

## NATAL PHILOPATRY AND APPARENT SURVIVAL OF JUVENILE SEMIPALMATED PLOVERS

ERICA NOL,<sup>1,3</sup> SIMONE WILLIAMS,<sup>1</sup> AND BRETT K. SANDERCOCK<sup>2</sup>

**ABSTRACT.**—Natal philopatry is rare in long-distance migrant shorebirds and requires long-term population studies to detect. We report on the rate of natal philopatry from a 18-year study of Semipalmated Plovers (*Charadrius semipalmatus*) marked as hatchlings to an arctic breeding site near Churchill, Manitoba. About 2% (27/1271) of banded hatchlings returned to the Churchill area to breed. There was no male/female bias in rates of philopatry: 17 male and 10 female hatchlings recruited into the local breeding population. The annual rate of recruitment of hatchlings varied between 0 and 10.7%. Age of first encounter on breeding areas ranged from 1 to 8 years (median age 4) suggesting either unusually delayed age at first breeding, or low detection rates for philopatric hatchlings. The maximum age of a recruited (known-age) hatchling was 9 years. Natal dispersal distances did not differ between males and females, and averaged 5 km between hatching and breeding locations. We used a time-since-marking mark-recapture model to calculate apparent survival of hatchlings. Apparent survival in the interval after first capture was  $\phi_1 = 0.0475$  (95% CI: 0.030–0.075), whereas apparent survival ( $\phi_{2+}$ ) of birds during subsequent intervals was 0.866 (95% CI: 0.764–0.927). Low rates of natal philopatry suggest little advantage to site familiarity for juveniles, and agree with theoretical predictions for migratory species with widespread habitat availability. Received 15 June 2009. Accepted 7 October 2009.

Natal philopatry is rare in long-distance migrant birds and requires either long-term population studies or large sample sizes to detect (Thompson and Hale 1989, Renner and McCaffery 2008). Using known-age birds in survival analyses avoids the complications of assuming age of first breeding in population viability analyses and, with sufficiently large sample sizes, allows precise estimates of age-specific survival (Sidhu et al. 2007), probability of breeding (Sedinger et al. 2001, 2008), and life-expectancy (Lavers et al. 2007). Analyzing natal philopatry can also help evaluate hypotheses about the adaptive significance of gender bias in natal dispersal rates and distances (Greenwood and Harvey 1982, Weatherhead and Forbes 1994, Sutherland et al. 2000).

Studies of arctic-breeding birds are disadvantaged in documenting natal philopatry and dispersal because of inaccessibility of breeding areas and low encounter probabilities (Renner and McCaffery 2008). Possibly as a consequence, studies of temperate breeding shorebirds typically report higher rates of encounter of breeding juveniles, especially if the species is of conservation concern (e.g., *Charadrius alexandrinus* and *C. melodus*; Larson et al. 2000, Colwell et al. 2007b, Stenzel et al. 2007).

The Semipalmated Plover (*C. semipalmatus*) has been the subject of an 18-year population study near Churchill, Manitoba. This small shorebird breeds in open gravel, tundra, beaches, and riverbeds throughout the sub-arctic regions of North America (Nol and Blanken 1999). Semipalmated Plovers migrate long distances from sub-arctic breeding areas to a large, dispersed wintering range that spans coastal areas of the southern United States, Mexico, Central America, and northern and central South America. Unlike many *Charadrius* plovers, there is currently no evidence to suggest this species is declining (Morrison et al. 2006, Bart et al. 2007). An earlier study of this species suggested low rates of natal philopatry and no gender bias in these rates (Flynn et al. 1999). Our objectives are to: (1) update knowledge of these factors, (2) evaluate natal dispersal distances, and (3) estimate apparent juvenile and adult survival based on a known-age sample. We also estimate the earliest age of first breeding and report on a longevity record based on a known-age hatchling.

