

**POPULATION DYNAMICS OF SEMIPALMATED PLOVERS (*CHARADRIUS*
SEMIPALMATUS) BREEDING AT CHURCHILL, MANITOBA.**

A Thesis Submitted to the Committee in Graduate Studies
in partial Fulfillment of the Requirements for the
Degree of Master of Science
in the Faculty of Arts and Science

TRENT UNIVERSITY
Peterborough, Ontario, Canada

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ABSTRACT

POPULATION DYNAMICS OF SEMIPALMATED PLOVERS (*CHARADRIUS SEMIPALMATUS*) BREEDING AT CHURCHILL, MANITOBA.

Debra. S. Badzinski

This thesis describes the population dynamics of breeding Semipalmated Plovers (*Charadrius semipalmatus*) at Churchill, Manitoba. The objectives of this study were: (1) estimate rates of local survival and fecundity, (2) identify factors affecting survival and fecundity and (3) estimate population growth rate (λ) and determine sensitivity of λ to changes in demographic parameters. Local survival rates were not sex specific but there was significant annual variation that was correlated with hatching success. All reproductive parameters except fledging success, showed significant annual variation. Previous breeding experience affected fledging success, but not hatching success. Pairs with an experienced male fledged more chicks than did all other pairs, but female experience did not affect reproductive success. Population growth rate ($\lambda=0.846\pm0.046$) was most sensitive to changes in adult survival, juvenile post-fledging survival and pre-fledging survival. The model predicted a population decline of more than 15%, but annual population censuses showed no population change.

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CHAPTER 1

GENERAL INTRODUCTION

BACKGROUND

Animal populations fluctuate because of the addition of individuals by recruitment and immigration and the loss of individuals through mortality and emigration. An understanding of the extent to which demographic parameters are influenced by biotic and abiotic factors is of critical importance for studies of population demography as well as for understanding evolution of life-histories (Lebreton et al. 1992). Many different factors that operate either extrinsically (e.g., environment) or intrinsically (e.g., density dependence) to the population may induce temporal variation in population size (Lima and Jasic 1999). Environmental variation is both temporally and spatially unpredictable and results in fluctuations in population size when environmental variables affect survival and reproductive rates or immigration and emigration (Akçakaya et al. 1999). Several studies have found that environmental variables, such as temperature and rainfall, directly affect bird population dynamics (Peach et al. 1991, Thompson and Thompson 1991, Peach et al. 1994, Insley et al. 1997, Yalden and Pearce-Higgins 1997, Schekkerman et al. 1998). Although difficult to detect and quantify in natural populations, intrinsic population processes operating in a density-dependent manner (e.g., crowding, competition) also may cause fluctuations in population size through suppression of survival or reproductive rates (McCallum 2000).

In most species, breeding success and survival are the two most important life history traits because they exert the greatest influence on population size. The manner in which these two life-history traits combine to optimize fitness differs among species (Oro et al. 1999). For example, shorebirds typically have low fecundity, and high adult survival probabilities (Evans and Pienkowski 1984, Evans 1991, Hitchcock and Gratto-Trevor 1997, Sandercock and Gratto-Trevor 1997). Shorebird reproductive success tends to fluctuate highly among years (Evans and Pienkowski 1984). Annual variation in several components of shorebird reproductive success, including probability of breeding (Gratto-Trevor 1991), clutch size (Nol et al. 1997), viability of eggs (Tomkovich 1995), hatching success (Knopf 1996), pre-fledging growth rates (Schekkerman et al. 1998), and pre-fledging survival (Schekkerman et al. 1998, Knopf and Rupert 1996) have been attributed to annual variation in weather conditions on breeding grounds. Most among year variation in shorebird reproductive success, however, results from variation in nest predation rates (Parr 1980, Evans and Pienkowski 1984, Haig 1992, Warriner and Paton 1995).

Unlike reproductive success, shorebird survival rates are apparently not influenced by weather conditions on the breeding grounds because species with high probability of survival tend to forego breeding during unfavourable conditions instead of jeopardizing future survival (Sandercock and Gratto-Trevor 1997). Weather conditions on the wintering grounds, however, significantly affect shorebird local survival rates (Holland and Yalden 1991, Peach et al. 1994, Insley et al. 1997). This is because environmental factors such as temperature, precipitation and wind affect the availability and distribution of invertebrate prey (Pienkowski 1983, Evans and Pienkowski 1984),

which then may affect shorebird survival rates and consequently population size. Furthermore, high densities of shorebirds on wintering grounds may result in increased intra- and interspecific competition for food that may further exacerbate weather related effects.

Several studies have found a relationship between shorebird population size and extrinsic factors (e.g., unfavourable weather conditions), which increase wintering ground mortality and suppress or prevent reproduction on breeding grounds, but few have found a relationship between population size and density-dependent factors (Evans and Pienkowski 1984). However, Yalden and Pearce-Higgins (1997) found that although the population size of Golden Plovers (*Pluvialis apricaria*) was influenced by winter weather, density dependent factors during the previous year explained more variation in the population's growth rate. There also is evidence to suggest that other aspects of shorebird demography, including foraging rates (Goss-Custard 1980), territory acquisition (Harris 1970, Holmes 1970), and nest predation rates (Page et al. 1983) are affected by population density.

Because fluctuations in local population size result from interactions between different population factors, identification of biotic and abiotic factors influencing survival and reproductive success are critical for understanding bird population dynamics (Lebreton et al. 1992). With a basic understanding of a species' life-history, population models can be developed and then used to assess the relative impact of varying rates of survival and fecundity on population growth and size as well as to ascertain the most important life-history parameters. Population models also can be used to investigate population change over time, interaction of populations with their environment and

probability of population increase or decrease. Development of a realistic population model for any species depends upon obtaining accurate estimates of several essential demographic parameters such as survival rates, age at first breeding, fecundity and immigration.

A population of Semipalmated Plovers (*Charadrius semipalmatus*) breeding at Churchill, Manitoba has been studied since 1987, and as such, contributes one of the longest-term studies of small nearctic shorebirds. During each breeding season, Semipalmated Plover breeding success was monitored and birds were colour banded to permit identification of individual birds and to estimate local survival rates. Information was also collected on reproductive ecology, behaviour and energetics. In this thesis I used demographic data from 1992-1998, the years with most complete colour-banding and nest monitoring, to describe the population dynamics of Semipalmated Plovers.

STUDY SPECIES

Semipalmated Plovers are small shorebirds that breed in sub-arctic and arctic regions of North America, and winter in coastal areas of the southern United States, central, and South America (Nol and Blanken 1999). Nesting habitat is characterized by sparsely vegetated areas such as coastal mudflats, outcrop ridges and gravel ridges (Flynn 1997). Semipalmated Plovers are monogamous within a breeding season, and more than 50% of pairs are monogamous between breeding seasons (Flynn et al. 1999). Because unpaired males are rarely observed on breeding grounds, an equal sex ratio is assumed in the Churchill study population (Nol and Blanken 1999). Extra-pair paternity is rare and

intra-specific brood parasitism has never been observed in this species (Zharikov and Nol 2000).

Male Semipalmated Plovers are territorial, and in the spring settle on breeding territories earlier than do females (Flynn et al. 1999). Once females arrive, pair bonding occurs and nest construction begins. In sub-arctic regions, most egg laying occurs in the first week of June and most young fledge by early August. Clutch size is typically four eggs, but females occasionally lay reduced clutches with two or three eggs. .

Semipalmated Plovers are determinate layers, clutches containing more than four eggs have never been found. Due to short sub-arctic breeding seasons, Semipalmated Plovers are only able to rear one brood per season, and there is little opportunity to re-nest following depredation of their first clutch. Males and females share equally in incubation; while one parent incubates, the other forages nearby at coastal mudflats or inland ponds.

The average incubation period is 24 days, and eggs usually hatch within 24 hours after pipping (when the chick breaks through the eggshell) (Nol and Blanken 1999). Parents lead their precocial chicks to nearby mudflats or ponds to forage soon after hatch. Semipalmated Plovers exhibit biparental care; parental duties include leading chicks to suitable foraging areas, brooding chicks, and warning chicks of predators. Females abandon their mates and broods approximately one to two weeks after hatch, but males remain with their brood until fledging (Nol and Blanken 1999).

Semipalmated Plovers are unusual among plovers in that breeding is apparently delayed until two, or, more commonly, three years of age (Flynn et al. 1999). Other

plover species of similar size, about 45 g (e.g., Ringed Plover (*Charadrius hiaticula*), Piping Plover (*Charadrius melodus*), Snowy Plover (*Charadrius alexandrinus*)) begin breeding at one year of age (Pienkowski 1984, Wilcox 1959, Page et al. 1995). Adult philopatry (tendency to return to same breeding site in subsequent years) in Semipalmated Plovers is relatively high but natal philopatry is among the lowest reported for shorebirds (less than 2% of birds banded as chicks return to breed) (Flynn et al. 1999). Males are more site tenacious than are females. Females are less likely to return to the same territory if they experienced breeding failure in the previous year, but males typically return to the same territory year after year regardless of previous breeding success (Flynn et al. 1999).

STUDY OBJECTIVES

My first objective was to estimate local survival rates for adult Semipalmated Plovers breeding at Churchill, Manitoba based on resightings of colour-marked birds from 1992-1998. My second objective was to identify biotic and abiotic factors that influence local survival rates. To accomplish these objectives, I determined (in Chapter 2):

1. if local survival probabilities are correlated with environmental variables such as temperature and precipitation, or with breeding success
2. if Semipalmated Plover local survival rates are time, sex and/or age specific.

My objectives for the study of Semipalmated Plover reproductive success (Chapter 3) were to determine whether there was significant annual variation in several reproductive parameters (clutch size, hatching success, hatchability, nest predation and

fledging success) and to test the hypothesis that breeding experience influences reproductive success. Based on an accumulation of studies documenting the importance of age and experience to breeding in birds, I predicted that experienced individuals would hatch more eggs, fledge more chicks, and nest earlier in the season than would inexperienced birds.

Finally, by using matrix-modelling techniques, I constructed a model to calculate the growth rate of the Semipalmated Plover population (Chapter 4). The model incorporated several life-history parameters, including reproductive success, adult and juvenile local survival rate, and breeding propensity. I also performed a sensitivity analysis to explore the effect of each demographic factor on the population growth rate.

STUDY AREA

The study area was located at Churchill, Manitoba (58° 45' N, 95° 04' W) (Figure 1.1) on the West Coast of Hudson Bay. The study area encompassed 384 km², but only about one quarter of this area was considered suitable nesting habitat (Flynn et al. 1999). Semipalmated Plovers reach their highest nest densities at or near the coast, but nest at low densities up to 16 km inland (E. Nol pers. comm.). Coastal nest sites are characterized by open gravel and shale areas surrounded by small patches of low-lying willow (*Salix* spp.) and birch (*Betula* spp.). Inland nesting sites, however, have lower visibility due to the presence of willows, birches, white spruce (*Picea glauca*), and tamarack (*Larix laricina*) around the gravel nesting sites (Sullivan Blanken and Nol 1998). Although most Semipalmated Plovers nest on gravel areas or directly on the tundra, they occasionally nest on mudflats, or near the boreal forest edge.

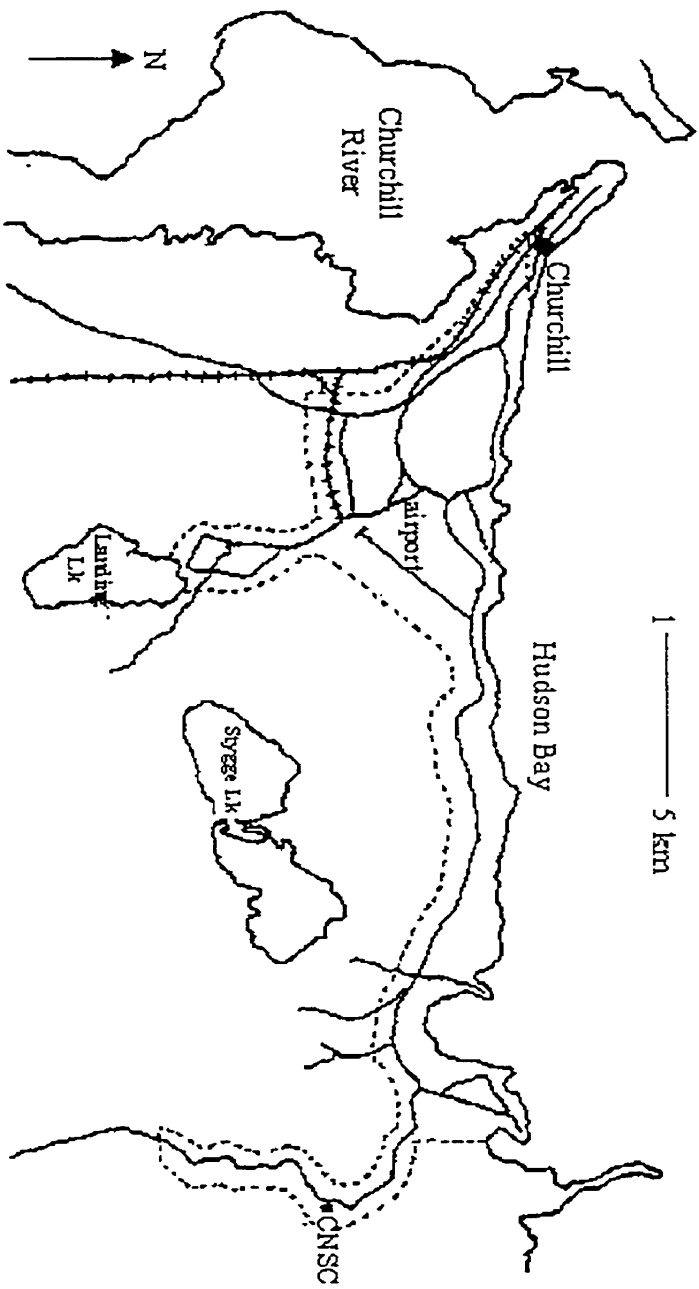


Figure 1.1 – Map of Churchill, Manitoba, with the study area indicated by the dashed line.

CHAPTER 2

FACTORS INFLUENCING LOCAL SURVIVAL OF SEMIPALMATED PLOVERS (*CHARADRIUS SEMIPALMATUS*) BREEDING AT CHURCHILL, MANITOBA.

ABSTRACT

Local survival of breeding adult Semipalmated Plovers (*Charadrius semipalmatus*) was estimated from the resighting of colour-banded adults (males: $N=142$; females: $N=152$) at Churchill, Manitoba from 1992 to 1998. SURGE was used to calculate survival and resighting probabilities and to determine whether survival was correlated with annual conditions on the breeding grounds. Male Semipalmated Plovers had significantly higher resighting rates (0.85) than did females (0.64), either because females are more likely to temporarily emigrate, or more likely to forego breeding and remain on wintering grounds than are males. Similar to other shorebird species, male and female local survival rates did not differ. The most parsimonious survival model (with the lowest Akaike's Information Criterion) contained two relative age classes in which survival of newly banded birds was separated from that of previously banded birds. Overall, the constant local survival rate of adult Semipalmated Plovers was 0.71, but there was significant annual variation. Annual variation in survival was not correlated with mean date of clutch completion, or mean temperature on the breeding grounds, but was correlated with hatching success (mean number of eggs hatched/nesting attempt).

