Why don't female purple sandpipers perform brood care? A removal experiment

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In most monogamous sandpiper species, females share parental care but leave the brood earlier than males, a feature unusual among birds in general. In the purple sandpiper (*Calidris maritima*), females almost always leave the brood at hatching and never share brood care. Males perform uniparental brood care from hatching until well after fledging. In this paper, we report the results of a mate-removal experiment conducted on the purple sandpiper in high Arctic Svalbard and discuss the implications for the evolution of their mate desertion strategy. By removing males from nests near hatching, we tested 2 hypotheses: 1) Males assume brood care because females, who always have a net benefit from deserting, have a fixed brood desertion strategy, whereas males do not; 2) females desert the brood because they cannot perform uniparental brood care as well as males and/or because they are under physiological stress at hatching due to egg laying and incubation activities hypothesis). We found that when experimentally deserted, most female purple sandpipers assumed brood care. Parental behavior and the growth and survival of the chicks suggested that the attending females were not under physiological stress after hatching and did not seem less able than males to perform brood care. Thus, we found no support for either hypothesis. We suggest that uniparental brood desertion is a consequence of strong selection for uniparental brood care in this species and that the actual sex roles may result from rather marginal differences between the sexes in the fitness consequences of care and desertion. *Key words:* brood desertion, *Calidris maritima*, ESS parental care models, male parental care, mate-removal experiment, parental investment, purple sandpiper, reproductive strategies, sex roles, shorebirds, uniparental care. *[Behav Ecol 21:275–283 (2010)]*

D esertion of dependent young by a female parent is not a common phenomenon among birds or mammals. Among monogamous species where one sex sometimes deserts the young, it is generally the male (Clutton-Brock 1991), because males most often have a higher reproductive potential through additional mating opportunities than do females (Trivers 1972; Gross and Sargent 1985). A major exception to this trend is exemplified by the shorebirds, in which females of all polyandrous species ($n = 12$–16), and a substantial number of monogamous, single-clutched species ($n > 149$) desert their broods before males (Erckmann 1983; Oring and Lank 1984; Miller 1985; Gratto-Trevor 1991; Székely and Reynolds 1995). Among some monogamous Arctic sandpipers, for example, dunlin (*Calidris alpina*; Soikkeli 1967), semipalmated sandpiper (*Calidris pusilla*; Ashkenazie and Safriel 1979; Gratto-Trevor 1991), and western sandpiper (*Calidris mauri*; Holmes 1973), females participate in brood care but leave the brood in the care of the male some time after hatching. If 2 parents are not much better at caring for the brood than one, and the deserting parent has a good chance of mating again, uniparental brood care could evolve as an evolutionarily stable strategy (ESS) of parental investment (Maynard Smith 1977). In these sandpipers, therefore, one parent must be nearly as good at caring for the brood as 2, at the time of desertion. It has also been hypothesized that selection promotes the removal of one adult from the vicinity of the nest because it results in a reduction of intrafamilial competition for food in the breeding area (Pitelka et al. 1974). However, this does not offer a satisfactory explanation for why the deserting sex is almost always a female and why females in many other monogamous shorebirds leave the brood earlier than males. Few studies have attempted to investigate female brood desertion experimentally. Experimental studies of species in which brood desertion by one sex is a normal part of the breeding strategy can elucidate the evolutionary dynamics of mate desertion, particularly if timing of desertion and response of the partner are taken into account.

In this study, we investigated potential factors influencing which sex assumes uniparental brood care duties in the purple sandpiper (*Calidris maritima*) in Svalbard, Norway. The purple sandpiper is a monogamous, high Arctic shorebird whose breeding biology is similar to that of a number of other monogamous Arctic sandpipers. However, purple sandpiper behavior differs from that of many other shorebirds in at least one important respect: Broods are never attended by both parents. That is, nearly all females leave the brood at hatching or soon after and do not participate even briefly in biparental brood care, as do many other monogamous female shorebirds (Pierce 1997a). During a previous study (1986–1988, 1993–1994), all accompanied broods captured ($n = 102$) were attended to by a single parent, which, in more than 94% of the cases, was the male; in rare cases, uniparental female care was recorded (Pierce 1997a). Females were last seen on the breeding grounds on average 3–4 days after their clutch hatched or was lost. During the study, no replacement or second clutches were found, nor did remating occur within a season (Pierce 1997a). Further, the species is characterized by sexual monogamy (Pierce and Lifjeld 1998). Most purple sandpipers return year after year

to the same breeding area and are highly faithful to their territory and their partner, that is, divorce rarely occurs (Pierce 1997b). Székely (1996) suggested that studies of species in which the desertion behavioral trait is variable are particularly informative because the trait can be experimentally manipulated. In contrast, purple sandpipers exhibit very little variation in the deserter's timing and sex, that is, females almost always desert at hatching. It is precisely the simplicity of this system that lends it suitable for analyses of sexual differences in costs and benefits of desertion because variation (within reasonable limits) caused by individual differences, time during the season, or remating opportunities does not need to be controlled for. The main objective of this study was to test 2 dominant hypotheses about the evolution of male brood care in the purple sandpiper by conducting a mate-removal experiment at the time of hatching. To specifically formulate these hypotheses, and to make predictions from them about the desertion decisions of male and female purple sandpipers, we used a logical approach similar to that used in game theory models by Maynard Smith (1977) for parental investment and by Lazarus (1990) for the evolution of mate desertion. Here, we describe our approach in general terms.