### METHODS

**Study Sites and Species.**—Field work was conducted each year from the beginning of June to mid-August in 18 years including 1988 and 1992 to 2008. We regularly searched 11 major breeding sites in the area south and east of Churchill, Manitoba, Canada (58° 45' N, 95° 04' W), spanning ~ 20 km of coastal beaches and two inland sites in an area of 34.2 km<sup>2</sup> (Fig. 1). Each field season, researchers walked

<sup>1</sup>Biology Department, Trent University, Peterborough, ON, K9J 7B8, Canada.

<sup>2</sup>Division of Biology, Kansas State University, Manhattan, KS 66506, USA.

<sup>3</sup>Corresponding author; e-mail: enol@trentu.ca

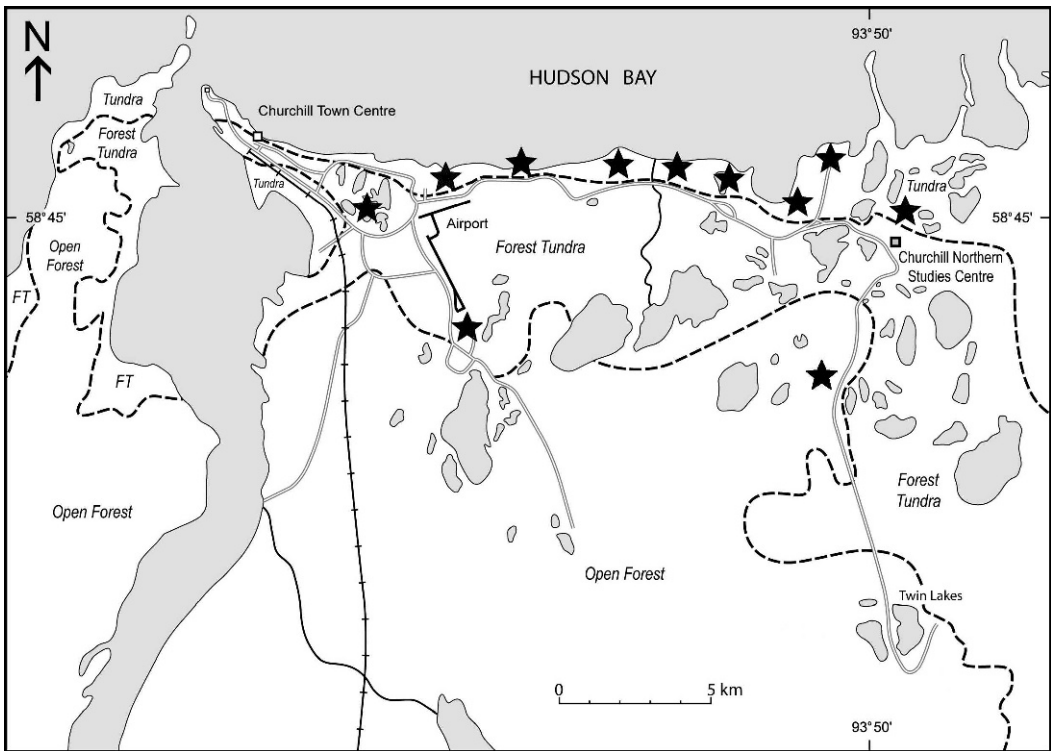


FIG. 1. Churchill, Manitoba area showing the 11 major study sites (★).

potential nesting areas in search of Semipalmated Plovers. The nests of Semipalmated Plovers in 1988 and from 1992 to 2000 were assigned identification (ID) numbers sequentially as they were found within the 11 areas, and locations of nests were drawn on field maps and aerial photos. Nests of Semipalmated Plovers were assigned ID numbers from 2001 to 2008 and the locations were recorded using a Global Positioning System (GPS). In early June, observers searched for previously banded Semipalmated Plovers and recorded the band combinations of color-marked birds using 20–40 X spotting scopes. Any nesting Semipalmated Plovers that were unbanded, or needed clarification of identification (e.g., faded color bands) were captured using circular walk-in traps with a keyhole entrance, made of hardware cloth, that were placed over the nest. Once adults were captured, they were banded with an aluminum band and given a unique color combination of bands or faded color and aluminum bands were replaced. Gender of adults was assigned using the number of brown feathers in the crown and supercilium with females having more brown feathers than males (Teather and Nol

1997). Gender assignments were confirmed by behavioral postures with males using display flights or mounting females during copulations.