INTRODUCTION

To understand a species' population ecology, it is necessary to identify the intrinsic and extrinsic factors that are associated with annual changes in survival and fecundity. Survival rates of birds may vary with age (Botkin and Miller 1974, Kus et al. 1984, Loery et al. 1987, Kanyamibwa et al. 1990, Francis et al. 1992, Blums et al. 1996, Cézilly et al. 1996, Insley et al. 1997, Warnock et al. 1997), sex (Cézilly et al. 1996, Sandercock and Gratto-Trevor 1997), reproductive status (Francis et al. 1992), and physical condition (Aebischer and Coulson 1990), and at the population level survival rates often exhibit marked temporal variation. Biotic factors (e.g., population density, competition, and predation rates), and abiotic factors (e.g., climatic variables) may also influence survival probabilities (Lebreton et al. 1992). Climatic variables such as temperature, precipitation and wind directly affect the abundance and distribution of food resources, which may in turn affect survival of birds (Pienkowski 1983, Evans and Pienkowski 1984, Yalden and Pearce-Higgins 1997). Determination of factors that influence a species' survival and the derivation of precise, unbiased survival estimates are both crucial to understanding the dynamics of animal populations (Lebreton et al. 1992).

Long-term studies show most shorebirds have a life-history strategy that includes low reproductive output, high annual survival rates and delayed age at first breeding (Skagen and Knopf 1993, Thompson and Hale 1993, Sandercock and Gratto-Trevor 1997, Warnock et al 1997). Most smaller shorebird species breed for the first time at one or two years of age, but larger species may delay breeding for up to five years (Evans and Pienkowski 1984, Marks and Redmond 1996). Most arctic nesting shorebirds lay a four

egg clutch and there is little among and within year variation in clutch size (Evans 1991, Székely et al. 1994, Nol et al. 1997). Hatching success of shorebird nests is stochastic, fluctuating among years in response to climatic variables and predation rates.

Furthermore, because of short breeding seasons, arctic and subarctic breeding shorebirds rarely have an opportunity to renest following depredation of their first clutch, and in years of late snow melt or inclement weather may forego breeding altogether (Evans and Pienkowski 1984, Nol et al. 1997).

Shorebird populations are typically characterized by unpredictable breeding performance, high mortality in their first year of life, low reproductive output and high adult survival rates (Evans and Pienkowski 1984, Yalden and Pearce-Higgins 1997). Species with this type of life-history strategy typically have relatively stable populations, but are vulnerable to sudden population declines caused by small increases in adult mortality (Harris and Wanless 1991). For many monogamous shorebird species, there is little difference between male and female survival rates (Oring and Lank 1984, Gratto et al. 1985, Grant 1991, Thompson and Hale 1993), which may be due to equal reproductive investment between the sexes (Brunton 1988).

High elasticity of adult survival is ubiquitous among long-lived vertebrates (e.g., Crouse et al. 1987, Brault and Caswell 1993, Hiraldo et al. 1996, Hitchcock and Gratto-Trevor 1997, Crooks et al. 1998); a relatively small proportional change in this parameter can have a marked effect on population size. Hitchcock and Gratto-Trevor (1997) used demographic matrix modelling techniques to explore possible causes of a population decline in Semipalmated Sandpipers (*Calidris pusilla*) breeding at La Pérouse Bay, Manitoba. The results of their model showed that only increases in adult survival and/or

immigration would have been successful in averting the population decline. Changes in reproductive parameters, including increased chick survival, increased chick production, and lower age at first breeding were ineffective at restoring population growth rate to a stable level (Hitchcock and Gratto-Trevor 1997).

Survival rates of shorebirds are inherently difficult to estimate, primarily because there are few long-term population studies with colour-marked individuals. In addition, most studies have estimated shorebird survival rates by assuming resighting probability was close to one, and equated return rates of colour-banded birds with survival probabilities (e.g., Oring and Lank 1984, Grant 1991, Peach et al. 1994, Flynn et al. 1999 but see Thompson and Hale 1993, Paton 1994, Sandercock and Gratto-Trevor 1997, Warnock et al. 1997). Return rates, however, are the product of true survival rate, degree of site fidelity, temporary emigration, and rate of resighting, so should be used only as minimum estimates of survival. Because changes in survival probabilities can have a large effect on shorebird population size, it is important to obtain accurate survival estimates.

Recent statistical techniques and programs (e.g., SURGE, MARK) used to analyze capture-recapture data produce separate estimates of local survival and recapture rates (Lebreton et al. 1992). Local survival rate estimates produced by this method are the product of true survival rate and rate of local site fidelity; such estimates are an improvement over return rates which potentially underestimate true survival (Sandercock and Gratto-Trevor 1997, Warnock et al. 1997). This method also allows the effects of factors such as sex, age, and climatic variables on survival and resighting rates to be assessed.

The main objective of this study was to calculate annual variation in local survival and resighting rates of adult Semipalmated Plovers (*Charadrius semipalmatus*), a seasonally monogamous shorebird breeding in the Hudson's Bay lowlands near Churchill, Manitoba. I also determined if sex, age class or annual conditions on the breeding grounds influenced survival and/or resighting rates.

METHODS

NEST SEARCHING

All areas with suitable nesting habitat that were accessible by road were searched with equal effort from 1993 to 1997. No vehicle was available in 1992, so the entire study area was not thoroughly searched. This resulted in low banding effort and no accurate estimation of population size. Semipalmated Plovers are determinate layers, clutches containing more than four eggs have never been found. However, females occasionally lay less than four eggs. Semipalmated Plover nests consist of a small scrape on the ground. Nests were located by walking through the study area and sighting adults performing distraction displays, or by observing foraging adults fly to the nest site. All suitable nesting habitats were searched at least twice in June of each year. Because adult Semipalmated Plovers rarely leave their nests unattended, it was unlikely that many nests were undetected using this method.

Most nests (90%) were located during incubation, so eggs were measured and weighed to estimate hatch date based on a regression between the index of specific gravity and the ratio of mass to volume (Flynn 1997). To reduce probability of nest predation, nest locations were either marked at a distance with natural material such as

rock cairns and wood or were mapped. Nests were subsequently monitored every two to four days to determine their fate. To reduce disturbing incubating adults, nests were observed from a distance with a spotting scope. Clutches that disappeared between visits were assumed depredated unless another cause was apparent (e.g., destroyed by tides, trampled by humans, other animals, or motor vehicles). Just prior to estimated hatch date, nests were visited at least daily to check for pipped eggs. Date of clutch completion for each nest was estimated by subtracting 24 days (the mean incubation period) from the hatch date of the nest.

NEST TRAPPING AND BANDING

During incubation, adults were nest-trapped with either a Potter trap or a walk-in keyhole nest trap. The circular walk-in nest trap was constructed from hardware cloth and contained a net top made of either cotton or nylon netting. The square Potter trap was made of 2 mm wire and had a treadle placed over the nestcup that triggered a drop door. To prevent the possibility of nest desertion, birds were not trapped early in the incubation period. Traps were continuously monitored so that birds were removed immediately upon entering, and traps were removed if the adult did not return within 20 minutes. Adult birds were leg-banded with unique combinations of an aluminium Canadian Wildlife Service (CWS) band and 1-3 coloured plastic bands (Size XCL, A.C. Hughes Ltd.). During hatch, chicks were caught by hand and each was banded with an aluminium CWS band and a brood-specific combination of coloured plastic leg bands. Most nestlings were banded one or two days after hatch. Adult plovers were sexed on the

basis of plumage colouration (Teather and Nol 1997), whereas nestlings could not be sexed by plumage.

Every year, a small number of birds were not banded, either because their nest was depredated before they could be trapped or because we were unable to trap certain 'wary' birds. The proportion of unbanded adult birds in the population was small every year (1993-1998, mean unbanded birds in population=12%).

RESIGHTINGS

During each breeding season, colour-banded Semipalmated Plovers were resighted in the field by either having their unique colour-band combination identified with a spotting scope or being recaptured on the nest (hereafter collectively referred to as a 'recapture occasion'). Occasionally, birds were resighted on coastal mudflats and inland ponds but no nest was found. If a colour-band was lost, the individual was recaptured, identified by its CWS band and the colour-bands were replaced.

Semipalmated Plovers are highly site tenacious (Flynn et al.1999), which facilitated the identification of birds that had lost colour-bands. Colour-band loss was infrequent (<5% of birds), and the majority of the individuals that lost colour-bands (>95%) were subsequently re-banded. Therefore, local survival estimates were not likely biased by band loss.

STATISTICAL ANALYSES

SURVIVAL AND RESIGHTING RATES

Survival rates were calculated from resightings of colour-banded Semipalmated Plovers from 1993 to 1998. Capture-histories were constructed for all colour-banded birds, where the first '1' from the left represents the initial banding occasion, and each subsequent digit represents one breeding season from 1992-1998 during which resightings and recaptures occurred (Appendix 1). A zero in the capture history indicates that the bird was either dead, or alive and not resighted that year. Birds banded as nestlings were included in the capture history when they were first observed as a breeding adult.

Analysis of capture histories involved a two-step process following methodology outlined in Lebreton et al. (1992). RELEASE was used to assess goodness-of-fit (GOF) to a Cormack-Jolly-Seber (CJS) model, in which survival and recapture probabilities vary between years, and was applied to each sex separately. The validity of the CJS model depends upon several assumptions being upheld (for detailed description of model assumptions see Pollock 1981, Seber 1986 and Lebreton et al. 1992). The two most important assumptions of the CJS model are that all individuals in the population have the same time-specific survival and recapture probabilities. The complete GOF test involves four components that detect variation in survival (Tests 3.SR and 3.SM) and recapture probabilities (Tests 2.CT and 2.CM) of different individuals (for detailed description of the component tests see Cooch et al. 1996). Most importantly, Test 3.SR tests if individuals banded in a given year have the same probability of being resighted in

subsequent years as do those banded in previous years. Several effects including trap dependence, marking effects, presence of transients in the population, and age effects on survival can cause Test 3.SR to be rejected (Cooch et al. 1996, Prevot-Julliard et al. 1998). Trap dependence occurs when some individuals in the population have low capture rates (i.e. are unlikely to be trapped and/or resighted) while others have high capture rates, whereas marking effects occur when the act of marking a bird causes an increase in immediate mortality (Cooch et al. 1996). Finally, if transient birds are present in the population when marking occurs, but depart the study area shortly after, then newly banded birds will have a consistently lower probability of being resighted than will previously banded individuals. Only those GOF tests that contained sufficient data to calculate a χ^2 value were included.

Once a satisfactory starting model was identified, SURGE was used to obtain maximum likelihood estimates of local survival and recapture rates. Models were fitted in order of decreasing complexity. This modelling approach reduces a model with a large number of parameters that provides little biological insight into the data, into a model with fewer parameters that still explains significant variability in the data and is biologically meaningful (Kanyamibwa et al. 1990, Burnham and Anderson 1992).

The fit of a model was described by deviance ($DEV = -2 \ln(L)$ where L is the maximum likelihood) of the model and the number of estimable parameters (NP). The model with the lowest Aikake's Information Criterion ($AIC = DEV + 2*NP$) was selected as the best fitting model because the AIC provides an unbiased criterion for model selection (Burnham and Anderson 1992, Lebreton et al. 1992, Cooch et al. 1996). Pairs of nested models were formally compared using the likelihood-ratio statistic, which is

obtained as the difference in deviance of the two models. This statistic is distributed as a χ^2 , with the difference in the number of estimable parameters used as the degrees of freedom. If the Likelihood Ratio Test (LRT) was not significant, the reduced model was accepted and tested against other models with fewer parameters. By using both the AIC and LRT, any nonsignificant effects were removed and the most parsimonious model was selected.

MODEL NOTATION

Model notation follows Lebreton et al. (1992); different models are defined by the subscripts on the survival (ϕ) and recapture (p) probability parameters. A model with time dependence in local survival is written as ϕ_t , whereas a model with constant survival is written as ϕ_c . The effects of sex (s), year of study (t), age class (2ac) and environmental variables on survival and resighting were tested. Differences between sexes or age classes were sometimes constrained to be a constant difference in every year by using an additive model. Comparing an additive (e.g., $\phi_{\text{sex}+\text{time}}$) and saturated model (e.g., $\phi_{\text{sex}*\text{time}}$) is similar to testing the significance of an interaction term in a two-way ANOVA (Warnock et al. 1997).

MODELLING PROCEDURE

In modelling local survival and resighting rates, I started with a fully saturated model that included sex, time, and age class ($\phi_{2ac*s*t}$, $p_{2ac*s*t}$), and then fit progressively simpler models. Because natal philopatry is very low for Semipalmated Plovers (<2% of hatchlings returned to the study area to breed, Flynn et al. 1999), I did not know the

absolute age of first-time breeders. So, to test for relative age effects on survival, I separated birds into two relative age classes to compare local survival from year of first capture to the following year (age class one) with local survival in subsequent years (age class two) (Johnston et al. 1997, Sandercock and Gratto-Trevor 1997, Warnock et al. 1997). Although this model is termed a two 'age-class' model, only birds banded as adults were included. The model compared survival of newly banded birds with that of previously banded birds, but the absolute age of the birds was unknown.

EXTERNAL CONSTRAINTS

Relationships between Semipalmated Plover survival and resighting rates and conditions on breeding grounds were tested using SURGE. SURGE incorporates environmental covariates into the model, thus taking into account the non-independence of successive annual survival estimates (Insley et al. 1997). A logit-link function is used to reconstitute survival or resighting estimates as a function of the external variable (for more detail see p.77 of Lebreton et al. 1992, and chapter 6 in Cooch et al. 1996). I tested three different external variables. The first external variable was mean daily air temperature (mean daily air temperature for June and July), which was used to determine if temperatures on the breeding grounds affect local survival. Second, I used mean date of clutch completion in each year as a proxy for seasonal breeding ground conditions. In years of late snowmelt birds are forced to either delay nesting or forego breeding altogether (Nol et al. 1997). Therefore, I predicted that local survival would be lower in late years, either because of high costs of breeding during unfavourable weather conditions, or because birds may disperse to areas where conditions are more favourable.

The final external variable tested was hatching success (mean number of eggs hatched per nest). There are two reasons why annual local survival and hatching success may be correlated. Low hatching success may be the result of high egg predation rates, which may in turn cause a higher than average number of adult birds to be taken by predators. Alternatively, low hatching success may be an impetus for dispersal such that birds are more likely to disperse following nest failure thereby lowering local survival rate estimates. Weather data were obtained from the Environment Canada weather station at Churchill, Manitoba.

