.

Nesting phase.—Although it is the most common shorebird in Svalbard (Løvenskiöld 1964; Pierce 1993, 1997), Purple Sandpiper nests are sparsely distributed. Nest densities for 11 sites totaling 31.0 km² ranged from 0 (in 2.8 km²) to 2.9 nests/km² (in 5.1 km²) and averaged 1.1 nests/km² ($SD = 0.9$, $n = 37$). These densities are much lower relative to other shorebirds that breed in Svalbard, such as Ruddy Turnstone (*Arenaria interpres*) and Dunlin (*Calidris alpina*), which have nested elsewhere in densities of 3 to 7 and 15 to 75 pairs/km², respectively (Cramp and Simmons 1983). To estimate the degree of breeding synchrony, the completion dates for clutches found in 1994 ($n = 38$) and 1995 ($n = 51$) were combined, because the differences were nonsignificant ($t = 0.25$, $P = 0.80$). Pairs completed their clutches highly asynchronously, starting as early as 2 June and lasting until 17 July, a time span of 45 days (Fig. 3). The median clutch completion date was 19 June ($SD = 9.1$, $n = 89$). The resulting breeding-synchrony index (Kempnaers 1993) for both years combined was low. On average, only 26.4% of the females in the Purple Sandpiper population were fertile per day during the breeding season. Despite a low copulation frequency, male Purple Sandpipers were com-

pletely successful at fertilizing the eggs in their clutches. Clutches that survived to hatching during this study ($n = 26$) each consisted of four eggs, all of which hatched. Clutches observed during a previous study in Svalbard (1986 to 1988; Pierce 1993) had a similarly high hatching success ($95 \pm 0.4\%$, $n = 37$).

DISCUSSION

The Purple Sandpiper is a relatively long-lived shorebird with a socially monogamous, territorial mating system, long-term pair bonds, and a high level of paternal investment. Our results suggest that Purple Sandpipers do not exhibit paternity-assurance behaviors during the female's fertile period, and they rarely engage in mixed reproductive strategies. We found little or no evidence for mate-guarding behaviors by either males or females, and copulation rates were low. In our genetic analyses, we found that only 1 of 82 offspring resulted from an extrapair fertilization. Thus, Purple Sandpipers in Svalbard must be characterized as genetically as well as socially monogamous.

Mate guarding.—Møller (1991) classified many shorebird species (22 of 29 listed), including the Purple Sandpiper, as exhibiting mate-guarding behaviors. To date, however, few studies detailing this behavior in shorebirds have been published (Oring et al. 1994). Our results show that between the female's pre-fertile and fertile periods, there were no differences in the proportion of time that pairs spent in close proximity to each other, in the proportion of site changes initiated by females, and in whether males followed their mates or vice versa. In fact, males initiated significantly more site changes than females, which contrasts with mate-guarding theory. During the fertile period, the behaviors and movements of pairs foraging together often appeared to be cooperative and coordinated. Several observations indicated that, even during the female's fertile period, pairs spent time foraging in completely separate areas, precluding the possibility of the male's preventing any EPC attempt on his mate. Males generally seemed to spend more time on the territory, whereas females foraged at length on the territory but also flew off to other tundra and coastal foraging sites (sometimes unaccompanied by the male). This is understandable because males generally spend much time

early in the season engaged in territorial displays and defense activities, like chasing and fighting with other males. Purple Sandpipers, in not guarding their mates, are similar to Eurasian Oystercatchers (*Haematopus ostralegus*; Heg et al. 1993), Spotted Sandpipers (*Actitis macularia*; Oring et al. 1994), and Eurasian Dotterels (*Charadrius morinellus*; Owens et al. 1995). In these species, pairs associated closely, but none exhibited mate-guarding behaviors that intensified during the fertile period, during which females were rarely if ever observed to seek or accept EPCs.

Copulation frequency.—Non-guarding species have been associated with the strategy of frequent copulation as a compensatory paternity guard, i.e. "to make the best of a bad situation" (Birkhead and Møller 1992). However, Purple Sandpipers in Svalbard apparently exhibited a low frequency of copulation. It is not likely that copulations were simply missed by observers, because the arctic tundra generally offers good visibility. Although males of two other shorebird species (polyandrous) did not intensify mate guarding during the fertile period, copulation rates were not high (1.3/day, Spotted Sandpiper [Oring et al. 1994]; 5.3/day, Eurasian Dotterel [Owens et al. 1995]). That copulation rates generally are low in Purple Sandpipers is supported by the fact that they have smaller testes (length) relative to body size compared with 17 other sandpipers (family Scolopacidae, subfamily Calidridinae) with various mating systems (Cartar 1985). Across avian genera, Møller (1991) found that copulation rates of females were positively correlated with testis size (mass) of males. However, he also found that testis size decreased as mate-guarding behavior increased, and as species were more socially dispersed, neither of which was supported in this study. Purple Sandpipers do not perform mate guarding, and because they are not solitary nesters, but territorial, EPCs between neighbors are possible. Despite low copulation rates, Purple Sandpipers achieved almost total fertilization success of clutches (hatching success was nearly 100%). In this species, therefore, frequent copulation is unnecessary for achieving high fertilization success.

Ecological factors.—The absence of mate-guarding often is assumed to result from the males being unable or somehow constrained

from doing so (i.e. Birkhead and Møller 1992). Purple Sandpipers nested in low densities ($\bar{x} = 1.1/\text{km}^2$). This alone could not have prevented or constrained males from guarding their mates, nor could it have reduced the risk of EPCs, because territories often had shared boundaries. During time-budget observations, we often observed other individuals of both sexes intruding onto territories (males were chased away). In addition, females moved to such distances from the territory that males could not possibly gain information on extra-pair activities, should they have occurred there. Males were mostly absent from the nest during the first three days after clutch completion (Pierce 1997), and with their paternity in the clutch assured, males potentially could have sought EPCs. Paternity analyses indicated that they did not seek EPCs, or if they did, they were almost entirely unsuccessful.