Chicks were banded in the nest with unique aluminum bands and, depending on the year of study, with either brood-specific or individual color band combinations.

*Statistical Analysis.*—We assigned the location of the natal site as the UTM of the center of one of the 11 nesting areas for older nest and banding records without reliable GPS locations (in years prior to 2000) (Fig. 1), and the location of the first breeding site as the UTM of the center of the site at which we first encountered them breeding. We used a binomial test to examine whether there was a bias in the gender of returning hatchlings, and *t*-tests to compare natal dispersal distances of males and females.

We used a two-stage ‘time-since-marking’ model for live encounter data using Program MARK to calculate annual probabilities of apparent survival ( $\phi$ ) and encounter (*p*). The time-since-marking model separates apparent survival in the first interval after capture ( $\phi_1$ ) from apparent survival in subsequent intervals

( $\phi_{2+}$ ) (Larson et al. 2000). We modeled apparent survival as a function of year of marking and gender because these factors are important in other plovers (Larson et al. 2000), and treated the encounter rate as a nuisance parameter. We tested for possible overdispersion before testing reduced models by using the median  $\hat{c}$  procedure to calculate a variance inflation factor for the global starting model (Cooch and White 2004).

### RESULTS

Twenty-seven of 1,271 (2.1%) banded hatchlings from 1988 to 2008 returned to breed in the Churchill area. Rates of return were low in all years, but reached 10% in 2000 and 2001 (Table 1). Ten local females and 17 males recruited into the breeding population, a ratio that was not significantly different than 1:1 (Binomial test,  $P = 0.09$ ). The age ( $\pm$ SE) at which birds were first encountered breeding ranged widely from 1 to 8 years (median 4 years) and did not differ between males and females (males:  $3.9 \pm 0.4$  years, females:  $4.2 \pm 0.6$  years;  $t = 0.38$ ,  $P = 0.65$ ). The maximum age of a recruited (known-age) hatchling was 9 years. The distance ( $\pm$ SE) between natal sites and nesting sites where we first encountered philopatric individuals did not differ between males and females (males:  $5.8 \pm 1.4$  km, median = 4.2 km, range: 0.7 to 12.6 km,  $n = 11$ ; females:  $3.7 \pm 1.8$  km, median = 0.8 km, range: 0.3 to 12.7 km,  $n = 7$ ;  $t = 0.93$ ,  $P = 0.37$ ).

Our estimate of  $\hat{c}$  for the global model indicated there was little evidence of overdispersion ( $\hat{c} < 1$ ), and we set the variance inflation factor to  $\hat{c} = 1$  and used AIC<sub>c</sub> for model selection. The minimum AIC<sub>c</sub> model for the survival analysis from Program MARK included two capture periods for apparent survival ( $\phi$ ) and a constant encounter rate ( $p$ ). Apparent survival in the first interval after capture ( $\phi_1$ ) was 0.048 (95% CI: 0.030–0.075), whereas survival ( $\phi_{2+}$ ) for birds during subsequent capture periods was 0.866 (95% CI: 0.764–0.927). Encounter probabilities ( $p$ ) were relatively low, 0.174 (95% CI: 0.113–0.230). The next best model included a time effect for encounter probabilities but was 28.8 AIC<sub>c</sub> units from the top model and received no weight relative to the top model ( $w_1 < 0.01$ ).

### DISCUSSION

The frequency of returning Semipalmated Plovers marked as hatchlings is among the lowest reported for shorebirds (Thompson and Hale

TABLE 1. Number of newly banded Semipalmated Plover chicks per year and number of new adult recruits from that year's cohort.