RESULTS

BANDING SUMMARY

Local survival and resighting rates of adult Semipalmated Plovers were calculated from the capture histories of 134 adult female and 122 adult male Semipalmated Plovers from 1992-1998 (Appendix 1). The oldest known breeding birds were two females that survived to at least ten years of age. These females were banded as adults in 1988 (assumed to be at least 2 years old), and were last observed breeding on the study area in 1996. Two other females survived to age nine, whereas the oldest breeding males were eight years old. Birds that were banded outside of the study area were excluded from analyses, as were the small number of adult birds banded in 1988. Due to low natal return rates, juvenile survivorship was not modelled. Five birds banded as chicks were included in the capture histories when they were first resighted as breeding adults.

GOODNESS-OF-FIT TESTS

Resighting probabilities were high; the majority of birds were resighted in the year immediately following banding. There were sufficient data to perform one set of GOF tests from RELEASE (test 3.SR). The results of test 3.SR for males and females showed no evidence of heterogeneity of capture (males: $\chi^2=9.38$, $df=5$, $P=0.10$; females: $\chi^2=6.90$, $df=5$, $P=0.23$); and therefore the data met CJS model assumptions.

LOCAL RESIGHTING RATE

I first modelled resighting rate (p), so that the best fit of p was found before modelling survival. There was no significant age-class effect (model 2 vs. 1; Table 2.1) and no significant interaction between sex and time (model 3 vs. 2; Table 2.1) in resighting rate. The most parsimonious model (i.e. lowest AIC) was one with no annual variation in resighting rate but a significant sex effect (model 6 vs. 5; Table 2.1). The resighting rate of males was 21% higher than that of females (males: $p=0.85$, 95% CI: 0.76-0.91; females: $p=0.64$, 95% CI: 0.54-0.73).

LOCAL SURVIVAL

Local survival rates of male and female Semipalmated Plovers were not significantly different (model 7 vs. 5; Table 2.1) and there was a significant interaction between age class and time. The additive model (where survival was constrained to be a constant difference) was significantly different from the unconstrained model (model 8 vs. 7; Table 2.1). For adult Semipalmated Plovers, the most parsimonious model was one

containing two age classes (both with time-dependence) in local survival and sex-dependence in resighting rate (model 7; Table 2.1).

In 1993 and 1994, newly banded birds (age class one) had lower local survival rates than did previously banded birds (age class two), whereas the opposite trend occurred in 1995. In 1996 and 1997, local survival did not differ between the age classes (Table 2.2). For birds in age class one, local survival was high in 1996, and low in 1992, 1994 and 1997, whereas survival was high in 1994 and 1996 and low in 1995 and 1997 for birds in the second age class (Table 2.2). To remove any bias on survival estimates caused by the presence of young or transient breeders, survival estimates were obtained from age class two (ϕ_2). Based on age class two, the estimated constant local survival rate of Semipalmated Plovers was 0.71 (95% CI: 0.64-0.78), but survival varied annually from 0.49 in 1997 to 1.0 in 1993 (Table 2.2).

EXTERNAL CONSTRAINTS

To determine if annual variation in local survival was related to annual breeding ground conditions, survival estimates were constrained to be a linear function of several external variables. To remove any bias on survival estimates caused by the presence of young or transient breeders, linear constraints were only applied to age class two. Annual variation in local survival was not correlated with mean temperature (model 9 vs. 7; Table 2.1) or mean date of clutch completion (model 10 vs. 7; Table 2.1). Hatching success was a good predictor of probability of survival to the next year (model 11 vs. 7; Table 2.1), and had the lowest AIC of all models tested (AIC=812.87). Years in which Semipalmated Plovers experienced high hatching success on the breeding grounds

Semipalmated Plovers experienced high hatching success on the breeding grounds corresponded to years with high probability of survival to the next breeding season (Figure 2.1). Hatching success and local survival were highest in 1993 and 1994, and lowest in 1995 and 1997 (Figure 2.1).

DISCUSSION

Recently, there have been many advancements to the basic CJS model. For example, statistical techniques and programs for analysis of mark-recapture data have been developed that allow the evaluation of the effects of factors such as sex, age, time, and environmental variables on survival and resighting. Because the CJS approach separates estimates of local survival from resighting rates, it is a definite improvement over using return rates as a crude estimate of minimum survival. Return rates of adult shorebirds are commonly reported in the literature (e.g., Pienkowski 1983, Oring and Lank 1984, Haig and Oring 1988, Thompson and Hale 1989, Grant 1991, Thompson et al. 1994, Flynn et al. 1999) but these estimates should only be considered reliable if resighting probabilities of both sexes are nearly 100%, a condition that is rarely met in most studies. Resighting probabilities are probably low for many shorebird species, especially those that nest at low densities over a large geographic area. Furthermore, if the study area is small and suitable nesting habitat is available nearby, birds are unlikely be resighted if they emigrate beyond the study area.

Table 2.1 - Model selection for local survival and resighting rates of adult Semipalmated Plovers banded at Churchill, Manitoba from 1992 to 1998. Model fit is described by deviance (DEV), number of parameters (NP) and Aikake's Information Criterion (AIC). Results obtained from SURGE. Nested models are compared with likelihood ratio tests (LRT) and best-fitting models are shown in bold.

Model	DEV	NP	AIC	LRT	DF	χ^2	P
Modelling Resighting							
1. $\phi_{2ac*s*t}, p_{2ac*s*t}$	771.02	40	851.02				
2. $\phi_{2ac*s*t}, p_{s*t}$	777.77	32	841.77	2 vs. 1	8	6.75	0.564
3. $\phi_{2ac*s*t}, p_{s+t}$	778.03	28	834.03	3 vs. 2	4	0.26	0.992
4. $\phi_{2ac*s*t}, p_t$	786.92	27	840.92	4 vs. 3	1	8.89	<0.005
5. $\phi_{2ac*s*t}, p_s$	783.94	24	831.94	5 vs. 3	4	5.91	0.206
6. $\phi_{2ac*s*t}, p_c$	792.20	23	838.20	6 vs. 5	1	8.26	<0.005
Modelling Survival							
7. ϕ_{2ac*t}, p_s	790.84	13	816.84	7 vs. 6	11	6.90	0.807
8. ϕ_{2ac+t}, p_s	805.60	9	823.60	7 vs. 6	4	14.76	<0.010
Modelling survival with external variables							
9. $\phi_{1t}, \phi_{2temp}, p_s$	819.23	10	839.23	9 vs. 6	3	28.39	<0.001
10. $\phi_{1t}, \phi_{2date}, p_s$	819.24	10	839.24	10 vs. 6	3	23.40	<0.001
11. $\phi_{1t}, \phi_{2h.s.}, p_s$	792.87	10	812.87	11 vs. 6	3	2.03	0.566

Notes: 2ac=two age classes, c=constant, t=time dependence, s=sex dependence, ϕ_1 =survival of birds in age class one, ϕ_2 =survival of birds in age class two, temp=mean daily air temperature, h.s.=hatching success (mean number eggs hatched per pair).

Table 2.2 - Annual estimates of local survival rate (with 95% confidence interval) of adult Semipalmated Plovers breeding at Churchill, MB from 1992-1997 in the year immediately following banding (ϕ_1), and in subsequent years (ϕ_2). Parameter estimates obtained from model 7 ($\phi_{2ac \cdot t}, p_s$) using SURGE. Survival estimates represent the probability of survival to the next breeding season.

Year	<u>Newly banded birds (ϕ_1)</u>		<u>Previously banded birds (ϕ_2)</u>	
	Probability of survival to next breeding season	95% CI	Probability of survival to next breeding season	95% CI
1992	0.46	0.26-0.67	—	—
1993	0.70	0.55-0.82	1.00	1.00-1.00
1994	0.54	0.39-0.68	0.94	0.59-0.99
1995	0.61	0.41-0.77	0.54	0.41-0.67
1996	0.91	0.58-0.99	0.88	0.63-0.97
1997	0.50	0.32-0.68	0.49	0.35-0.63

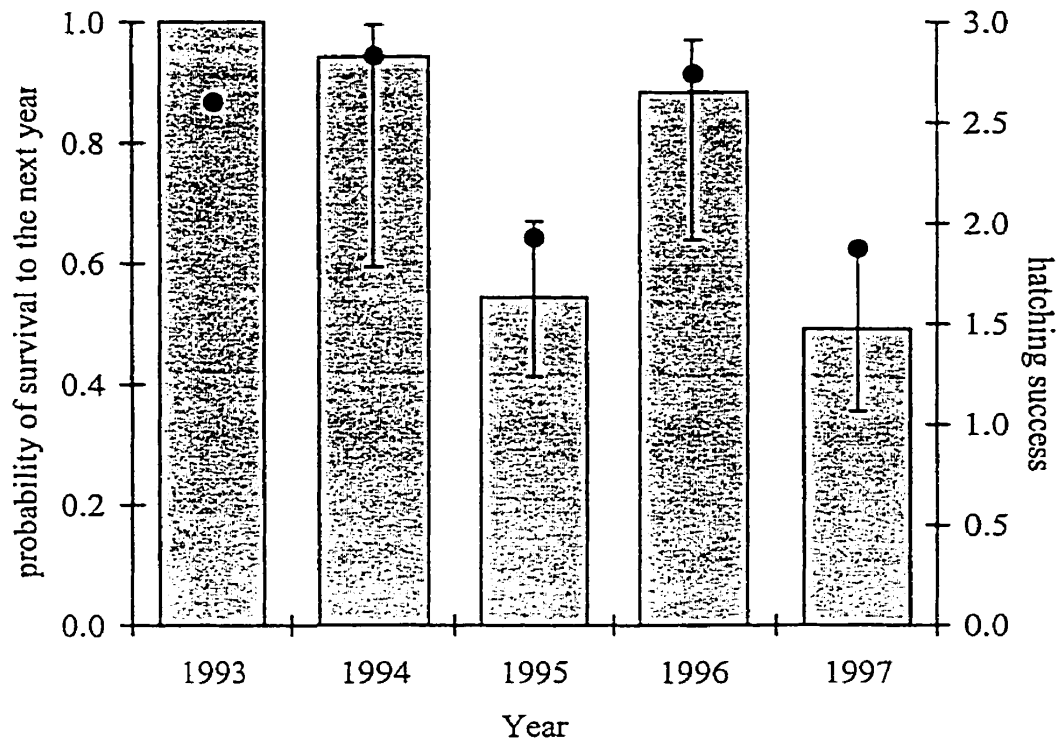


Figure 2.1 – Relationship between adult Semipalmated Plover local survival (males and females combined) and mean hatching success at Churchill, Manitoba from 1993 to 1997. Local survival rate estimates (with associated 95% confidence intervals) taken from SURGE, model $\phi_{1t}\phi_{2h,s}p_s$ (model 11, Table 2.1) are represented by bars and show the probability of survival to the next year. Hatching success is shown by the black dots and is equal to the mean number of eggs hatched per pair. Years with low hatching success (1995 and 1997) correspond with years in which local survival rates were lower than average.

As expected, estimates of local survival of Semipalmated Plovers at Churchill were considerably higher than were return rates previously reported by Flynn et al. (1999) for the same population. The difference between return rates and local survival was greater for females than for males. Female return rates underestimated local survival by more than 35% in some years (Flynn et al. 1999, this study). When resighting rates differ among years or between groups of individuals (e.g., sex, age), using return rates as an estimate of survival could result in the acceptance of false conclusions. In the present study, for example, an examination of return rates alone, would lead one to falsely conclude that female Semipalmated Plovers have higher mortality rates than do males. However, when a capture-recapture model that accounts for lower female resighting rates was used, it was revealed that there were no sex differences in local survival.

Although modern capture-recapture models produce more reliable estimates of survival than do return rates, local survival is still underestimated because permanent emigration from the study area cannot be distinguished from mortality. Because breeding site fidelity is typically quite high among adult shorebirds (Oring and Lank 1984) and habitat adjacent to the study area was searched for colour-marked individuals each year, local dispersal is probably not underestimating local survival of Semipalmated Plovers at Churchill, Manitoba. However, there are likely some individuals that permanently emigrate long distances and are thus never resighted. Male and female Snowy Plovers (*Charadrius alexandrinus*), for example, have been found during the breeding season 50 to 1140 km (median=175 km) away from their regular breeding site (Stenzel et al. 1994). At Churchill, female Semipalmated Plovers occasionally move more than 4 km between years (Flynn et al. 1999)

Scale of the study is another important consideration when interpreting the results of survival analyses. At the local population scale, mortality and emigration have identical effects, whereas at the species level it is important to determine the relative importance of mortality and emigration so a species' entire population can be monitored. For this reason, the scale of this study was restricted to the local breeding population of Semipalmated Plovers around Churchill, Manitoba.

RESIGHTING PROBABILITIES

Resighting rates of Semipalmated Plovers were relatively high and did not vary among years. This suggests that despite the large study area, good coverage was achieved each year and search effort was consistent among years. Male Semipalmated Plovers were resighted at a significantly higher rate than were females. A best-fitting mark-recapture model for Snowy Plovers also contained higher male resighting rate, but the difference between the sexes was considerably less than that of Semipalmated Plovers (Paton 1994). In fact, resighting rates for both sexes were lower than that of Semipalmated Plovers (male Snowy Plovers: $p=0.68$; female Snowy Plovers: $p=0.52$) (Paton 1994). Compared to Semipalmated Plovers, Snowy Plovers are much less site faithful and they breed in more unpredictable habitat (Warriner and Paton 1995). These two factors are likely responsible for the lower resighting rates.

Higher male resighting rates may occur if males are more active than are females on the breeding grounds, and thus are more likely to be resighted by researchers (Prévot-Julliard et al. 1998). Male Semipalmated Plovers are more conspicuous than females during the pre-laying period because they perform aerial displays and vocalizations above

their nesting territory, and aggressively defend a territory against intruding conspecifics (Sullivan Blanken and Nol 1998). Incubation duties are shared equally among the sexes and in every year of study both members of a pair were identified (by resighting or recapture). Additionally, Semipalmated Plovers nest and feed in open habitats and are quite conspicuous, so it is unlikely that many birds present on the study area were missed during a 'recapture occasion'. For this reason, lower female resighting rates of Semipalmated Plovers are not likely due to sex differences in conspicuousness. Differences in trapability between male and female birds can also cause sexual differences in resighting rates. However, male and female Semipalmated Plovers are equally likely to be trapped, and most resightings consisted of observations of colour-marked birds as opposed to trapping (pers. obs.).