Cost–benefit analysis of brood desertion in the purple sandpiper

The mating system of a species is in large part determined by coevolution of the male's and female's parental investment strategies, which are both dependent on costs and benefits of caring for, or deserting the brood (Maynard Smith 1977; Lazarus 1990). However, the decision by one sex to desert, and thus the costs or benefits the deserter gains, vary according to the outcome of that decision on its mate and whether or not the mate deserts in turn. First, the benefit of providing brood care is the net reproductive success (RS) gained from the current brood. This net RS may not be equal for males and female purple sandpipers but is likely to be much higher throughout most of the breeding season than leaving the brood to no care. The species apparently never exhibits biparental care; thus, we do not consider it here. Second, the benefit of desertion, or the increment increase in net RS a deserting male or female may gain above that gained by continuing parental care, would be the avoidance of parental investment costs (i.e., physiological stress, risk of mortality, and reduced ability to invest in future reproduction) and the potential of obtaining additional breeding attempts in the same or future seasons. This potential gain is not necessarily greater for males than for females. Because purple sandpipers in Svalbard usually breed only once each season (Pierce 1997a), males do not have greater desertion benefits in terms of additional mating opportunities or possible extrapair young in second clutches of deserting females, as, for example, in spotted sandpipers (*Actitis macularia*; Oring et al. 1992). Thus, a female, for example, should desert the brood to the male's care if the net RS benefits she gained by deserting plus the RS gained from male brood care outweighed the net RS she could gain by assuming uniparental care; the reverse is also true for the male. This assumes, in either case, that the mate being deserted is willing to assume brood care.

Hypotheses for female brood desertion in the purple sandpiper

Forced male brood care hypothesis
Male purple sandpipers perform uniparental brood care because females always desert at hatching. In other words, males

are in a "cruel bind" because female brood desertion is a fixed strategy (cf. Maynard Smith 1977). Our male-removal experiment directly tests this hypothesis, which predicts that if the male experimentally deserted the nest at hatching, the female would, in turn, also desert the brood (Prediction 1). This would occur if the female's net benefits of leaving the brood parentless outweighed her benefit of assuming sole parental care. A deserted male, however, may be selected to perform uniparental brood care if deserting the brood would result in a relatively lower fitness (cf. Trivers 1972; Dawkins 1976; Lazarus 1990).

Poorer female parent hypothesis
Male purple sandpipers are willing to perform uniparental brood care because they can achieve a higher RS than through uniparental female brood care. This hypothesis assumes that biparental care is no more productive than uniparental care. If there were no net benefits for a female to leave the offspring parentless, then it would pay her to assume brood care should the male desert the nest at hatching. However, costs of assuming uniparental brood care may be greater for females than males if, for example, physiological stresses from egg laying and incubation left females less able to perform brood care ("stressed female" hypothesis; cf. Graul et al. 1977; Maynard Smith 1977; Ashkenazie and Safriel 1979; Lenington 1980; Myers 1981; Brunton 1988; Gratto-Trevor 1991; Székely and Williams 1995; Pierce 1997a). Further, both sexes may benefit from female desertion at hatching if 1) the female can significantly improve the survival of the offspring by maximizing investment in incubation, egg size, or quality and that 2) this investment reduces her physiological capacity to care for the young, relative to the male, and by deserting, 3) the female can increase her probability of survival to the next year, whereas the male can increase the likelihood of reuniting with his mate (Ashkenazie and Safriel 1979; Gratto-Trevor 1991; Székely 1996; Pierce 1997a). Therefore, if experimentally deserted females that assume brood care are physiologically stressed, they should pay a significant cost of reproduction (Røskaft 1985), resulting in significantly greater weight loss, lower survival rates, or reduced success in future reproductive attempts compared with brooding males (Prediction 2).

Alternatively, females' brood care costs and desertion benefits may not be greater but similar to that of males. Nonetheless, males may be able to achieve a greater net RS from uniparental brood care than females would, perhaps due to differences in inherent morphological or behavioral characteristics ("differential parental capacity" hypothesis; Pierce 1997a). Males of biparental shorebird species are purported to be better parents because they may be more successful than females at defending or protecting the young from predators (Székely 1996), and territorial males may be more familiar with foraging sites and better able to expel foraging competitors. If brooding females are indeed less capable parents than males, then females forced to brood via male-removal experiments should show reduced antipredator responses and attendance times, or achieve lower chick growth or survival rates (Prediction 3).

MATERIALS AND METHODS

Study area

Purple sandpipers were studied on Spitsbergen Island, in the Svalbard archipelago in the Norwegian high Arctic. Svalbard lies only some 1000 km from the North Pole. Thus, summers are short (about 10–12 weeks), and 24 h sunlight occurs from April to September. The tundra vegetation reaches only a few

centimeters high and below the thin layer of soil is year-round permafrost. We conducted the mate-removal experiment from early June to late July 1995 in the Adventdalen valley, near a mining town, Longyearbyen (78°13′N, 15°35′E). Here, purple sandpipers have been studied in 1988 and yearly from 1993 to 2002 (see Pierce 1993, 1997a, 1997b; Pierce and Lifjeld 1998). Summer temperatures in the valley commonly lie between 3 and 7 °C. At the mouth of Adventdalen river is a large expanse of mudflats where shorebird flocks gather in spring and fall. The study area and vegetation are described in detail elsewhere (Pierce 1993, 1997a). A few observational data used in this study were collected near the Ny Ålesund research station (78°55′N, 11°56′E) during a previous study (1986–1987).