Year	Newly banded chicks	Min. number of recruits from cohort (%)
1988	57	1 (1.75)
1992	31	0 (0)
1993	87	3 (3.44)
1994	92	1 (1.08)
1995	81	1 (1.23)
1996	106	2 (1.89)
1997	75	2 (2.67)
1998	58	2 (3.45)
1999	25	0 (0)
2000	28	3 (10.70)
2001	38	4 (10.50)
2002	44	1 (2.27)
2003	94	1 (1.06)
2004	50	2 (4.00)
2005	105	2 (1.90)
2006	103	0 (0)
2007	122	0 (0)
2008	75	0 (0)

1989, Flynn et al. 1999). Our estimate was similar to an earlier estimate from the same study area using observation data for returning juveniles from 1988 to 1996 (1.57%,  $n = 455$ , Flynn et al. 1999) despite a sample size that has nearly tripled. Our hatchlings were banded within 48 hrs of hatching, and low rates may be due to high mortality in the period after hatching when young are unable to thermoregulate or fly, and are vulnerable to inclement weather conditions and predators (Thompson and Hale 1989, Flynn et al. 1999, Sandercock et al. 2005, Colwell et al. 2007a). Our survival estimates obtained for the first sample period were also low compared to that reported for the temperate congeners: Piping Plover (*C. melodus*) and Snowy/Kentish Plover (*C. a. alexandrinus*) (survival from hatching to the following year,  $\phi = 0.15$ , Sandercock et al. 2005;  $\phi = 0.18$  for true survival of *C. a. nivosus*, Stenzel et al. 2007;  $\phi = 0.32$  for *C. melodus* banded as juveniles  $\geq 16$  days of age, Larson et al. 2000). Predator control can reduce mortality of hatchlings for both temperate North American species (Stenzel et al. 2007). However, large differences between these rates and those of Semipalmated Plovers may also be due to greater permanent emigration (through greater natal dispersal) from the Churchill study area, rather than lower survival, because this population of Semipalmated Plovers appeared to be stable over the study

period (E. Nol, unpubl. data) and otherwise could probably not sustain mortality of this magnitude. The difference between these survival rates among congeners also mirrors that seen in comparing natal philopatry and dispersal rates between migratory and resident passerines (Weatherhead and Forbes 1994, Sutherland et al. 2000). Lower rates of natal philopatry in long-distance migrants like Semipalmated Plovers may be due to dispersal costs accrued when they migrate south and relinquish familiarity with their natal area. It may only be important to find similar, but not necessarily familiar habitat when they return to breed (Weatherhead and Forbes 1994).

There was substantial variability in number of recruits into the breeding season among hatchling cohorts, but a model of survival with time-dependence was not supported. A similar absence of time effects was also found for Kentish Plover in southern Turkey (Sandercock et al. 2005) and, in both cases, may have been due to sparse data with low numbers of philopatric young. Alternatively, variation in the number of recruiting individuals may be more common when resources for breeding birds fluctuate widely (e.g., Black-throated Blue Warbler, *Dendroica caerulescens*; Rodenhouse et al. 2003) or where interference competition results in exclusion of potential recruits (Arcese et al. 1992). Low fecundity of arctic-breeding shorebirds may keep populations below the carrying capacity of breeding areas (Piersma and Baker 2000), but as yet we know little about the possible role of density-dependence in this group of birds.