Female Semipalmated Plovers may have lower resighting rates than do males because they are more likely than are males to temporarily emigrate beyond the study area. Among monogamous birds, the sex that secures and defends the territory is usually more site tenacious because familiarity with an area is thought to facilitate the acquisition and maintenance of a territory (Greenwood and Harvey 1982). Higher adult male site-tenacity and female-biased dispersal is a widespread phenomenon among monogamous male-territorial shorebirds. Studies have shown that males of many monogamous shorebird species exhibit stronger site tenacity than do conspecific females (Holmes 1971, Lenington and Mace 1975, Gratto et al. 1985, Redmond and Jenni 1986, Haig and Oring 1988, Johnson et al. 1993, Jackson 1994, Paton and Edwards 1996). Male Semipalmated Plovers return to their breeding grounds to defend a territory before arrival of females, and remain faithful to that territory during successive breeding seasons, while

females are less site tenacious, and move greater distances between years (Flynn et al. 1999).

Many factors influence a female's decision on whether to move to a new nest site or remain at the old site. Females of many shorebird species (e.g., Semipalmated Plovers, Snowy Plovers, Piping Plovers (*Chardrius melodus*), Semipalmated Sandpipers), are less likely to return to a previous nest site if her mate does not return, or if she failed to breed during the previous breeding season (Gratto et al. 1985, Haig and Oring 1988, Paton and Edwards 1996, Flynn et al. 1999). Previous nest success does not usually influence a male plover's decision of whether to return to a territory in successive years; he may return to the same territory despite nest failure during the previous year (Paton and Edwards 1996, Flynn et al. 1999). Males may remain faithful to a breeding territory because they are familiar with the distribution of food resources and predator safe areas, or because of familiarity with conspecifics (e.g., mates, relatives) (Oring and Lank 1984, Gratto et al. 1985, Jackson 1994, Paton and Edwards 1996). Males may also remain faithful to a nest site because they are unable to establish a territory in an unfamiliar location (Greenwood and Harvey 1982). A male plover must acquire a 'good' nest site to attract a mate, but female plovers are not as tied to a territory and thus are free to choose among available breeding opportunities (Flynn et al. 1999). A female may disperse to a new nest site if her chance of breeding successfully is increased or risk of mortality is decreased (Jackson 1994, Flynn et al. 1999), and she may use cues such as previous nesting success, nesting density, success of conspecifics and quality of her mate to decide whether to move to a new nest site (Paton and Edwards 1996). Higher female dispersal results in more females than males moving beyond the study area and hence being

resighted at a lower rate. Although female Semipalmated Plovers are more likely than males to temporarily emigrate, there are no sex differences in rates of permanent emigration because local survival (which is the product of mortality and permanent emigration) did not differ between males and females.

Lower female resighting rates can also arise if females skip breeding seasons and remain at lower latitudes. There are records of Semipalmated Plovers over-summering in their wintering range, but the sex and age of these individuals are unknown (Nol and Blanken 1999). In other shorebird species, most over-summering birds are sexually immature, first-year birds, but adults of some species over-summer (McNeil et al. 1994, Summers et al. 1995). Like Semipalmated Plovers, female Greater Flamingos have lower resighting rates than do males (Cézilly et al. 1996). This may be because females have higher reproductive costs than do males, which is expressed as reduced probability of breeding in the year following a successful breeding season (Cézilly et al. 1996). Females of long-lived bird species (e.g., Waved Albatross (*Diomedea irrorata*), Antarctic Fulmar (*Fulmaris glacialoides*), Lesser Snow Goose (*Anser caerulescens caerulescens*)) are less likely to nest the year following a successful season, presumably because of costs associated with breeding (Rechten 1986, Weimerskirch 1990, Viallefont et al. 1995). Although this phenomenon has not been documented for any shorebird species, it is possible that female plovers skip breeding seasons when they cannot meet the energetic requirements for breeding that year. A female may skip a breeding season if she is in poor physical condition and thus unable to undertake a long migration and incur reproductive costs. By skipping a breeding season, she sacrifices present reproduction in favour of survival to the next breeding season and future breeding opportunities. A

summer survey of wintering grounds would be useful to determine if any adult females are over-summering.

ABSENCE OF SEX DIFFERENCES IN LOCAL SURVIVAL

Studies of male-territorial, monogamous shorebirds have found no sexual differences in adult return rates or slightly higher male return rates (Oring and Lank 1984, Gratto et al. 1985, Thompson and Hale 1989, Grant 1991). Sexual differences in return rates alone cannot be accepted as conclusive evidence for differential survival rates between sexes because, as in this study, resighting rate may be sex-dependent. Local survival rates of male and female Semipalmated Plovers did not differ, which agrees with several other shorebird survival studies (Root et al. 1992, Thompson and Hale 1993, Paton 1994, Insley et al. 1997, Warnock et al. 1997). Local survival of female Semipalmated Sandpipers, however, was consistently lower than that of males (Sandercock and Gratto-Trevor 1997), and females experienced higher mortality on the breeding grounds than did males (Gratto-Trevor 1991). Higher mortality of breeding females is common among waterfowl, and is usually attributed to energetic costs of egg production and incubation, and/or high susceptibility of incubating females to predators (Sargaent and Raveling 1992). This may not be true of shorebirds because both males and females incubate.

Although incubation is shared equally between male and female Semipalmated Plovers, females invest a significant amount of energy into egg production (a four egg clutch represents more than 75% of a female's body mass) (Nol and Blanken 1999). Conversely, male plovers expend more energy in territory defence and remain with the

brood a week longer than do females. Intersexual differences in reproductive investment may not be reflected in survival rates if females have evolved behavioural mechanisms to compensate for the added costs of egg production (Cézilly et al. 1996). One such mechanism for female Semipalmated Plovers may be reduction in time spent on arctic breeding grounds (Gratto-Trevor 1991). Females arrive later in spring and depart earlier at the end of the breeding season than do males. Ashkenazie and Safriel (1979) found that Semipalmated Sandpipers breeding in Alaska had an energy deficit by the end of incubation and suggested that females that deserted the brood early to migrate to better feeding areas would have higher survival rates. Other possible fitness benefits of early female departure are decreased predation risk and increased availability of food on staging areas (Boates and Smith 1989, Schneider and Harrington 1981, Gratto-Trevor 1991).

There are high apparent energetic costs of breeding for Semipalmated Plovers, because when faced with unusually harsh weather on breeding grounds, plovers may be unable to acquire sufficient energy reserves to sustain egg production and long bouts of incubation (Nol et al. 1997). Consequently, plovers may forego breeding and/or lay smaller clutches (Nol et al. 1997), presumably to improve their probability of survival to the next breeding season. If lower female resighting rates in this study are the result of females skipping breeding seasons when they are unable to meet the energetic requirements of breeding, this could be another behavioural adaptation that allows females to maintain survival rates equal to that of males.

COMPARISON WITH OTHER SHOREBIRD SPECIES

It is important to consider interspecific differences in site tenacity when comparing survival rates among shorebird species because local survival estimates confound mortality and emigration (Sandercock and Gratto-Trevor 1997). Many ecological, environmental and demographic factors can influence a species' site tenacity. Species that are territorial, have a monogamous mating system and exhibit biparental care tend to have the highest rates of site fidelity, whereas environmental factors such as habitat stability and increased predation, and demographic factors such as a skewed sex ratio will result in lower levels of site tenacity (Oring and Lank 1984).

The estimated 71% local survival rate of adult Semipalmated Plovers (ϕ 2) is comparable to survival estimates of other male territorial shorebirds, including wintering Dunlin (*Calidris alpina*) in California (74%; Warnock et al. 1997), breeding Redshanks (*Tringa totanus*) in Scotland (age 2: 67%, age 3+: 74%; Insley et al. 1997), breeding Redshanks in England (males: 72%, females: 67%, Thompson and Hale 1993), breeding Snowy Plovers in Utah (69%; Paton 1994), breeding Piping Plovers in Great Plains region (66%; Root et al. 1992), and breeding Piping Plovers in Massachusetts (74%, USFWS 1996). Local survival of adult Semipalmated Sandpipers breeding at La P rouse Bay was lower than that of Semipalmated Plovers (Semipalmated Sandpipers: males: 61%, females 56%; Sandercock and Gratto-Trevor 1997). This may be partly due to the smaller size of Semipalmated Sandpipers (Semipalmated Sandpipers weigh about half as much as do Semipalmated Plovers), however, there were probably other contributing factors, since the Semipalmated Sandpiper population was in decline at the time (Hitchcock and Gratto-Trevor 1997). Body size may be an indicator of mortality in

shorebirds, with smaller species having lower survival rates than larger species (Boyd 1962). Possible reasons for higher mortality rates of smaller shorebird species are increased energetic demands and greater vulnerability to a wider range of aerial predators (Bélisle and Giroux 1995, Warnock et al. 1997).

AGE EFFECTS ON LOCAL SURVIVAL

The best-fitting unconstrained survival model for Semipalmated Plovers contained a two-age class term with time-dependence in both age classes. Many studies have found that birds have lower survival in the year immediately following banding than in subsequent years (Insley et al. 1997, Johnston 1997, Warnock et al. 1997). Lower survival of newly banded birds can result from a banding/trapping effect (Pradel et al. 1995, Warnock et al. 1997), heterogeneity in capture (Francis and Cooke 1992, Prévot-Julliard et al. 1998) or the presence of transients in the populations of banded birds (Johnson et al. 1997). If transient birds are included in capture histories, survival in the year immediately following banding will be artificially lower because birds that are passing through the study area are banded and then never resighted (Johnson et al. 1997, Warnock et al. 1997). The presence of transients is a common problem in mist-net studies conducted during migration (e.g., Warnock et al. 1997) but is likely not an issue in my study because only breeding birds were banded. However, it is possible that transient breeders en route to more northerly breeding grounds may have “short-stopped” to breed at Churchill in some years. Transient breeding Lesser Snow Geese have been observed in the Akimiski Island Snow Goose colony in southern James Bay (Abraham et al. 1999) and in the La Pérouse Bay colony near Churchill, Manitoba (F. Cooke pers.

comm.). When weather conditions further north are unfavourable, Snow Geese shorten their migration and breed further south, returning to their regular breeding grounds in subsequent years (Abraham et al. 1999). Transient breeders have never been reported in shorebird populations, but their presence could easily go unnoticed.

Trapping and marking may negatively affect survival of some shorebird species. For example, Dunlin and Western Sandpipers are more prone to raptor predation in the days immediately following capture (Warnock and Takekawa 1996, Warnock et al. 1997). Nest-trapping and banding Semipalmated Plovers does not appear to negatively impact their subsequent survival, because birds typically return to the nest quickly after trapping and were usually observed at the nest for several days post-handling. Additionally, survival of newly banded birds was equal to or greater than that of previously banded individuals in 1995, 1996 and 1997, and the age class effect in 1993 could have been an artefact of a small sample size of age class two birds.

In 1994, survival of newly banded birds was considerably lower than that of previously banded individuals ($\phi_1=0.54$, $\phi_2=0.94$) despite higher than average hatching success and warmer than average weather conditions on Churchill breeding grounds (Nol et al. 1997). The absolute age of newly banded birds was unknown, so, it is possible that a high proportion of birds banded in 1994 were young or inexperienced birds that subsequently dispersed to other areas or died. Higher energetic costs for first-time breeders may cause higher mortality (Viallefont et al. 1995, Prévot-Julliard et al. 1998), but if this were true for Semipalmated Plovers, then survival of newly banded birds should have been consistently lower than that of previously banded individuals. Future

research will ascertain whether lower survival of newly banded Semipalmated Plovers occasionally occurs, or if 1994 was truly an anomalous year.

ANNUAL VARIATION IN LOCAL SURVIVAL RATES

There was significant annual variation in survival of Semipalmated Plovers breeding at Churchill, which is typical of shorebird populations (Root et al. 1992, Thompson and Hale 1993, Paton 1994, Sandercock and Gratto-Trevor 1997 but see Warnock et al. 1997). Annual variation in local survival was not correlated with annual variation in mean date of clutch completion or mean daily temperature on the breeding grounds. Annual variation in Semipalmated Sandpiper local survival at La Pérouse Bay was also not correlated with weather conditions on the breeding grounds and authors suggested that this might be partly due to the relatively short duration of their study ($N=8$ years) (Sandercock and Gratto-Trevor 1997). Failure to find a correlation between survival of Semipalmated Plovers and environmental conditions may be due to a small sample size ($N=6$ years), because the appropriate variables were not measured (e.g., wind speed, wind chill, availability of mudflats), or because interactions among abiotic factors were not considered.

Shorebird survival is likely to be more influenced by selection factors operating elsewhere in the annual cycle. There is unlikely to be any strong correlations between environmental conditions on the breeding grounds and shorebird survival because life history theory predicts that in long-lived species, environmental stress will affect fecundity before affecting adult survival (Benton and Grant 1996, Oro et al. 1999). Several long-term studies (more than 15 years) of wintering shorebirds (Peach et al.

1994, Insley et al. 1997, Yalden and Pearce-Higgins 1997) and other wintering bird species (Clobert et al. 1988, Kanyamibwa et al. 1990, Cézilly et al. 1996) have found correlations between survival rate and environmental variables. However, no studies have found a correlation between adult shorebird survival and environmental conditions on the breeding grounds.

Weather conditions on wintering grounds, where shorebirds spend six months of the year, have a much greater influence on local survival than do breeding ground conditions. High density of shorebirds and competition for resources may further exacerbate any weather effects. Environmental factors such as temperature, precipitation and wind affect the availability and distribution of invertebrate prey (Pienkowski 1983, Evans and Pienkowski 1984), which may in turn affect shorebird survival. Adult local survival of wintering Golden Plovers was correlated with mean monthly air temperature (Yalden and Pearce-Higgins 1997), and survival of Redshanks and Lapwings (*Vanellus vanellus*) was correlated with both rainfall and temperature on wintering grounds. High mortality of Redshanks occurred during winters that were either significantly wetter or drier than average or were unusually cold (Insley et al. 1997). Winter weather was also an important cause of mortality among populations of Golden Plovers (Yalden and Pearce-Higgins 1997). Heavy rainfall and cold temperatures reduce the availability of invertebrates near the surface of the mud, and consequently depress shorebird foraging rates (Pienkowski 1983, Insley et al. 1997). Heavy mortality of shorebirds may occur during prolonged periods of inclement weather (e.g., heavy rainfall, strong wind, unusually cold temperatures) because of a reduction in prey availability and excessive heat loss. First-year birds and birds in poor physical condition may be particularly

susceptible to cold weather mortality because of inadequate fat reserves (Insley et al. 1997).

Local survival of Semipalmated Plovers at Churchill, MB and return rates of Semipalmated Plovers to Prudhoe Bay were lower than average in 1998, the breeding season immediately following an El Niño Southern Oscillation (ENSO) event (Nol and Blanken 1999). Changes in marine water temperature, such as those that occur during an ENSO can have a large impact on the marine intertidal ecosystem (Sanford 1999). For example, only a slight decrease in water temperature dramatically reduced the effects of a keystone predator (Sea Star, *Pisaster ochraceus*) on its principal prey, which could potentially cause large-scale ecological changes (Sanford 1999). Changes in oceanographic conditions that occur during ENSO alter food availability and cause high mortality in some seabird species (e.g., Snow Petrel, *Pagodroma nivea*) (Chastel et al. 1993). If growth and survival of invertebrate prey are also affected by ENSO, then shorebird survival could be similarly affected. The impact of wintering ground conditions on Semipalmated Plover survival deserves further study.