Study species

The purple sandpiper is the most common shorebird in Svalbard (Løvenskiold 1964; Pierce 1997a). Females closely resemble males except that they are larger (typically by 3–4%; Payne and Pierce 2002), particularly in bill length (1–31% larger, $n = 73$ pairs; Pierce 1997b). Males occupy and actively defend large breeding territories on the tundra and perform aerial displays above them early in the season. Males court females through ground and flight chases (see Pierce 1997a). Nests, which are small, deep cups scraped into the tundra, occur at very low densities (mean = 1.1 nests/km^2; standard deviation [SD] = 0.9, $n = 11$ searched sites totaling 31.0 km^2; this study). They are very difficult to discover because incubating birds are highly camouflaged and most flush only at distances of 50 cm or less. The eggs are relatively heavy; a fresh clutch usually weighs about 65% of the female's body weight (Pierce 1993) and varies little in size (mean = 3.84 eggs ± 0.35, $n = 37$). Clutches are laid asynchronously during a season (i.e., 3 June–18 July 1995). Incubation is shared by males and females fairly equally overall for 21–22 days, and the nest is virtually never left unattended (Pierce 1997a). The arctic fox (*Alopex lagopus*) is responsible for most clutch depredation, although arctic skuas (*Stercoraria parasiticus*) and even grazing reindeer (*Rangifer tarandus*) may cause some losses. Only on very rare occasions do purple sandpipers renest after clutch predation. When some clutches found during 1986–1988 and 1993–1995 were depredated ($n = 14$), males in particular remained at length in the area, but none were found later with a brood (Pierce 1997b). Only during one summer (1999) with exceptionally favorable weather did 3 pairs ($n = 20$ nests) renest after clutch depredation (Pierce EP, unpublished data). Chicks leave the nest the day after hatching and become independent when 28–34 days old (Pierce 1993). The attending parent must not only warm the chicks extensively during 7–10 days until they can thermoregulate but also stay alert for predators and lead chicks to foraging sites. The main predators of chicks are likely to be arctic skuas and foxes, but occasionally glaucous gulls (*Larus hyperboreus*) also take chicks. No pairs have been found to renest after brood loss (Pierce EP, unpublished data).

General methods

From 1993 to 1995, a total of 73 female and 103 male adult purple sandpipers were captured and banded with unique color codes. Each bird was weighed to the nearest gram and lengths of bill, maximum wing, and foot (tarsus joint/"knee" to toe-tip) were measured according to methods in Pierce (1997a). Captured birds were sexed by bill length, which overlaps little between sexes (see Pierce 1997a) and additionally by a combination of the biometrical measurements, because females generally are larger than males in all measurements. A bird's sex was often verified by previous years' knowledge, comparison with its mate's biometrical measurements, or by behavioral observations, such as courtship, territorial activity, or aerial displays. One member of each pair was given a small dot of paint on the forehead feathers to enable identification from a distance during incubation. All located nests and broods were plotted on detailed maps of Adventdalen valley (scale 1:10 000, Store Norske Spitsbergen Kulkompani AS), from which distances were measured.

Mate-removal experiment

Nest searches were made by pairs of people systematically walking throughout 11 chosen sites, dragging a rope to flush nesting birds. Each chosen site was naturally delimited (by, e.g., moraine, riverbed, or mountains) and therefore encompassed most (if not all) territories. More than 500 work hours were spent searching the sites, which totaled 31.0 km^2 in area, and 34 nests were found. Indication of any missed nest was given by sightings of young, unbanded chicks in previously searched sites. Broods are relatively easy to discover, and further, each site was searched or traversed nearly daily by 5–7 observers during 75 days. All located nests were randomly designated as "male removal" or "female removal" in which the male or female, respectively, was removed at or near hatching. Although females normally leave around hatching (Pierce 1997a), females were removed from some nests ("female removals") to control for the effect of the experiment (i.e., physical manipulation of the breeding pair). Although as many as 34 nests were located, 22 could not be used in the experiment: Eleven nests were depredated, 2 nests hatched early, in 4 nests, the mate-removal procedure failed (see Results), 2 nests were unmanipulated in order to observe interactions of pair members from hatching to nest departure, and the rest were excluded due to smaller clutch size ($n = 1$) or unusually late hatching dates ($n = 2$). Among the nests that survived until 2 days before hatching ($n = 12$), 8 nests were randomly designated as male removal, and 4 as female removal. In both groups, all nests contained 4 eggs and were distributed throughout the study area. The 2 groups did not differ significantly with respect to mean egg sizes of clutches (Mann–Whitney U tests, widths: $U_{4,8} = 11.0$, $P = 0.40$; lengths: $U_{4,8} = 12.5$, $P = 0.55$), hatching dates ($U_{4,8} = 12.5$, $P = 0.55$), the minimum age of each bird (males: $U_{4,8} = 13.0$, $P = 0.61$; females: $U_{4,8} = 9.0$, $P = 0.23$), nor body weights, which were taken once during incubation (males: $U_{4,8} = 15.5$, $P = 0.93$; females: $U_{4,8} = 6.5$, $P = 0.11$).

When unknown, the hatching date of a clutch was estimated by floating the eggs and comparing float angles with a scale based on previous measurements of known-age eggs (see Pierce 1997a). Hatching dates can be estimated with an accuracy of ±0.6 days when eggs are floated during the first week of incubation and ±2.0 days when floated later (Pierce 1997a). Because incubation bouts last 13–17 h (Pierce 1997a), removals had to be timed in relation to the mate's return. Therefore, sex of incubating birds in each nest was recorded, from a distance, 1–2 times daily throughout incubation to estimate changeover times. During the final 2 days of incubation in all manipulated nests, one bird was removed 1–4 h before its mate's return. To prevent damage from cold, eggs were replaced with false eggs and temporarily stored in an incubator. When the mate returned and settled on the nest for at least 1 h, it was flushed off and the original eggs returned. All flushed birds ($n = 12$) returned to the nest within 30 min. Whenever possible, manipulations were made before the hatching phase began (i.e., in 12 of 16 attempted mate-removal experiments). Removed birds were initially kept in an outdoor aviary, to prevent their return to the nest. However,

the first 2 birds did not adapt to captivity and were thus released. Subsequently, all others were placed in a small, dark cage in quiet for 24 h. If the mate assumed brood care by that time, we clipped the primaries of the captive (removed) bird and released it 4–5 km away on the mudflats at low tide, near other foraging shorebirds. At least 8 of 12 removed, wing-clipped birds returned the following year.