Territorial shorebirds are often assumed to have male-biased natal philopatry (reviewed in Colwell et al. 2007b) because of a resource-defense mating system (Greenwood 1980). However, bias towards philopatric recruiting juvenile males, where it occurs, is usually small (Gratto et al. 1985, Reed and Oring 1993, Colwell et al. 2007b, Stenzel et al. 2007; but see Redmond and Jenni 1982). The advantages of familiarity with the natal site should be approximately equal for males and females of monogamous, bi-parental incubating species. Female Snowy Plovers share in incubation duties but typically desert the brood and, at times, re-nest with other males (Page et al. 1995). In this species, where females are presumed to have a relatively low attachment to the territory, the return rate of juvenile females to the local study area to breed is only 12% lower than for juvenile

males, but still 64% (Stenzel et al. 2007). This difference reversed in winter with juvenile males more likely to disperse (54%) from wintering areas than juvenile females (44%). Thus, a re-evaluation of the theoretical basis for gender-biased natal dispersal in birds is probably needed (Redmond and Jenni 1982, Sutherland et al. 2000).

Most Semipalmated Plovers appear to delay breeding beyond 1 year although, contrary to the results from the previous study on this species (Flynn et al. 1999), at least one male bred in its first year. Delayed age at maturity differs from other studies of migratory shorebirds, where most individuals attempt to breed in their first year (reviewed in Sandercock et al. 2005). This suggests that a large proportion of the Churchill population may over-summer on wintering areas (e.g., McNeil et al. 1994), similar to reports for three species of calidridine sandpipers in Africa and Central America (Summers et al. 1995, O'Hara et al. 2002).

The precise age of first breeding is difficult to ascertain because numbers of philopatric young were low and re-encounter probabilities of banded hatchlings are low (Sandercock et al. 2005). Age-specific variation in breeding propensity with higher rates of philopatry can be estimated with robust design models (Sedinger et al. 2001, 2008), but our data were not adequate for this approach. Most hatchlings were banded with an aluminum band and a single color band. Band loss and color fading after 3–4 years reduces the probability of observing these individuals if breeding in the Churchill study area. That two hatchlings were not detected in the local breeding population until the age of 8 years strongly suggests that some birds are temporarily leaving the population and then returning. In another study of this species on Akimiski Island, Nunavut, a breeding male underwent a long-distance (30 km) dispersal event. This also suggests, that despite generally greater nest site tenacity by males than females (Flynn et al. 1999, Lishman et al. in prep), males can and will disperse between breeding attempts in the same or different years. These difficult to document movements will continue to result in lower estimates of adult and juvenile survival for shorebirds breeding in mostly inaccessible habitats across the North American arctic, and reaffirm the importance of scale of the study area for documenting dispersal events (Greenwood and Harvey 1982, Jackson 1994, Sandercock and

Gratto-Trevor 1997, Colwell et al. 2007b, Stenzel et al. 2007).

Apparent survival estimates for philopatric individuals at intervals after the first return were high, and much higher than previous estimates from an adult sample from this population (Badzinski 2000; adult estimate of 0.71, CI: 0.64–0.78). Estimates of apparent survival for birds marked as adults may include first-time breeders of a wider range of ages that have lower survival rates. Alternatively, philopatric individuals may have higher site fidelity as adults than individuals that immigrate into our study sites as adults. Variation in individual strategies for space use have been reported for wintering Grey Plovers (*Pluvialis squatarola*), where individuals are either territorial or non-territorial, and do not change strategies during their lifetime (Turpie 1995). Our mean estimate of apparent adult survival is also higher than reported for the congeners Piping Plover (Larson et al. 2000,  $s = 0.77$  for known-age juveniles), Snowy Plover ( $s = 0.69$ , Stenzel et al. 2007), and Kentish Plover ( $s = 0.58$ , Sandercock et al. 2005). Similarly, survival rates of known-age Pacific Golden Plovers (*Pluvialis fulva*; territorial:  $s = 0.90$ , non-territorial,  $s = 0.82$ ) were 10–15% higher than those from a sample of unknown-age adults (territorial,  $s = 0.80$ , non-territorial,  $s = 0.67$ , Johnson et al. 2001). Variation in individual strategies for space use and apparent differences in age of first reproduction invite further research on the demography of short- versus long-distance migrant shorebirds to identify possible trade-offs in life history strategies, and to evaluate the consequences of life-history variation for planning conservation efforts.

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