EFFECT OF HATCHING SUCCESS ON LOCAL SURVIVAL

Of all models tested, the best-fitting survival model contained a two age class term with survival in the second age class constrained to be a function of hatching success. In other words, hatching success appears to be a good predictor of adult Semipalmated Plover local survival. Years in which many nests were depredated, and thus hatching success was low, corresponded to years with low survival rates. Nest depredation may be an impetus for dispersal, in that unsuccessful birds disperse to new

nesting areas beyond the boundaries of the study area (Thompson and Hale 1989, Gratto et al. 1985, Payne and Payne 1990, Haas 1998, Flynn et al. 1999). High predator density or abundance, low hatching success of conspecifics, or poor individual success in 1995 and 1997 may have been indicators of a poor nesting area and thus encouraged Semipalmated Plovers to permanently emigrate. A previous study found that nesting success and divorce influenced return rates of female, and to a lesser extent male Semipalmated Plovers, to the Churchill study area (Flynn et al. 1999). High hatching success resulted in higher return rates in the subsequent year. Furthermore, females that experienced breeding failure and changed mates in the subsequent breeding season dispersed farther distances than did successful females that changed mates (Flynn et al. 1999). Semipalmated Plovers may be using a 'decision rule' (Haas 1998) in that individuals select nest sites and decide whether or not to disperse based on their prior nesting experience.

PREDATION

There are several predators of Semipalmated Plover eggs and young, including Raven (*Corvus corax*), Rough-legged Hawk (*Buteo lagopus*), Arctic Fox (*Alopex lagopus*) and Red Fox (*Vulpes vulpes*) (Sullivan Blanken and Nol 1999). An artificial nest study (using Japanese Quail eggs) conducted in 1998 also revealed Short-tailed Weasels as likely egg predators (D. Badzinski, unpublished data). Similar to other arctic-nesting birds, Semipalmated Plover nest predation rates may fluctuate in response to microtine levels, with high predation in years of low microtine numbers as predators (particularly foxes) seek alternate prey sources (Norton 1972, Gratto-Trevor 1992,

Underhill et al. 1993, Nol and Blanken 1999). A relationship between Arctic Fox, lemmings and breeding birds was first suggested by Larson (1960) who noticed that Arctic regions with few or no lemmings supported few breeding birds, and the birds' anti-predator strategies were highly developed. However, in areas where lemmings were present, the avifana was richer, and breeding birds performed less intensive distraction displays (Underhill et al. 1993). This observation led to the formation of the Roselaar-Summers hypothesis (Summers 1986, Dhondt 1987, Underhill et al. 1993), which suggested that breeding productivity of shorebirds and Brent Geese (*Branta bernicula bernicula*) was directly related to the abundance of lemmings and foxes. In particular, Summers and Underhill (1987) suggested that lemming abundance *per se* is not the critical factor, but the change in lemming abundance. In a year following a lemming peak in which lemmings have declined or are declining, predation rates are intensified because foxes switch from being territorial to nomadic, and predators (mammalian and avian) move into the area from regions that did not experience a lemming peak in the previous year (Underhill et al. 1993). The density of collared lemmings (*Dicrostonyx richardsoni*) at Churchill, Manitoba dropped dramatically from 12.5 lemmings/ha in 1994 to 0.9 lemmings/ha in 1995 remained low in 1996 (0.5 lemmings/ha) and began to increase in 1997 (2.2 lemmings/ha) (Roth 1998). Low survival of adult shorebirds, and high levels of nest depredation in 1995 may have been a direct result of predators switching to Semipalmated Plovers and their eggs as alternate prey.

The correlation between nest success and local survival of Semipalmated Plovers is probably caused by two different factors. High rates of nest failure may cause birds to permanently emigrate to nesting areas with lower predation risk. Secondly, in some

years, predator densities may be high and/or predators are forced to switch to alternate food sources, causing high rates of egg and adult predation and consequently lower adult survival.

This study demonstrates that breeding ground conditions, particularly predation rates influence Semipalmated Plover hatching success, which in turn influences local survival. Local survival rates are likely more influenced by weather conditions on the wintering grounds than on breeding grounds, and changes in oceanographic conditions that occur during El Niño years could also influence survival. Further investigation into factors promoting dispersal from the study area is needed. In particular, research should focus on explaining why female Semipalmated Plovers are more likely than are males to temporarily emigrate.

CHAPTER 3

ANNUAL VARIATION IN SEMIPALMATED PLOVER (*CHARADRIUS SEMIPALMATUS*) REPRODUCTIVE SUCCESS AND THE INFLUENCE OF PREVIOUS BREEDING EXPERIENCE

ABSTRACT

Annual variation in clutch size, egg predation rate, hatching success, and fledging success of Semipalmated Plovers (*Charadrius semipalmatus*) breeding at Churchill, Manitoba was studied from 1992 – 1998. I tested whether breeding experience of individuals affects hatching success, fledging success, and nesting chronology. My prediction was that experienced individuals would hatch more eggs, fledge more chicks, and nest earlier in the season than would inexperienced birds. Clutch size, hatchability, hatching success, and nest predation showed significant annual variation. Clutch size was lower in two years, suggesting that reductions in clutch size of shorebirds are more common than previously believed. Hatchability of nests ranged from 80% - 98%, and on average, was lower than that of many other shorebirds. Low clutch size and hatchability in 1992 and 1998 may be linked to El Niño events during the previous winters. There was no detectable annual variation in number of chicks fledged per nesting attempt or number of chicks fledged per brood. On average, pairs produced 0.92 fledglings/nesting attempt and 1.87 fledglings/brood. Fledging success, but not hatching success improved with breeding experience, but the effect varied between the sexes. Pairs with an experienced male fledged more chicks than did either inexperienced pairs or those with an experienced female. Previous breeding experience had no effect on laying date.

INTRODUCTION

Many life-history traits, such as timing of nesting, acquisition of mates, egg size, clutch size and fledging success, vary among birds of different age and previous breeding experience (Hepp and Kennamer 1993). Many studies have been unable to examine the independent effects of age and breeding experience, but those that were able to control for age found that breeding experience increased reproductive success (e.g., Wooler et al. 1990, Pyle et al. 1991, Hepp and Kennamer 1993, but see Croxall et al. 1992).

Experienced birds may nest earlier in the season and have higher reproductive success than do inexperienced conspecifics. For example, experienced female Wood Ducks (*Aix sponsa*), initiated nests earlier, produced larger clutches and hatched more eggs than did inexperienced females (Hepp and Kennamer 1993). Previous breeding experience also affects reproductive success of female polyandrous Spotted Sandpipers (*Actitis macularia*). Experienced female Spotted Sandpipers acquire more mates, hatch more eggs and fledge more chicks than do inexperienced females (Oring et al. 1983).

Four main hypotheses have been proposed to explain why avian reproductive success improves with age (Nol and Smith 1987). First, the breeding experience hypothesis predicts that reproductive success will improve with experience whereas, second, the age hypothesis predicts that age-related improvements in skills such as foraging efficiency and predation avoidance, will allow older birds to fledge more young. Third, older birds may increase reproductive effort in later years to because of declining survival rates and thus reduced probability of future breeding opportunities (the residual reproductive value hypothesis). Finally, the selection hypothesis attributes higher reproductive success of older birds to differential survival of successful and unsuccessful

breeders (Nol and Smith 1987). If successful breeders have higher survival rates than do unsuccessful breeders, then older age classes will contain a high proportion of successful individuals. These hypotheses are not mutually exclusive, because several factors likely act together to increase performance of older birds (Wooler et al. 1990, Forslund and Pärt 1995).

A positive relationship between breeding experience and reproductive success has been documented for a wide variety of bird species, including waterfowl (e.g., Baillié and Milne 1982, Forslund and Larsson 1992, Hepp and Kennamer 1993), seabirds (e.g., Wooler et al. 1990, Pyle et al. 1991, Croxall et al. 1992), raptors (Newton et al. 1981, Korpimäki 1988), and passerines (see review Nol and Smith 1987, Harvey et al. 1988, Sasvári and Hegyi 1993), but has been demonstrated for only two shorebird species (Redshank (*Tringa tetanus*), Thompson and Hale 1989; and Spotted Sandpiper, Oring et al. 1983, Oring et al. 1994). This does not necessarily indicate that age-dependent reproduction is uncommon among shorebirds, but more likely reflects the difficulties associated with measuring shorebird reproductive success and a lack of long-term studies with known-age individuals.

For arctic-nesting shorebirds, among and within year variation in clutch size is low (Székely et al. 1994). Most species lay four eggs, and reductions in clutch size are rare (but see Redmond and Jenni 1986, Nol et al. 1997, Sandercock et al. 1999). Shorebird hatching success, on the other hand, varies significantly among species, and within a species hatching success tends to fluctuate among years in response to changes in environmental conditions (e.g., weather, predator abundance) (Evans and Pienkowski 1984, Redmond and Jenni 1986).

Although estimates of hatching success are available for most shorebird species, few studies have been able to follow the survival of chicks from hatch to fledge. Shorebird chicks are precocial, and have cryptic colouration and behaviour, so, it is very difficult to re-locate chicks once they leave the nest. Because chick mortality is highest during the first few weeks of life (Evans and Pienkowski 1984), hatching success may be a poor measure of reproductive success. Therefore, it is important to obtain estimates of shorebird fledging success.

The reproductive success of colour-marked Semipalmated Plovers (*Charadrius semipalmatus*), nesting in the sub-arctic region of Churchill, Manitoba has been studied for seven breeding seasons (1992-1998). In this paper, I will describe annual variation in clutch size, egg predation rate, hatching success, and fledging success of Semipalmated Plovers. I will also test the prediction that individuals with previous breeding experience hatch more eggs, fledge more chicks and nest earlier in the season than do inexperienced birds.

METHODS

NEST SEARCHING

Nesting success of Semipalmated Plovers at Churchill, Manitoba was monitored for seven years (1992-1998). All areas with suitable nesting habitat that were accessible by road were searched with equal effort from 1993 to 1997. No vehicle was available in 1992, so the entire study area was not thoroughly searched. This resulted in low banding effort and no accurate estimation of population size. Semipalmated Plovers are determinate layers, clutches containing more than four eggs have never been found.

However, females occasionally lay less than four eggs. Semipalmated Plover nests consist of a small scrape on the ground. Nests were located by walking through the study area and sighting adults performing distraction displays, or by observing foraging adults fly to the nest site. All suitable nesting habitats were searched at least twice in June of each year. Because adult Semipalmated Plovers rarely leave their nests unattended, it was unlikely that many nests were undetected using this method.

Most nests (90%) were located during incubation, so eggs were measured and weighed to estimate hatch date based on a regression between the index of specific gravity and the ratio of mass to volume (Flynn 1997). To reduce probability of nest predation, nest locations were either marked at a distance with natural material such as rock cairns and wood, or the locations were mapped. Nests were subsequently monitored every two to four days to determine their fate. To reduce disturbing incubating adults, nests were observed from a distance with a spotting scope. Clutches that disappeared between visits were assumed depredated unless another cause was apparent (e.g., destroyed by tides, trampled by humans, other animals, or motor vehicles). Just prior to estimated hatch date, nests were visited at least daily to check for pipped eggs. Once eggs are pipped, hatching usually occurs within 12 hours, but can take up to four days (Sutton and Parmelee 1955). The date at which a complete clutch was laid and incubation began (date of clutch completion) for nests that were located during incubation was estimated by subtracting 24 days (mean period of incubation) from hatch date.

NEST TRAPPING AND BANDING

During incubation, adults were nest-trapped with either a Potter trap or a walk-in keyhole nest trap. The circular walk-in nest trap was constructed from hardware cloth and contained a net top made of either cotton or nylon netting. The square Potter trap was made of 2 mm wire and had a treadle placed over the nestcup that triggered a drop door. To prevent the possibility of nest desertion, birds were not trapped early in the incubation period. Traps were continuously monitored so that birds were removed immediately upon entering, and traps were removed if the adult did not return within 20 minutes. Adult birds were leg-banded with unique combinations of an aluminium Canadian Wildlife Service (CWS) band and 1-3 coloured plastic bands (Size XCL, A.C. Hughes Ltd.). During hatch, chicks were caught by hand and each was banded with an aluminium CWS band and a brood-specific combination of coloured plastic leg bands. Most nestlings were banded one or two days after hatch. Adult plovers were sexed on the basis of plumage colouration (Teather and Nol 1997) whereas nestlings could not be sexed by plumage.

Every year, a small number of birds were not banded, either because their nest was depredated before they could be trapped or because we were unable to trap certain 'wary' birds. The proportion of unbanded adult birds in the population was small every year (1993-1998, mean unbanded birds in population=12%).

FLEDGING SUCCESS

Pre-fledging survival of Semipalmated Plover chicks was monitored for four years (1995-1998). Parents lead the chicks away from the nest within 24 hours of

hatching to forage on mudflats along Hudson Bay or at inland ponds, so these areas were searched extensively to locate family groups. To minimize disturbance, families were observed from a distance with a spotting scope. Family groups were observed every 3-4 days to determine the number of chicks present. Semipalmated Plover chicks are difficult to locate because they are cryptically coloured, and crouch down in response to the alarm calling of parent birds. To avoid underestimating fledging success by including chicks that were missed during an observation period but were actually still alive, I only included family groups in which the same number of chicks was recorded on multiple occasions. If both parents were observed without chicks, and exhibited no parental behaviour (i.e. alarm calls, distraction displays) on more than one occasion, the chicks were assumed to be dead. Male Semipalmated Plovers remain with the brood until fledging, whereas females leave at approximately 15 days after hatch (Blanken and Nol 1999). Semipalmated Plovers are capable of flight 21-24 days after hatch (E. Nol pers. comm), so for this study, I defined pre-fledging survival as survival to 21 days.

TERMINOLOGY

For this study, clutch hatching success was defined as the percentage of nests that hatched at least one young (number of nests hatching at least one young/total number of nests), and included depredated, destroyed and abandoned nests. Egg hatching success, or hatchability was the percentage of eggs laid that hatched successfully, excluding nests that hatched no eggs (total number of eggs hatched from successful nests/total number of eggs laid in successful nests). Clutch hatching success reflects total nest loss due to predation, abandonment, and destruction, whereas egg hatching success is a measure of how many eggs failed to hatch, because of infertility, neglect, or damage. For this study,

I defined fledging success as the percentage of nesting attempts that fledge at least one young (total number of young fledged/total number of eggs laid), and pre-fledgling survival as the percentage of hatched chicks that survived to fledging (total number of fledglings/total number of chicks hatched). Finally, a bird was classified as experienced if it was known to have bred at Churchill in a previous year (i.e., it was banded previously).