After each mate removal, the time of hatching and nest departure was noted. Antipredator behaviors of manipulated adults with broods were recorded during 3 observer approaches during 0–3, 4–6, and after 7 days posthatch. Responses were defined as "strong" (score = 3) if the adult alarmed from a short distance (i.e., approached the observer within 20 m) and gave a full rodent run display (description in Duffey and Creasey 1950) with loud, constant alarm calls. The response was "medium" (score = 2) if the adult gave alarm calls of short duration, approached the observer no closer than 20 m and gave a crouched run and/or had an alert posture. A "weak" response (score = 1) was when alarm calls were weak or absent, the attending parent did not attempt to approach and only had an alert posture (no alarm display). We attempted to capture and weigh all broods and attending parents once to record chick growth and adult condition. To minimize any possible effect of disturbance, attending females were captured at least a week after hatching and capture attempts limited to 30 min or less. Chick growth (weight) and survival (brood size) of manipulated broods were all measured at various times, and thus, male-removal and female-removal broods were not directly comparable. Instead, therefore, we took the differences between each manipulated brood's mean weight or brood size to those of all known-age unmanipulated broods ($n = 120$ chicks in 37 broods captured 1986–1988 and 1993–1995) measured during the same age interval.

Manipulated broods were observed daily with binoculars from a car or from a distance without disturbing the brood (i.e., >50 m). We recorded brood size, fate, and the number of days the parent attended. Brood positions were plotted on a map, and distance from the nest cup was averaged for each 3-day interval after hatching. Distances moved per interval were averaged for male- and female-attended broods and plotted against days after hatching, as were distances moved by unmanipulated broods observed 1994–1995 ($n = 18$). The territory was defined as the area within a radius of 600 m from the nest cup, the mean area of territorial activity (cf. Pierce 1997b). We estimated the number of days each female-attended brood spent within the territory limits and compared it with that of male-attended broods for which we had the data ($n = 16$, 1994–1995). Brood fate was considered 1) successful if at least one offspring was observed as an independent juvenile, 2) depredated if an attending adult gave medium or strong antipredator responses and was later resighted alone near the same area giving weak antipredator responses, or 3) abandoned if the attending bird gave weak responses from hatching and then disappeared altogether. To investigate possible long-term effects of the experiment, fieldwork was also conducted the following year (1996), although with reduced intensity (2 persons working for 30 days). Because purple sandpipers show high territory fidelity (Pierce 1997b), territories of 1995 were specifically searched to observe and find nests of experimental adults.

Unsuccessful mate-removal experiments

Four of 16 attempted mate-removal experiments were unsuccessful. In the first experiment conducted, a removed male was released at the mudflats 5 km away with the primaries of only one wing clipped. In less than 24 h, the male returned to the territory where the female had assumed brood care; the experiment was thus discontinued. This strong drive to return to the nest was also shown by a removed female with one wing clipped that returned to the nest site from 6 km away; her mate, however, had already moved elsewhere with the brood, and the experiment was thus not disrupted. In 2 male-removal nests and 1 female-removal nest, experiments were discontinued when birds did not return and settle in the nest within 2–4 h after removal of the incubating mate. The removed birds were then released at the nest with their primaries intact.

RESULTS

Test of "forced male brood care hypothesis"

Time from hatching to nest departure
Normally, a paired male and female will continue to incubate in shifts throughout the 1- to 3-day hatching phase (Pierce 1993, 1997a) until the male leaves with the brood about 1 day after hatching (Pierce 1993). In this study, some nests hatched later than predicted, and birds whose mates were removed completed incubation without assistance. Times from mate removal to start of hatching varied 0–2 days between clutches but were nonetheless similar in male-removal and female-removal groups (Mann–Whitney $U_{4,8} = 12.5$, $P = 0.55$; Table 1). However, females did not delay nest departure waiting for their mates' return. Females in 8 male-removal nests (0.5–1 day: $n = 7$; 1–2 days: $n = 1$) were similar to males in 4 female-removal nests (0.5 day: $n = 2$; 1 day: $n = 2$) in time spent from hatching to nest departure (Mann–Whitney $U_{4,8} = 9.0$, $P = 0.23$).

Female brood care
Of male-removal nests ($n = 8$), all females assumed brood care, except for one who presumably abandoned her brood 4 days after mate removal (see below). Except for this bird, all females departed the nest within a day after hatching while attending the brood in a manner very similar to males, that is, leading and periodically brooding the chicks, keeping constantly alert and, if necessary, distracting potential predators.

Female behavior after hatching
Although they are rarely seen near the nest 2 or more days after hatching, some unmanipulated females exhibit parental care behavior toward newly hatched chicks but not in coordination with the pair male (i.e., not biparental). Female parental behaviors were recorded after hatching at 17 unmanipulated nests during this and previous studies (1986–1988 and 1993–1995). On the hatching day and/or the day after, some females were seen brooding the chicks in the nest ($n = 3$), but most either remained on the territory while the male brooded ($n = 7$) or were not seen ($n = 7$) and had probably departed earlier. When alone with a newly hatched brood, females displayed strong antipredator responses and parental behaviors ($n = 8$) or gave strong antipredator responses near the brood 1–3 days after hatching, while the male attended ($n = 2$). In this study (1995), 2 unmanipulated nests were observed continually from hatching start to nest departure (about 48 h). Pair members continued to switch incubation duties until the day after hatching, when the chicks' down had dried (cf. Pierce 1997a for description of incubation changeover). When males then assumed brooding, they did not switch although the female returned to the area and called. Further, in 3 male-removal nests, females remained on the territory after hatching, gave strong distraction displays when the male alarmed, and took over brooding the young within minutes after the male was removed. These females also continued brood care until the chicks were successfully fledged.