Lack of breeding synchrony has been suggested to increase the opportunity for EPCs (e.g. Westneat et al. 1990, Birkhead and Møller 1992) and to promote mate-guarding strategies (van Rhijn 1991, Birkhead and Møller 1992), although Stutchbury and Morton (1995) suggested that the opposite is more likely. In Purple Sandpipers, the high degree of breeding asynchrony (on average, only 26% females fertile per day) may preclude males from seeking EPCs, such that mate guarding is unnecessary. Females, though, can seek EPCs because the average daily number of sexually active males probably greatly exceeds the number of fertile females. If the quality of a male's territory was the most important criterion for a female's mating choice, then a high degree of asynchrony would allow the female greater time to visit and assess various territories and their owners. Whether breeding synchrony has influenced mating strategies in Purple Sandpipers may depend more, however, on the benefits of EPCs and the mate-choice criteria of females.

Paternity.—Birkhead and Møller (1992) proposed that among species that do not mate-guard, the frequency of EPCs should be high relative to species that guard their mates. In spite of the lack of close mate guarding during the female's fertile period, male Purple Sandpipers obtained complete paternity in their clutches—we found only one extrapair fertilization, i.e. 1.2% of all offspring sampled. This strongly indicates that it was not necessary for

males to "guard" their mates closely in order to obtain a high certainty of paternity, even though the risk of EPC was not completely absent (see also Chek et al. 1996), and that males invested heavily in offspring by assuming all brood care from hatching for three weeks or longer. Clearly, the investment by males in mate guarding was not a prerequisite for their high level of parental investment, as conjectured by Møller (1991) and Birkhead and Møller (1992); i.e. males were not less "predisposed" to parental care because they did not perform, or were constrained from, mate guarding. Moreover, a male's large investment in parental care was paralleled by a high certainty of paternity. This agrees with findings in other long-lived, monogamous species with low reproductive rates and extensive biparental care (see below). Our results are consistent with the findings that a low frequency of EPP is associated with a low divorce rate (Cezilly and Nager 1995), which in turn is associated with high survival or return rates (Pierce unpubl. data).

Costs and benefits of EPCs.—Much recent literature has focused on the adaptive significance of EPC behavior (cf. Birkhead and Møller 1992). However, in the Purple Sandpiper and other long-lived species with extensive parental care, various selection pressures evidently have resulted in the evolution of intrapair, and not extrapair, fertilizations. Studies of such species often evoke mechanistic explanations for the lack of EPP (i.e. Northern Fulmar [*Fulmarus glacialis*]; Hunter et al. 1992) and suggest that EPCs must be beneficial but that birds were prevented from engaging in them (i.e. copulation interruption by relatives in the Black Vulture [*Coragyps atratus*]; Decker et al. 1993), that EPC costs were too high (potential loss of the nest site in Eastern Screech-Owls [*Otus asio*]; Lawless et al. 1997), or that strict monogamy is somehow related to a small clutch size through a decreased probability of extrapair fertilization success, or of detecting EPP (Leach's Storm-Petrel [*Oceanodroma leucorhoa*]; Mauck et al. 1995). It is likely that, at least in the Purple Sandpiper, females do not solicit or accept EPCs. In this context, it may be useful to consider the potential costs and benefits of pair faithfulness (i.e. in *not* seeking EPCs). The most parsimonious explanation is simply that females do not benefit from obtaining an EPC,

such as fertilization insurance, material benefits, or avoiding costs of some kind. Females are not likely to gain genetic benefits by EPCs if there is little genetic variation among individuals in the population. According to Baker (1992), shorebirds exhibit much lower levels of genetic variation than is typical of birds, and he described the Purple Sandpiper as being particularly "genetically depauperate". Thus, females may have no genetic or other benefits to gain from EPCs. Additionally, the potential costs of EPCs to females could be high. Besides the time and energy constraints during egg laying, a female that engages in EPCs may risk the pair male providing less or poorer care for her offspring (cf. Birkhead and Møller 1992). Even such a minimal risk may affect female behavior in species that make a single reproductive effort where paternal care is critical to offspring survival. Given that females are unwilling to engage in EPCs, then the costs to males of seeking EPCs would be high because they would have to leave their territory unguarded and also overcome both the female and perhaps her mate as well. If the costs of seeking EPCs outweigh the benefits (if any) for both sexes, then neither sex should seek EPCs, and both should invest in their offspring. In such a scenario, the interests of the pair would coincide, and cooperative breeding behavior should evolve.

In conclusion, the level of EPP in Purple Sandpipers was low. Paternity-assurance behaviors such as mate guarding and high copulation frequency were not necessary for achieving a high certainty of paternity or fertilization success. As suggested by Chek et al. (1996), the absence of paternity-assurance behaviors may persist due to the low rate of EPP. Furthermore, it cannot be said that mate guarding led to increased paternal investment in reproduction, because males invested heavily in parental care despite a lack of mate guarding. A high level of paternal investment can, however, be associated with high certainty of paternity. Whether mate-guarding behavior actually reduces the frequency of EPCs is questionable (Oring et al. 1994). Even if effective, males would not be under strong selection pressure to evolve paternity-assurance behaviors unless a significant risk of EPCs by their mates existed. As long as females can control sexual behaviors (e.g. by rejecting copulation attempts) and do not seek EPCs, selection pres-

sure for mate guarding will be weak or absent (Chek et al. 1996).

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