EFFECT OF BREEDING EXPERIENCE ON REPRODUCTIVE SUCCESS

To determine if breeding experience influences Semipalmated Plover hatching and/or fledging success, I classified each breeding pair into one of the following experience levels:

- 1) inexperienced (both male and female are inexperienced)
- 2) experienced female (female is experienced, male is inexperienced)
- 3) experienced male (male is experienced, female is inexperienced)
- 4) experienced (both male and female are experienced)

Although some birds were banded in 1992, intensive banding efforts did not begin until 1993. So, in 1993 all unbanded birds on the study area would have been considered inexperienced. For this reason, I only used data from 1994-1998 for this analysis.

STATISTICAL ANALYSES

The distribution of number of eggs laid, number of hatched eggs and number of young fledged deviated strongly from normality and could not be made normal through transformations. Therefore, I used non-parametric statistical methods to test for annual

variation in Semipalmated Plover reproductive success. Specifically, Kruskal-Wallis tests (PROC NPAR1WAY, SAS Institute Inc. 1990) were used to determine if clutch size, number of eggs hatched per nesting attempt, number of chicks fledged per nesting attempt, number of eggs hatched per successful nest, and number of chicks fledged per brood varied among years.

To determine if number of eggs hatched or number of young fledged per nesting attempt, varied among pairs of different experience levels, I used a log-linear model which treated the number of hatched eggs or number of fledged young as a multinomially distributed random variable (PROC CATMOD, SAS Institute Inc. 1990) (Hitchcock and Gratto-Trevor 1997). This procedure is analogous to ANOVA with the exception of the test statistic, which is asymptotically distributed as a χ^2 distribution (Hitchcock and Gratto-Trevor 1997).

To test my hypothesis that experienced birds nest earlier in the season, I used an ANOVA (PROC ANOVA, SAS Institute Inc. 1990). To account for significant year-to-year variation in date of clutch completion (hereafter DOC) (ANOVA, $F_{6,221}=20.67$, $P<0.001$) (Figure 3.1), dates were first standardized using the following formula:

$\frac{(x_i - \bar{x})}{\bar{x}}$, where x_i is the DOC for each nest and \bar{x} is the mean DOC. A negative DOC

indicates that a nest is laid earlier than the population average and positive dates indicate that the pair nested later than average.

All means are presented ± 1 standard error. All tests were two-tailed and were considered significant at $P<0.05$. P -values reported from Kruskal-Wallis tests were adjusted for ties (Zar 1996).

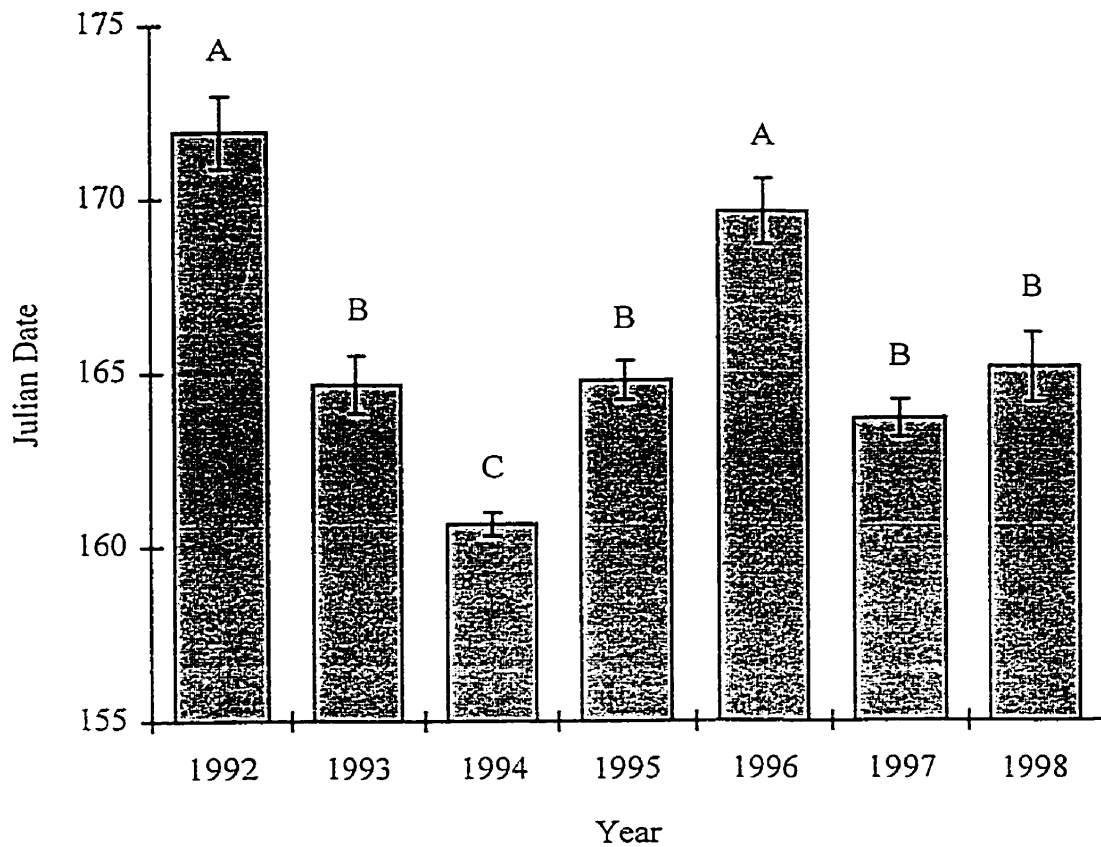


Figure 3.1 – Annual variation in mean date of clutch completion (± 1 SE) for a colour-banded population of Semipalmated Plovers nesting at Churchill, Manitoba from 1992-1998. Dates are Julian dates where 152=1 June for all years except the two leap years (1992 and 1996) where 154=1 June. Bars with different letters are significantly different from each other.

RESULTS

CLUTCH SIZE

There was significant annual variation in Semipalmated Plover clutch size from 1992 to 1998 (Kruskal-Wallis: $\chi^2=16.30$, $df=6$, $P<0.05$). Clutch size was smallest in 1992 (3.72 ± 0.11), followed by 1998 (3.83 ± 0.09) and 1997 (3.85 ± 0.06) (Table 3.1). In 1995, all Semipalmated Plovers laid four egg clutches, but in 1992 and 1997, a higher than average proportion of nests contained three egg clutches (Table 3.2). The proportion of nests with less than four eggs ranged from 0% in 1995 to 24% in 1992 (Table 3.2).

CLUTCH AND EGG HATCHING SUCCESS

There was significant annual variation in number of eggs hatched per nesting attempt (Kruskal-Wallis: $\chi^2=18.23$, $df=6$, $P<0.01$). Semipalmated Plovers hatched the greatest number of eggs per nesting attempt in 1994 (2.98 ± 0.26) and the fewest in 1997 (1.83 ± 0.24) (Table 3.1). Clutch hatching success varied from 52.4% in 1995 to 77.4% in 1994.

Rates of nest predation also varied annually ($\chi^2=12.60$, $df=6$, $P<0.05$) (Figure 3.2). In 1995 and 1997 a high proportion of Semipalmated Plover nests were depredated (47.6% and 43.1% respectively), whereas a low proportion of nests were depredated in 1994 and 1996 (16.3% and 15.8 % respectively) (Figure 3.2). Other causes of nest failure were abandonment (3% of nests from 1992-1998) and destruction by trampling (1.5% of nests from 1992-1998).

Table 3.1 - Summary of annual variation in reproductive success from 1992-1998 for a colour-marked breeding population of Semipalmated Plovers at Churchill, MB. Numbers in parentheses represent sample size, and means are presented ± 1 SE. Kruskal-Wallis tests were used to test for annual variation and *P*-values were adjusted for ties.

Reproductive Parameter	1992	1993	1994	1995	1996	1997	1998	<i>P</i>
Clutch Size	3.72 \pm 0.11 (18)	3.97 \pm 0.03 (37)	3.97 \pm 0.03 (35)	4.00 (22)	3.92 \pm 0.06 (38)	3.85 \pm 0.06 (40)	3.83 \pm 0.09 (41)	0.05
Clutch Hatching Success	70.6% (18)	70.0% (30)	77.4% (43)	52.4% (42)	76.3% (38)	53.4% (58)	74.4% (40)	
Eggs hatched per nesting attempt	2.00 \pm 0.37 (18)	2.60 \pm 0.35 (28)	2.98 \pm 0.26 (43)	2.02 \pm 0.31 (42)	2.68 \pm 0.27 (38)	1.83 \pm 0.24 (58)	2.22 \pm 0.25 (40)	0.05
Egg Hatching Success	86.4% (13)	94.0% (21)	97.8% (33)	96.6% (22)	87.9% (29)	89.1% (31)	80.2% (29)	
Eggs hatched per successful nest	2.92 \pm 0.21 (13)	3.71 \pm 0.14 (21)	3.88 \pm 0.06 (33)	3.86 \pm 0.10 (22)	3.52 \pm 0.14 (29)	3.42 \pm 0.14 (31)	3.07 \pm 0.17 (29)	0.05
Fledging Success	—	—	—	42.9% (34)	55.2% (29)	38.8% (49)	51.7% (29)	
Chicks fledged per nesting attempt	—	—	—	1.03 \pm 0.24 (34)	1.00 \pm 0.22 (29)	0.78 \pm 0.16 (49)	0.97 \pm 0.21 (29)	0.63
Chick survival	—	—	—	61.4% (15)	40.3% (18)	46.0% (24)	57.1% (17)	
Chicks fledged per brood	—	—	—	2.33 \pm 0.30 (15)	1.45 \pm 0.25 (18)	1.62 \pm 0.25 (24)	1.65 \pm 0.24 (17)	0.21

Table 3.2 – Distribution of eggs laid and eggs hatched by Semipalmated Plovers breeding at Churchill, Manitoba from 1992 to 1998.

Year	Eggs Laid			Nests with less than four eggs (%)	Eggs Hatched				
	2	3	4		0	1	2	3	4
1992	1	6	22	24	6	1	0	8	2
1993	0	1	36	3	9	0	2	2	17
1994	0	1	46	2	11	0	0	4	29
1995	0	0	37	0	21	0	0	1	23
1996	1	1	36	5	10	0	3	6	19
1997	0	6	34	15	25	1	2	11	17
1998	3	1	37	10	9	2	5	11	11

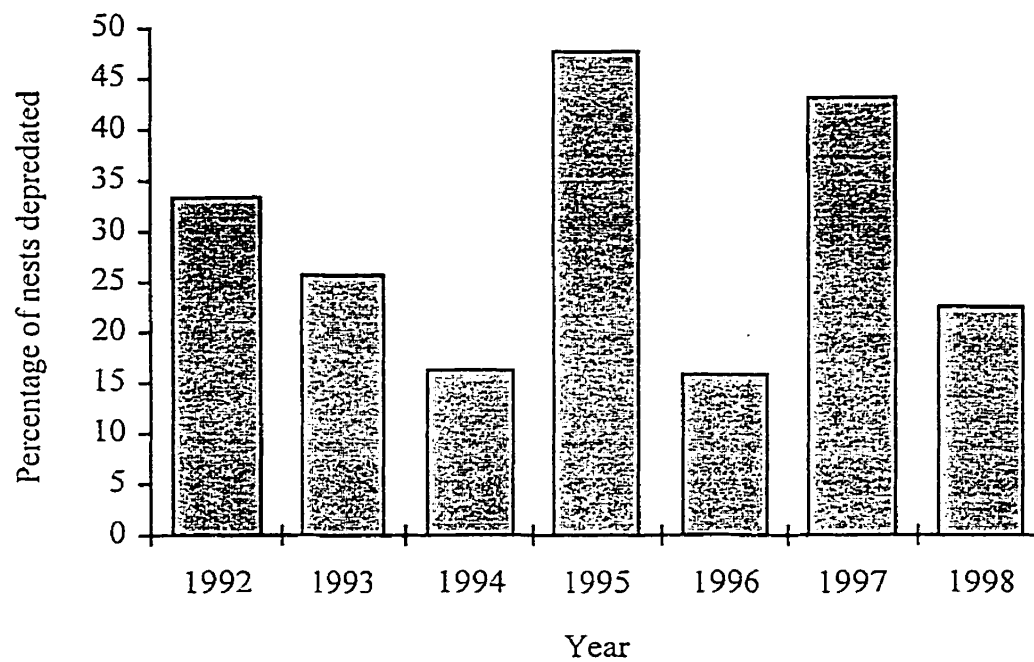


Figure 3.2 – Percentage of Semipalmated Plover nests that were depredated at Churchill, Manitoba from 1992-1998.

After excluding nests that failed to hatch any eggs, significant annual variation in number of eggs hatched per successful nest remained (Kruskal-Wallis: $\chi^2=37.02$, $df=6$, $P<0.001$) (Table 3.1). Hatchability was lowest in 1998 (80.2%) and 1992 (86.4%) when many Semipalmated Plover pairs failed to hatch their entire clutch (Table 3.2). In all other years egg hatching success was relatively high (range: 89.1% to 97.8%) and most successful pairs hatched a complete clutch (Table 3.1, 3.2).

FLEDGING SUCCESS AND PRE-FLEDGLING SURVIVAL

From 1995-1998, there was no detectable annual variation in number of chicks fledged per nesting attempt ($\chi^2=1.75$, $df=3$, $P=0.63$) or number of chicks fledged per brood (Kruskal-Wallis: $\chi^2=3.6$, $df=3$, $P=0.31$) (Table 3.1). On average, Semipalmated Plovers produced 0.92 fledglings/nesting attempt ($N=141$) and 1.74 fledglings/brood ($N=74$). Most pairs fledged one or two young, and few pairs fledged four young (Table 3.3). Of the pairs that hatched young, 7% subsequently lost their entire brood, 36% fledged one young, 29% fledged two young, and only 9% fledged four young (Table 3.3).

EFFECT OF BREEDING EXPERIENCE ON REPRODUCTIVE SUCCESS

Clutch hatching success. – The effect of breeding experience on clutch hatching success varied among years (Table 3.4). There was a significant year by experience interaction (Kruskal-Wallis: $\chi^2=30.94$, $df=12$, $P<0.01$), so each year was analyzed separately. In 1994 and 1995, there was no detectable difference in clutch hatching success among pairs of different experience levels (1994: $\chi^2=0.7$, $df=3$, $P=0.86$; 1995: $\chi^2=2.3$, $df=3$, $P=0.51$).

Table 3.3 – Number of Semipalmated Plover pairs nesting around Churchill, Manitoba that fledged 0, 1, 2, 3 and 4 young from 1995-1998. Only pairs that successfully hatched their clutch were included.

Year	Number of fledged young				
	0	1	2	3	4
1995	0	5	3	4	3
1996	3	8	3	3	1
1997	5	5	9	3	2
1998	2	6	5	4	0

Table 3.4 - Percentage of Semipalmated Plover pairs of different experience levels at Churchill, Manitoba that hatched 0, 1, 2, 3, and 4 eggs from 1994-1998.