Table 1

Behavior of experimentally deserted female and male purple sandpipers in Svalbard from mate removal near hatching to brood desertion

Days from removal to hatching	Antipredator response with days after hatching:			Time on territory (days after hatching)	Last day parent seen with brood	Brood fate
	0–3 (Response category)	4–6	>7			
Males						
0–1	Strong	Medium	—	—	7	Predated?
1	Strong	Strong	Strong	14	29	Fledged
2	Strong	Strong	Strong	21	19	Fledged
2	Strong	(No data)	Strong	10.5	33	Fledged
Females						
0	Strong	Strong	Strong	11	30	Fledged
0	Strong	(No data)	Strong	4	22	Fledged
0–1	Strong	Strong	Strong	21	27	Fledged
1	Strong	(No data)	Strong	1	19	Fledged
1	Weak	Weak	Strong	21	21	Prob. fledged
2	Medium	Medium	Strong	3	21	Fledged
2	Strong/weak*	—	—	—	2	Predated?
2	Weak	—	—	—	3	Abandoned?

One adult was observed twice during an interval; both responses are shown (*). Time on the territory is the number of days the brood was observed within 600 m of the nest cup. Fates of some broods (question marks) were not known but were assumed based on the attending birds' behavior the last day it was sighted (see text).

Test of "poorer female parent hypothesis"

Antipredator responses of brooding parents

Of females from male-removal nests, some ($n = 4$) gave weaker antipredator responses than males from female-removal nests (Table 1) during the first 6 days of brood attendance, that is, they gave alarm calls but not the full rodent run display, nor did they approach as closely as males did (<20 m). Three of these females had incubated continually for 2 full days after mate removal, and 2 lost their brood while 1 successfully fledged her young (Table 1). The fourth female with a weak response had experienced bad weather the day after hatching but remained to continue brood care until the young fledged. All other females whose mate was removed ($n = 4$) gave antipredator responses as strong as those of males, and after one week, males and females behaved similarly (Table 1). Two males whose mate was removed incubated continually for 2 days until hatching, but all males gave strong antipredator responses while attending the brood (Table 1). One male showed a medium response on day 6 (Table 1), but the brood was missing and probably depredated (see Materials and Methods). Overall, male and female antipredator responses did not differ significantly during any time interval (Mann–Whitney: days 0–3, $U_{4,8} = 8.0$, $P = 0.17$; days 3–6, $U_{3,4} = 4.5$, $P = 0.60$; >7 days, and $U_{3,6} = 9.0$, $P > 0.99$).

Time spent on the territory

Brooding males often stay on or near their territory and move away gradually when the offspring near fledging age (Pierce EP, personal observation). Males may gain benefits from lengthy territory maintenance, such as improved status, increased chances of attracting a mate the next year, and advantages in male–male competition. Because purple sandpiper clutches are laid very asynchronously (Pierce and Lifjeld 1998), early-nesting males would have greatest benefits, and if so, should remain longer on the territory than experimental females. Overall, females attending broods ($n = 40$ observations of 6 broods; 1–6 broods observed/3-day interval) moved more quickly away from the nest cup and left the territory sooner than unmanipulated

males ($n = 125$ observations of 18 broods; 3–13 broods observed/3-day interval; Figure 1). On average, females with broods spent 10.2 days (range = 1–21, standard error [SE] = 3.7) within the territory, while unmanipulated brooding males observed in 1995 spent 16.9 days (range = 4–28 days, SE = 1.8); the difference was not significant (Mann–Whitney $U_{6,16} = 27.5$, $P = 0.13$). Of birds attending a brood that hatched early, that is, eggs laid before that year's median hatching date, male-removal females spent significantly less time on the territory with their brood (mean = 7.2 days, range = 1–21, SE = 4.6; Mann–Whitney $U_{10,4} = 5.5$, $P = 0.040$) than attending males (mean = 20 days, range = 1–20, SE = 1.9).
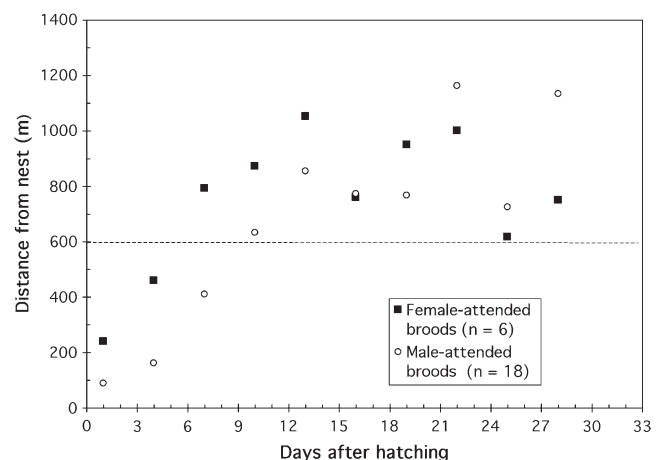
Figure 1
Distances that female- and male-attended purple sandpiper broods moved from the nest with time after hatching. Points represent averages of single distances of broods observed during 3-day intervals after hatching. The dashed line indicates the approximate size of a purple sandpiper territory.