Experience Level	Eggs Hatched					<i>N</i>	<i>P</i>
	0	1	2	3	4		
<u>1994</u>							
inexperienced	21.7	0	0	8.7	69.6	23	0.86
female experience	20.0	0	0	0	8.0	5	
male experience	28.6	0	0	14.3	57.1	7	
experienced	33.3	0	0	11.1	55.6	9	
<u>1995</u>							
inexperienced	61.5	0	0	0	38.5	13	0.51
female experience	0	75.0	0	0	25.0	4	
male experience	4.0	0	0	10.0	50.0	10	
experienced	33.3	0	6.7	0	0	15	
<u>1996</u>							
inexperienced	35.7	0	7.1	7.1	50.0	14	0.06
female experience	50.0	0	25.0	0	25.0	4	
male experience	25.0	0	0	12.5	62.5	8	
experienced	0	0	16.7	33.3	50.0	12	
<u>1997</u>							
inexperienced	33.3	4.8	4.8	28.6	28.6	21	0.06
female experience	33.3	0	0	0	66.7	3	
male experience	40.0	0	0	13.3	46.7	15	
experienced	68.4	0	5.3	15.8	10.5	19	
<u>1998</u>							
inexperienced	44.4	5.6	22.2	55.6	22.2	18	<0.001
female experience	0	0	20.0	40.0	40.0	5	
male experience	14.3	0	0	57.1	28.6	7	
experienced	0	0	0	57.1	42.9	7	

Experience was nearly significant in 1996 and 1997 (1996: $\chi^2=7.3$, $df=3$, $P=0.06$; 1997: $\chi^2=7.6$, $df=3$, $P=0.06$), and was significant in 1998 ($\chi^2=20.0$, $df=3$, $P<0.001$). In 1996 and 1998, experienced pairs had higher clutch hatching success than did birds of other experience levels, but in 1997 the opposite trend occurred. In 1996, all experienced pairs hatched at least two eggs and in 1998, all experienced pairs hatched at least three eggs. In 1997, however, experienced pairs had higher levels of nest failure than did birds of other experience levels.

Fledging success. - Because there was no significant annual variation in fledging success, data from all years (1995-1998) were combined for analysis. Fledging success varied significantly among pairs of different experience levels ($\chi^2=10.41$, $df=3$, $P<0.05$) (Table 3.5). Experienced pairs, and experienced male pairs were less likely to fledge no young and more likely to fledge three young than were experienced female pairs and inexperienced pairs. Only 36% of inexperienced pairs and 38% of female experienced pairs fledged at least one young, whereas 52% of experienced male pairs and 56% of experienced pairs fledged at least one young. There were no apparent differences in fledging success between inexperienced pairs and experienced female pairs (Table 3.5).

EFFECT OF EXPERIENCE ON LAYING DATE

There was no difference in nesting dates among birds of different experience levels (ANOVA, $F_{3,182}=1.46$, $P=0.22$). Mean standardized DOC was $+0.002\pm0.003$ for inexperienced pairs, $+0.008\pm0.007$ for female experienced pairs, -0.005 ± 0.003 for experienced male pairs and -0.0023 ± 0.0035 for experienced pairs.

Table 3.5 - Percentage of Semipalmated Plover pairs of different experience levels at Churchill, Manitoba that fledged 0, 1, 2, 3 and 4 young from 1995-1998. Sample sizes for each experience level are shown in parentheses.

Experience Level	Number of fledglings				
	0	1	2	3	4
inexperienced (50)	64.0	24.0	10.0	2.0	0
experienced female (11)	63.6	18.2	9.1	0	9.1
experienced male (40)	47.5	27.5	10.0	15.0	0
experienced (34)	44.1	20.6	11.8	14.7	8.8

DISCUSSION

CLUTCH SIZE AND HATCHING SUCCESS

Clutch size. – Shorebirds may forego breeding when environmental conditions on the breeding grounds are unfavourable, but rarely reduce their clutch size. However, among Semipalmated Sandpipers (*Calidris pusilla*) breeding at Nome, Alaska, reductions in clutch size are fairly common (Sandercock et al. 1999). The proportion of Semipalmated Sandpiper nests with fewer than four eggs ranged from 8 to 34% over four years. Semipalmated Sandpiper clutch size also declined seasonally; nests with a reduced number of eggs were initiated later in the season than were nests with four eggs (Sandercock et al. 1999). A reduction in mean clutch size of Long-billed Curlews (*Numenius phaeopus*) occurred during one breeding season in Idaho, and may have been a response to decreased habitat quality (Redmond and Jenni 1986). Increased density of vegetation forced curlews to travel greater distances in search of food and as a result females may have been unable to acquire sufficient nutrients to lay a full clutch. Similarly, in response to colder than average temperatures in 1992, Semipalmated Plover clutch size was reduced. Because birds require more food during cold temperatures and invertebrate prey may be less available when temperatures drop (Pienkowski 1983), female Semipalmated Plovers may have been unable to acquire sufficient energy to lay four eggs (Nol et al. 1997). Clutch size was also reduced in 1997 and 1998, but the effect was less pronounced than in 1992. In 1992, 24% of nests contained less than four eggs, whereas only 15% of nests in 1997 and 10% of nests in 1998 contained a reduced clutch. Although it is possible that partial predation may have caused the observed reduction in

clutch size, if this were true, partial nest loss would be expected in all years.

Furthermore, no eggs were lost from nests that were monitored during laying.

Reductions in shorebird clutch size have been only rarely reported, but my results suggest that clutch size of shorebirds may not be fixed, and that reductions occasionally occur. Large reductions in Semipalmated Plover clutch size likely occur only when environmental conditions are particularly unfavourable, but smaller reductions (e.g., 1997 and 1998) may reflect individual variation in female physical condition. Some females in the population, such as younger individuals or inefficient foragers, may be in poor physical condition and thus unable to lay a four-egg clutch.

Egg hatching success. – Hatchability of shorebird nests is typically high (close to 100%) (Evans and Pienkowski 1984), but hatchability of Semipalmated Plover nests were lower than those reported for other shorebirds. For example, egg hatching success of Snowy Plovers in California was 95% over six years (Warriner et al. 1986), and similar rates were reported for Ringed Plovers (*Charadrius hiaticula*) (92-96%) (Evans and Pienkowski 1984), Dotterel (*Charadrius morinellus*) (95%) (Pulliainen 1970), and Eurasian Golden Plovers (*Pluvialis apricaria*) (96%) (Ratcliffe 1976). In most years, hatchability of Semipalmated Plover nests was high, but in 1992 and 1998, egg hatching success was only 82% and 80% respectively. In 1992, some pairs abandoned eggs with fully developed chicks at hatch, perhaps as a form of brood reduction to cope with cold temperatures (Nol et al. 1997). When conditions are unfavourable, females may neglect eggs during incubation and/or abandon them at hatch so that brood size will be reduced (Nol et al. 1997). Larger broods require greater parental investment in the form of more

time spent brooding chicks, and during harsh weather conditions, females may be unable to meet energy demands of the brood (Nol et al. 1997).

In 1998, however, environmental conditions on the breeding grounds appeared normal, and yet many Semipalmated Plovers failed to hatch an entire clutch. Clutch size, hatchability and local survival rates (Chapter 2) were all lower than average in 1998. I hypothesize that the El Niño Southern Oscillation event in the winter of 1997-1998 may have negatively affected Semipalmated Plovers on their wintering and/or staging grounds. As a result, fewer birds survived and breeding female plovers were in poor condition and thus unable to incubate and rear four young (Chapter 2).

Clutch hatching success. – Clutch hatching success varies considerably among shorebird species, and within a species varies among habitats and years (Evans and Pienkowski 1984). In some years, coastal nesting shorebirds may suffer higher rates of nest loss than do inland nesters because of unpredictably high tides (e.g., Ringed Plovers, Evans and Pienkowski 1984). In this study, few Semipalmated Plover nests were lost to tides because coastal nests are located well above the high tide level and many plovers nest inland. Coastal nesting shorebirds also may be more vulnerable to nest predation, because some predators routinely search along the high-tide line for nests (Evans and Pienkowski 1984). At Churchill, more predators were observed at coastal nest sites than at inland nest sites (Sullivan Blanken 1996) and in some years coastal nesting Semipalmated Plovers suffered higher rates of nest predation than did inland nesters (E. Nol, unpublished data). However, this varies among years, and there was no consistent pattern.

Semipalmated Plover egg predation rate varied among years and was highest in 1995 and 1997 (48% and 43% of nests depredated respectively). Potential egg predators at Churchill include Ravens (*Corvus corax*), Arctic Fox (*Alopex lagopus*), and Red Fox (*Vulpes vulpes*) (Nol and Blanken 1999). Herring Gulls (*Larus argentatus*) and weasels (*Mustela sp.*) are also probable egg predators. Like other shorebird species, Semipalmated Plover nest predation rates may be correlated with lemming cycles (Underhill et al. 1993). Years in which lemming abundance has declined substantially from the previous year (e.g., 1995), predators may switch to eggs as an alternate prey source (see Chapter 2). A full understanding of this relationship needs to wait for more years of data.

Clutch hatching success estimates reported in this study may be inflated because nests that failed early in the season prior to being found were not included in calculations (Mayfield 1961). I believe that the number of undiscovered nests was small because the study area was thoroughly searched and few non-breeders were seen in the area. However, there were likely a few nests that were depredated before being discovered. Warriner and Paton (1995) found that observed clutch hatching success of Snowy Plovers was on average, 1.6 times higher than rates calculated from Mayfield's method, but I do not know if researchers searched for nests early in the incubation period. In future studies, Mayfield's method (Mayfield 1961) should be used to determine if observed hatching success is over-estimating true hatching success.

Semipalmated Plover hatching success was comparable to that of several temperate-nesting plover species. Mountain Plover hatching success (*Charadrius montanus*) (2.1-2.7 eggs hatched per nesting attempt) (Knopf 1996) is similar to that of

Semipalmated Plovers, whereas hatching success estimates reported for Wilson's Plover (*Charadrius wilsonia*) (25- 45%, Bergstrom 1988), Piping Plover (*Charadrius melodus*) (41-42%, Prindiville-Gaines and Ryan 1988), and Snowy Plover (*Charadrius alexandrinus*) (\bar{x} =47%, range: 13-69%, Warriner and Paton 1995) are lower than that of Semipalmated Plovers. Spur-winged Plovers (*Vanellus spinosus*) nesting in agricultural areas in Israel have slightly higher hatching success than do Semipalmated Plovers ($\bar{x} \pm \text{S.E.} = 86.4 \pm 21.2\%$) (Yogev et al. 1996). Temperate nesting shorebirds (e.g., Snowy, Wilson's, Piping plovers) typically have lower hatching success than do arctic nesting species (Evans and Pienkowski 1984), because of a greater variety of egg predators at temperate latitudes and because their nests may be more susceptible to human disturbance.

FLEDGING SUCCESS

Pre-fledging survival is one of the most difficult shorebird reproductive parameters to measure, so fledging success estimates were available for only a few species. In this study, observed fledging success may underestimate true Semipalmated Plover fledging success because pairs that fledged an unknown number of chicks were excluded from calculations.

Semipalmated Plover parental duties include brooding chicks, defending against predators and conspecifics, and leading chicks to feeding areas (Nol and Blanken 1999). Shorebird mortality is highest during the first few weeks of life because chicks must forage independently immediately after hatch (Evans and Pienkowski 1984). Their thermoregulatory ability is poorly developed and thus chicks depend almost entirely on

their parents for warmth (Grant 1991). Among Ringed Plovers, 53% of all chick mortality occurred in the first week after hatching, and 95% before chicks were two weeks old (Pienkowski 1984). Similarly, more than 80% of Whimbrel (*Numenius phaeopus*) chick mortality occurred within 14 days of hatch (Grant 1991).

Probable causes of Semipalmated Plover chick mortality include predation, starvation, exposure, drowning, and trampling. At Churchill, long day length and an apparent abundance of foraging areas make it unlikely that many chicks die of starvation. However, death due to starvation may be more prevalent when weather conditions at hatch are severe (e.g., heavy rain, strong wind, cold temperatures) (Evans and Pienkowski 1984). Although the depredation of a Semipalmated Plover chick has never been observed, it is likely that foxes, gulls and other aerial predators prey upon chicks. Semipalmated Plovers nesting in disturbed areas at Churchill may also die from trampling by humans and vehicles.

Semipalmated Plover fledging success is comparable to that of three other plover species. Piping Plover fledging success in the Atlantic region of the United States ranged from 0.97 to 1.69 fledglings per pair (USFWS 1996), Snowy Plovers fledged an average of 1.6 fledglings per successful brood (Warriner and Paton 1995), and survival of Ringed Plovers from hatch to fledge in Greenland varied from 40-60% (Pienkowski 1984). Fledging success estimates for other shorebird species (e.g., Long-billed Curlew, Whimbrel, Semipalmated Sandpiper) are also similar to or slightly lower than that of Semipalmated Plovers (Redmond and Jenni 1986, Grant 1991, Gratto-Trevor 1992).

DOES BREEDING EXPERIENCE INFLUENCE REPRODUCTIVE SUCCESS?

Hatching success – Parental breeding experience did not explain differences in Semipalmated Plover hatching success. I predicted that experienced birds would hatch more eggs than would first-time breeders, but this occurred only in 1996 and 1998. In all other years there was no detectable difference in hatching success among birds of different experience levels, and in 1997 hatching success of experienced and male experienced pairs was lower than that of female experienced and inexperienced pairs. Breeding experience also had little effect on Semipalmated Sandpiper hatching success (Hitchcock and Gratto-Trevor 1997). In some years, experienced female Semipalmated Sandpipers at La Pérouse Bay hatched more eggs than did inexperienced birds while in other years there was no experience effect.

I hypothesized that experienced pairs would be better than would inexperienced pairs at defending nests against predators. Like most shorebirds, Semipalmated Plovers rely on camouflage, and/or injury feigning to avoid predation. During incubation, parents typically respond to predators by running off the nest and then either flying away or standing far from the nest (Nol and Blanken 1999). Once away from the nest, the parent will stand quietly, call loudly, or occasionally feign injury. My results suggest that these predation avoidance strategies are innate, and do not improve with breeding experience. Other factors such as habitat (Prindiville-Gaines and Ryan 1988), nest site characteristics (Page et al. 1985), or nesting density (Page et al. 1983) probably have a greater influence on Semipalmated Plover hatching success.

Fledging success – Unlike hatching success, fledging success improved with breeding experience, although this varied between the sexes. Male reproductive success

improved with experience but female success did not. Pairs with an experienced male fledged more chicks than did either inexperienced or female experience pairs. Female Semipalmated Plovers remain with the brood for approximately 15 days after hatch (and sometimes less) whereas males stay with the brood until fledging (Nol and Blanken 1999). So, it follows that male breeding experience has a greater influence on Semipalmated Plover fledging success.