Chick growth

In the manipulated broods, not all chicks could be weighed because broods became increasingly difficult to capture or relocate as chicks matured or suffered mortality. However, those chicks captured ($n = 9$) from male-removal broods ($n = 6$) had mean weights similar to those of unmanipulated broods (Figure 2). Only the weight of one male-removal brood ($n = 1$ chick measured) fell below the 95% confidence intervals for mean weights of unmanipulated broods (Figure 2). The brood's attending female then weighed the least of the females from male-removal nests and was the only adult to incubate for 2 days plus attend a brood for more than 6 days (Table 1). Two broods from female-removal had normal weight gain shortly after hatching, but one chick reweighed much later was very light (Figure 2), due to a deformed leg.

Parental attendance times, brood fates, and chick survival

Almost all broods of females from male-removal nests ($n = 6$ of 8) were successful: At least 1 chick fledged in each. Females attended their broods until they fledged or well after, that is, 19–30 days, no differently than males from female-removal nests (Mann–Whitney $U_{8,4} = 12.5$, $P = 0.55$). Attendance times averaged 18 days ($n = 8$, SE = 4) for females and 22 days ($n = 4$, SE = 6) for males. Only 1 female presumably abandoned the brood 4 days after mate removal. Observed daily, she gave only weak antipredator responses and never took the brood more than 150 m from the nest. Two broods, 1 from a male-removal nest (hatched near an arctic skua nest) and 1 from a female-removal nest, were probably depredated. All the remaining broods from male-removal nests were successful and attended by the females for 19–33 days; well after the chicks could fly (Table 1). In female-removal nests, the experiment had no obvious influence on the behavior of males or their broods, relative to broods observed in all other years. Chicks in female-attended broods appeared to survive as well as chicks of males from female-removal nests, compared with averages of unmanipulated broods in the same age categories (Table 2; data from Pierce 1993). Female-attended broods did not differ more significantly in brood size (i.e., the latest confirmed brood size observation) from the average for same-aged unmanipulated broods than did male-attended broods from female-removal nests (Mann–Whitney $U_{7,4} = 9.5$, $P = 0.395$; Table 2). Further, 3 fully fledged juveniles (29–54 days old) from female-attended broods ($n = 3$ in which 1, 2, and 2 chicks were banded) and 3 (48–56 days old) from male-attended broods from female-removal nests ($n = 2$, 4 chicks banded in each) were resighted foraging alone well after brood bonds had dissolved.

Costs of brood care

Adult weight changes

Females lost weight during brooding but not relatively more than males. Females from male-removal nests lost an average 13.6% (from 9% to 19%) of their body weight between early incubation and brooding (respectively, 0–11 and 26–37 days after clutch completion), declining from a mean 71.7 to 62.3 g ($n = 4$, SD = 2.9, 1.5, respectively). However, all unmanipulated brooding males captured (1986–1995) and weighed once during the same periods as females, lost an overall average 14.2% of their body weight, declining from a mean of 66.9 g ($n = 15$, SD = 4.7) to 57.4 g ($n = 14$, SD = 4.3; Figure 3). Weighed during incubation and again after hatching, 2 unmanipulated males lost 14% and 21% of their weight, and one heavy male from a female-removal nest lost nearly 29% within 8 days after hatching (Figure 3). The differences between each female's weight and the average of unmanipu-
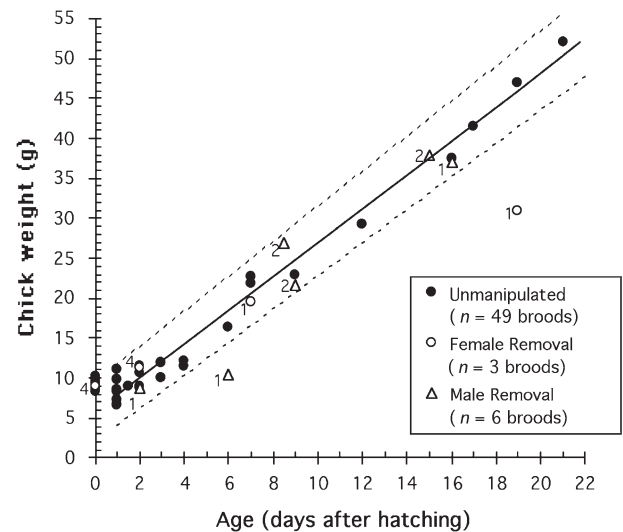

Figure 2
Body weight in relation to age of purple sandpiper chicks in manipulated broods. The solid line represents a regression on weights of unmanipulated chicks (brood averages), with 95% confidence intervals of their individual observations (dashed lines). Number of chicks weighed is given beside the manipulated brood symbols.

lated males during posthatching did not change significantly from weight differences during early incubation (Wilcoxon signed rank test, $z_{4,4} = -0.18$, $P = 0.85$).

Effects of the experiment in the following year

Data taken the following breeding season (1996) indicated that manipulated birds did not accrue substantial costs as a consequence of the experiment, although fewer field observations were made. Females from male-removal nests had the same minimum return (survival) rate as males from female-removal nests (50%; Table 3), similar to the mean of unmanipulated, banded birds resighted in the study area between 1993 and 1996 (females: 51.0%, $n = 51$; males: 59.3%, $n = 113$; Pierce 1997b). At least 3 of the females ($n = 4$) returned

Table 2

Survival of purple sandpiper chicks in broods from mate-removal nests, given in terms of brood size and compared with the average number of chicks in unmanipulated broods captured when within the same 2- or 4-day age interval (see Materials and Methods)

Brood age (days)	n chicks observed	Unmanipulated broods Brood size average per age interval (n, SD)
Male-removal broods		
2	0	3.7 (13, 0.6)
2	3	3.7 (13, 0.6)
4	4	3.3 (11, 1.0)
6	2	2.7 (12, 0.9)
9	2+	2.5 (6, 1.0)
12	3	2.5 (6, 1.0)
16	3+	2.8 (10, 1.0)
Female-removal broods		
2	4	3.7 (13, 0.6)
7	0	2.5 (4, 0.9)
7	3	2.5 (4, 0.9)
8	3–4	2.5 (4, 0.9)

Plus signs indicate a minimum number of chicks observed in the brood.
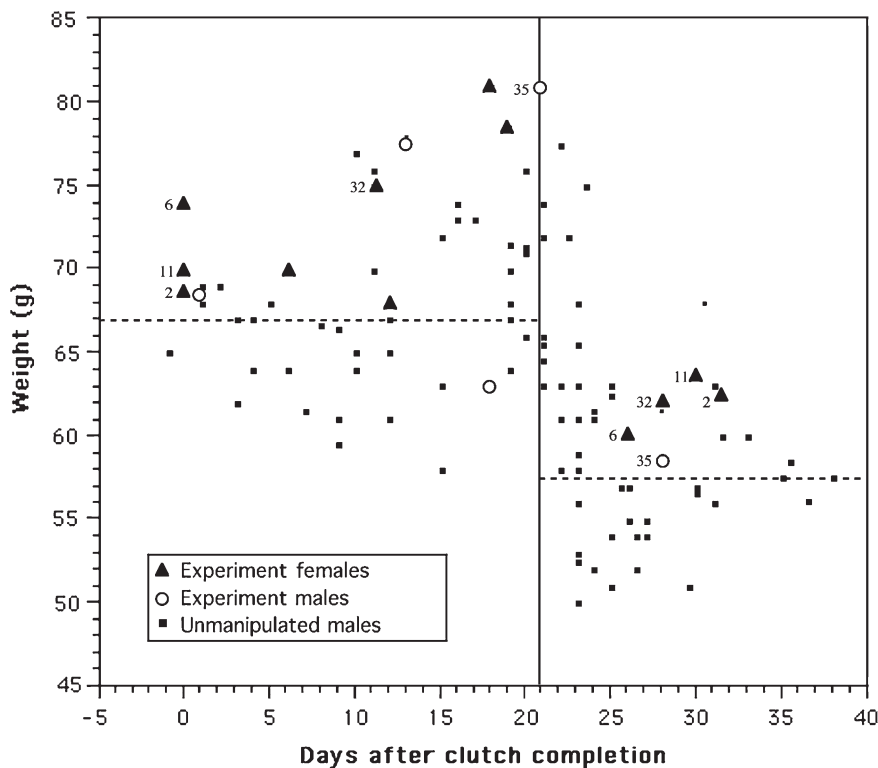
Figure 3
Body weights of female and male purple sandpipers experimentally deserted at hatching compared with single weights of unmanipulated males, from the start of incubation through the brooding phase. Nest numbers beside symbols identify individuals weighed before and after the hatching day (vertical line). For comparison, dashed horizontal lines indicate averages of unmanipulated males weighed during early incubation (days 0–11) and mid-brooding (days 26–37) phases.

to their previous territory, and at least 2 nested with the mates that had "deserted" them the year before. Both the latter females nested within 100 m of the previous year's nest and laid the same number of eggs within a week of the previous year's laying date (Table 3). One of these was weighed during incubation within 4 days of the previous year's capture and had a similar weight (+3 g). The other female stayed longer than usual after hatching (1.5 days) and gave unusually strong antipredator responses during brood capture. Although the attending male alarmed at 3 m, the female alarmed from 8 to 10 m and performed distraction

displays for 70–100 m away from the brood. Of female-removal nests, at least 1 pair reunited and nested near the previous year's nest cup (Table 3).

DISCUSSION

In Svalbard, we conducted a mate-removal experiment near hatching to test 2 hypotheses for female desertion in the purple sandpiper. Our results did not support Prediction 1 of the "forced male brood care hypothesis," that experimentally deserted females should in turn desert the brood. After hatching, all females but one assumed brood care and departed the nest at time intervals similar to males. Our results also indicated no support for the "poorer female parent hypothesis": 1) if males assume brood care because females are poorer parents due to a lowered physical capacity, then brooding females should show signs of physiological stress (Prediction 2), and/or 2) if females desert because they are less capable of brood care, then experimentally deserted females should exhibit reduced parental behavioral responses and shorter attendance times than males (Prediction 3). The brooding females' parental care behavior and performance, in terms of antipredator responses, attendance times, and chick weight-growth were similar to those of brooding males. Females were as successful as males in fledging at least one chick and avoiding total brood predation. Furthermore, female weight loss during chick rearing was similar or less than that of brooding males. If experimental females were physiologically stressed at hatching but "forced" to care for chicks that would otherwise perish, females could have deserted the chicks as soon as they could fly and survive unattended, that is, after 14 days. Instead, females attended broods for 19–34 days, times comparable with males. Except for a tendency to leave the territory sooner, parental behaviors of brooding females and males were very similar. Thus, we can conclude that female desertion at hatching is not an obligate strategy, forcing males in a "cruel bind" to assume brood care

Table 3
The fate in the following year (1995) of purple sandpipers manipulated in the mate-removal experiment

Males		Females		Both sexes		In relation to previous year:	
Sighted in study area	Kept territory	Sighted in study area	Kept territory	Nested	Kept mate	Clutch size	Hatching date
Female-removal Nests ($n = 4$)							
Yes	Yes	Yes	Yes	Yes	Yes	Same	(Predated)
Yes	—	No	—	—	—	—	—
Male-removal Nests ($n = 8$)							
Yes	Yes	Yes	Yes	Yes	Yes	Same	−4 Days
Yes	Yes	Yes	Yes	Yes	Yes	Same	−7 Days
Yes	Yes	Yes	—	Probably	—	—	—
No	—	Yes	Yes	—	—	—	—
Yes	Yes	No	—	Probably	—	—	—
Yes	—	No	—	—	—	—	—

Return rates are a minimum as the search intensity was much lower than in 1995. Four manipulated nests are not given because neither pair member was resighted. Dashed lines indicate where data were not obtained.

alone. Nor did the quality of brood care differ obviously between the sexes as a result of physiological stress or differences in parental capability. If such a difference exists, it must be small and a much larger sample size needed to detect it.

Although there has been some criticism of the "stressed female" hypothesis (Erckmann 1983), it has received considerable support (Graul et al. 1977; Ashkenazie and Safriel 1979; Lenington 1980; Myers 1981; Brunton 1988; Gratto-Trevor 1991; Székely and Williams 1995) but also criticism (Erckmann 1983). Maynard Smith (1977) assumed that if the ESS is for one parent to desert, it usually is the female, because her investment in the clutch makes her less able to care for the young than the male. In the semipalmated sandpiper, Arctic resources are thought to be more limiting for breeding females (Gratto-Trevor 1991), who are energetically stressed by the end of incubation (Ashkenazie and Safriel 1979); stresses from egg laying may have caused their observed higher mortality (Gratto-Trevor 1991). By departing early, females avoid further mortality risks and increase their chances of survival to subsequent seasons (Ashkenazie and Safriel 1979; Gratto-Trevor 1991). Székely and Williams (1995) found no support for this hypothesis in a study on female brood desertion in the temperate kentish plover (*Charadrius alexandrinus*) but predicted that the advantage might be particularly important among Arctic shorebirds. Our results, albeit low sample sizes, do not support this hypothesis (or our Prediction 2), because females were physically able to assume brood care and did not seem to be stressed from brood care duties during that season or the next. However, purple sandpipers are long lived (i.e., breed for 7 years or more; Pierce EP, unpublished data), and small reductions in lifetime expectancy and/or chick survival rate may lower a female's lifetime RS, thus providing sufficient selection pressure for male brood care to evolve. An ideal test of the "stressed female" hypothesis, although extremely difficult, is to compare the lifetime RS of deserted and unmanipulated females.

Males are thought to assume greater brood care as an investment if it increases the likelihood of female survival and of the pair reuniting the following year (Gratto-Trevor 1991). Regardless of survival, males could benefit simply if assuming brood care increased the likelihood that females remated with "them," and if reuniting facilitated pair formation and earlier nesting. Several studies have shown that mate-faithful pairs gain greater breeding success than newly formed ones (e.g., Coulson 1966, Choudhury 1995). In the purple sandpiper and semipalmated sandpiper, birds showed relatively high rates of return and of mate fidelity, and reuniting or older pairs were found to lay clutches significantly earlier than new or younger pairs (Gratto-Trevor 1991; Pierce 1997b). However, at least some experimental females in this study returned and reunited with their "deserting" mate, with similar laying dates as the previous year.

Of avian species with biparental incubation, only a relatively small number also show strict uniparental brood care, which is often considered to be correlated with additional mating opportunities gained by the deserting sex. The purple sandpiper represents an intriguing case, because females almost always desert at hatching. Yet in Svalbard, they breed only once per season, with very rare exceptions of renesting after a failed attempt (Pierce 1997a). Thus, it appears that neither sex can gain desertion benefits through additional matings. Rather, uniparental brood care may be selected for by predation. Because the purple sandpipers' tundra breeding habitat is extremely open with low vegetation cover (<6 cm), biparental broods run a greater risk of detection by predators than uniparental broods (cf. Pitelka et al. 1974).

How can we explain why males assume brood care and females desert and not vice versa? The behavioral mechanisms underlying female brood desertion may provide some important insights. For example, a few males observed after hatching simply ceased sharing parental duties and even showed some aggression toward the female (Pierce EP, unpublished data). Unmanipulated females showed parental behaviors when alone near newly hatched broods and also while the male attended. One removed female showed strong parental care drive when she flew 6 km back to the brood with the primaries of one wing clipped. This evidence suggests that females may not desert willingly but are, in fact, physically excluded from the brood by males. Hence, the sexual conflict seems to be over uniparental brood care (which must be more advantageous than biparental), not desertion. Desertion is simply a consequence for the loser (the female). This may be analogous to the classical territory owner–intruder contest, where a stable outcome is set by a conventional rule "the resident always wins" (Davies 1978). Further, game theory models predict that such contests, that is, male versus female brood care, can be settled by arbitrary cues to the benefit of both contestants (Maynard Smith and Parker 1976), cues with little bearing on cost–benefit asymmetries between the sexes. Such a cue in purple sandpipers could be an asymmetry in territory ownership (females are attracted to male territories).

Alternatively, the brood care conflict may be settled by a conventional rule: asymmetry in territory benefits. Male purple sandpipers are highly territorial, to some extent also during brooding. Prolonged territory residence may enhance male RS if it serves to 1) retain a mate, because females are highly site faithful, regardless of the male (Pierce 1997b); 2) advertise for future mates in case of female mortality, and/or 3) exclude competitors from nest and foraging resources important to both adults and young. Because clutches are laid over 45 days, late breeders may attempt to encroach the territory. Males, who chase such intruders away during brooding (Pierce EP, unpublished data), remained on the territory on average 17 days after hatching (Pierce 1997b), whereas brooding females left much sooner. Males also remain on the territory at length after clutch loss, even though renesting is extremely rare (Pierce 1997b). Males therefore may gain more from uniparental care than females because of both present and future reproductive events (Gross and Sargent 1985). That males possibly reap benefits via uniparental brooding deserves further exploration.

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