The Kentish Plover (*Charadrius alexandrinus*) is unusual among plovers in that either sex deserts, leaving the remaining parent to care for the brood alone (Székely 1996). By experimentally removing one parent, Székely (1996) found that male tended-broods had higher survival rates than did female-tended broods because male parents were better able to protect the brood from attacks by conspecifics and predators. Males of some other plover species (e.g., Killdeer (*Charadrius vociferus*) and Golden Plover (*Pluvialis apricaria*)) also protect young more intensively than do females (Byrkjedal 1987, Brunton 1990). Male Killdeer perform more intensive distraction displays and approach predators more closely than do females (Brunton 1990), and male Kentish Plovers are more successful than are females in keeping conspecifics away from the brood (Székely 1996). Although there are few sexual differences in Semipalmated Plover parental behaviour, male plovers fly and vocalize more than do females (Sullivan Blanken and Nol 1998). Flying and vocalizing more frequently may indicate that, like other plovers, male Semipalmated Plovers ward off potential predators more actively than do females.

An increase in reproductive success with breeding experience has been demonstrated for two other shorebird species. Spotted Sandpipers are polyandrous with

reversed sex roles (Oring et al. 1997). Females mate with up to four males, and the male is typically left to care for the clutch and brood alone (Oring et al. 1997). Female polyandrous Spotted Sandpipers with prior breeding experience acquire more mates, lay and hatch more eggs, and fledge more young than do inexperienced females (Oring et al. 1983). Hatching and fledging success of male Spotted Sandpipers does not differ between experienced and inexperienced birds (Oring et al. 1983), which is surprising because the male provides all or most of the parental care (Oring et al. 1983). Breeding success of female Redshanks (male success was not measured) is also related to breeding experience but contrary to my findings, experienced female Redshanks had higher hatching success than did inexperienced females (Thompson and Hale 1989).

Natal philopatry for Semipalmated Plovers at Churchill is one of the lowest rates reported for shorebirds (<2% of chicks banded as young return to breed, Flynn et al. 1999), and adult Semipalmated Plovers cannot be aged by plumage. Consequently, the age of most breeders was unknown. To test the independent effects of age on reproductive success, it is necessary to compare reproductive success of first-time breeders of different chronological ages (e.g., Wooller et al. 1990). This analysis was not possible for Semipalmated Plovers because of the small number of known-age birds. Thus, I was unable to separately examine the effects of age and breeding experience on reproductive success.

It is likely that both age and breeding experience influence Semipalmated Plover reproductive success. For some species, reproductive success increases with age because older birds lay larger and/or more eggs than do younger birds (Hamer and Furness 1991, Croxall et al. 1992, Desrochers and Magrath 1993). There is little variation in

Semipalmated Plover egg size and clutch size (Nol et al. 1997, this study) and hatching success is not affected by age or experience (this study). So, in this study, pre-fledging survival is the only reproductive parameter influenced by age and/or breeding experience.

Age-related increases in reproductive success have been attributed to improvements in skills such as foraging efficiency and predation avoidance (Nol and Smith 1987). Improvements in foraging efficiency of adults would not benefit precocial Semipalmated Plover young, however, improvements in predation avoidance and intraspecific competition may result in older birds fledging more young. Experienced male Semipalmated Plovers may be more efficient at protecting young from predators and conspecifics and better able to locate predator 'safe' foraging areas. These skills may be age-related, but I hypothesize that they are more likely due to knowledge accrued from prior breeding attempts.

One of the pre-requisites of the residual reproductive values hypothesis is that the proportion of adults that survive to breed again declines with age (Smith and Nol 1987). Semipalmated Plover survival rates are not age-related (Chapter 2), thus older Semipalmated Plovers do not need to increase their reproductive output. This hypothesis may be more relevant to long-lived birds (e.g., seabirds) whose survival rates decline with increasing breeding experience (Wooler et al. 1990).

The selection hypothesis, on the other hand may partly explain why reproductive success improved with breeding experience. Local survival of Semipalmated Plovers at Churchill is correlated with hatching success. Years in which Semipalmated Plovers experience high hatching success on the breeding grounds correspond to years with high survival probabilities (Chapter 2). Birds that fail to hatch any eggs may suffer high

mortality rates or permanently emigrate from the study area. So, it is possible that experienced pairs have higher apparent reproductive success because there are fewer 'poor' breeders in the population. Further investigation into the role of breeding experience and age on Semipalmated Plover reproductive success is needed.

CHAPTER 4

A DEMOGRAPHIC MATRIX MODEL FOR SEMIPALMATED PLOVERS (*CHARADRIUS SEMIPALMATUS*) BREEDING AT CHURCHILL, MANITOBA.

ABSTRACT

A matrix population model was constructed using demographic data from an intensively monitored breeding population of Semipalmated Plovers (*Charadrius semipalmatus*) at Churchill, Manitoba from 1992-1998. A simple, deterministic, density-independent model was used, and due to the limitations of this model, it should be considered a starting point for future, more sophisticated demographic analyses. The growth rate of the population was $\lambda=0.846\pm0.046$ which is significantly different from that of a stable population (i.e., $\lambda=1.0$). The model predicted a population decline of more than 15% per year, but annual population censuses showed no change in population size. The poor predictive ability of the model was likely due to high rates of immigration. The number of birds entering the population each year appeared to greatly exceed the number of birds emigrating. Sensitivity analyses revealed that population growth rate was most sensitive to changes in adult survival, juvenile post-fledging survival and pre-fledging survival. Despite an observed stable population, rates of survival and fecundity were insufficient to maintain the population, and the Churchill Semipalmated Plover population is reliant on an influx of birds from other populations. Therefore, changes in the demography of breeding populations in surrounding regions will also affect the Churchill population. Results of this model have important implications for shorebird conservation.

INTRODUCTION

Shorebirds have low reproductive rates and high adult survivorship, rendering them susceptible to population declines (Evans and Pienkowski 1984, Myers et al. 1987, Evans 1991, Hitchcock and Gratto-Trevor 1997). For many bird species, including shorebirds, adult survival probability is the demographic parameter to which the population growth rate is most sensitive (Lebreton and Colbert 1991, Hitchcock and Gratto-Trevor 1997). Only a very small change in adult survival probability can cause a stable population to decline (Hitchcock and Gratto-Trevor 1997). The combination of low annual reproductive output and high annual survival has important conservation implications because of the tendency for shorebirds to congregate in small geographic areas during migration and in winter (Myers et al. 1987). A large proportion of a species' population can be found at a single staging area (Myers et al. 1987), and as a result of human development, many of the sites used by shorebirds have been lost, severely diminished in size or otherwise degraded, which has the potential to decrease adult survival and consequently population size (Myers et al. 1987, Skagen and Knopf 1993, Morrison et al. 1994).

Three of nine Nearctic plover species (Piping Plover (*Charadrius melodus*), Mountain Plover (*Charadrius montanus*) and Snowy Plover (*Charadrius alexandrinus*)) are species of concern (designated as endangered or threatened) (Haig 1992, Warriner and Paton 1995, Knopf 1996), and two more (Killdeer (*Charadrius vociferus*) and Black-bellied Plover (*Pluvialis squatarola*)) are in decline (Sauer et al. 1999, Morrison et al. 1994). Population trend estimates for Lesser Golden-Plover (*Pluvialis dominica*), and American Golden-Plover (*Pluvialis fulva*) although uncertain, also show signs of decline

(Johnson and Connors 1996). Semipalmated Plover (*Charadrius semipalmatus*) is the only plover species whose numbers appear to be increasing (Nol and Blanken 1999). This population increase could be due to this species' versatility in food and habitat choice, its widespread coastal winter distribution or its habitat expansion in the sub-arctic (Nol and Blanken 1999). In sub-arctic regions of Canada, the availability of habitat for Semipalmated Plovers may be increasing due to the degradation of coastal marshes by burgeoning populations of arctic-nesting geese (Abraham and Jeffries 1997). Semipalmated Plovers use the open degraded habitat that is created by over-grazing and over-grubbing of the geese (Abraham and Jeffries 1997), although the degree to which this habitat is used is presently unknown.

Our ability to assess change in arctic shorebird populations is limited due to the remoteness and inaccessibility of breeding grounds, so few long-term studies have examined breeding populations of shorebirds (Page and Gill 1994). An examination of demographic parameters can provide insight into factors that limit a species population size and make it possible to describe and understand the population dynamics governing a species (Lebreton and Clobert 1991). With a basic understanding of a species' life history, matrix models can be used to assess the relative impact of varying rates of survival, mortality and fecundity in a population.

A breeding population of Semipalmated Plovers at Churchill, Manitoba has been intensively monitored since 1992, and unlike other shorebird populations nesting in the Hudson Bay lowlands (e.g., Semipalmated Sandpipers, Hitchcock and Gratto-Trevor 1997) has shown no signs of decline. This long-term dataset created a unique opportunity to investigate the demography of a stable shorebird population. In this paper,

I use demographic data for Semipalmated Plovers at Churchill, Manitoba to develop a structured matrix population model. Using a simple, deterministic, density-independent approach, I calculate the geometric growth rate (λ) of the population, its standard error, and the sensitivity of λ to changes in demographic parameters.

METHODS

NEST SEARCHING

Survival and reproductive success of a colour-marked population of Semipalmated Plovers at Churchill, Manitoba was studied from 1992-1998 (Chapters 2 and 3). All areas with suitable nesting habitat that were accessible by road were searched with equal effort from 1993 to 1997. No vehicle was available in 1992, so the entire study area was not thoroughly searched. This resulted in low banding effort and no accurate estimation of population size. Semipalmated Plovers are determinate layers, clutches containing more than four eggs have never been found. However, females occasionally lay less than four eggs. Semipalmated Plover nests consist of a small scrape on the ground. Nests were located by walking through the study area and sighting adults performing distraction displays, or by observing foraging adults fly to the nest site. All suitable nesting habitats were searched at least twice in June of each year.

Most nests (90%) were located during incubation, so eggs were measured and weighed to estimate hatch date based on a regression between the index of specific gravity and the ratio of mass to volume (Flynn 1997). To reduce probability of nest predation, nest locations were either marked at a distance with natural material such as rock cairns and wood or were mapped. Nests were subsequently monitored every two to

four days to determine their fate. To reduce disturbing incubating adults, nests were observed from a distance with a spotting scope. Clutches that disappeared between visits were assumed depredated unless another cause was apparent (e.g., destroyed by tides, trampled by humans, other animals, or motor vehicles). Just prior to estimated hatch date, nests were visited at least daily to check for pipped eggs. Once eggs are pipped, hatching usually occurs within 12 hours, but can take up to four days (Sutton and Parmelee 1955). The date at which a complete clutch was laid and incubation began for nests that were located during incubation was determined by subtracting 24 days (mean length of incubation) from hatch date.

PRE-FLEDGING SURVIVAL

Survival of Semipalmated Plover chicks from hatch to fledging was monitored for four years (1995-1998). Parents lead the chicks away from the nest within 24 hours of hatching to forage on the mudflats along Hudson's Bay or at inland ponds, so these areas were searched extensively to locate family groups. To minimize disturbance, families were observed from a distance with a spotting scope. Family groups were observed every 3-4 days to determine the number of chicks present. Semipalmated Plover chicks are difficult to locate because they are cryptically coloured, and crouch down in response to alarm calling parents. To avoid underestimating fledging success by including chicks that were missed during an observation period but were actually still alive, I only included family groups in which the same number of chicks was recorded on multiple occasions. Furthermore, if both parents were observed without chicks, and exhibited no parental behaviour (i.e. alarm calls, distraction displays) on more than one occasion, the chicks were assumed to be dead. Male Semipalmated Plovers remain with the brood

until fledging, whereas females leave at approximately 15 days after hatch (Blanken and Nol 1999). Semipalmated Plovers are capable of flight at 21-24 days (E. Nol pers. comm), so, for this study, I defined pre-fledging survival as survival to 21 days.

NEST TRAPPING AND BANDING

During incubation, adults were nest-trapped with either a Potter trap or a walk-in keyhole nest trap. The circular walk-in nest trap was constructed from hardware cloth with a net top made of either cotton or nylon netting. The square Potter trap was made of 2 mm wire and had a treadle placed over the nestcup that triggered a drop door. To prevent the possibility of nest desertion, birds were not trapped early in the incubation period. Traps were continuously monitored so that birds were removed immediately upon entering, and traps were removed if the adult did not return within 20 minutes. Adult birds were leg-banded with unique combinations of an aluminium Canadian Wildlife Service (CWS) band and 1-3 coloured plastic bands (Size XCL, A.C. Hughes Ltd.). During hatch, chicks were caught by hand and each was banded with an aluminium CWS band and a brood-specific combination of coloured plastic leg bands. Most nestlings were banded one or two days after hatch. Adult plovers were sexed on the basis of plumage colouration (Teather and Nol 1997) whereas nestlings could not be sexed by plumage.

Every year, a small number of birds were not banded, either because their nest was depredated before they could be trapped or because we were unable to trap certain 'wary' birds. The proportion of unbanded adult birds in the population was small every year (1993-1998, mean unbanded birds in population = 12%).

RESIGHTINGS

Survival rates were estimated from resightings of colour-marked birds. During each breeding season, colour-banded Semipalmated Plovers were resighted in the field by either having their unique colour-band combination identified with a spotting scope or being recaptured on the nest. Occasionally, birds were resighted on coastal mudflats and inland ponds but no nest was found. If a colour band was lost, the individual was recaptured, identified by its CWS band and the colour bands were replaced. Colour-band loss was infrequent (<5% of birds), and the majority of the individuals that lost colour-bands (>95%) were subsequently re-banded, so local survival estimates were not likely biased by band loss.

MATRIX POPULATION MODEL

To model the growth rate of the Semipalmated Plover population, I incorporated fecundity and survival estimates into a structured matrix population model. To avoid errors in rounding numbers off, and because some values were very similar in magnitude, in this paper, I presented all values with five significant figures. To simplify analysis of the population's sensitivity to variations in demographic parameters, I used a deterministic, density-independent model. Because of the simplicity of the model and the uncertainty associated with several parameter estimates, I did not forecast long-term population trends. A modified Leslie matrix was used to describe the dynamics of female Semipalmated Plovers only. I divided the female population into three age classes: one year olds, two year olds, and birds three years of age and older (3+). A three-age class model was necessary because many females appear to delay breeding until three years of

age (Flynn et. al. 1999), thus breeding propensity differs among age classes. A life-cycle graph describing the structure of the model is shown in Figure 4.1.

The growth of a population from time t to time $t+1$ was represented by the following equation:

$$N_{t+1} = A \cdot N_t$$

where A is a population projection matrix with elements a_{ij} that describe changes in population size due to mortality and reproduction (Gotelli 1995). For a three age class model, the matrix takes the form:

$$A = \begin{bmatrix} F_1 & F_2 & F_3 + \\ s_1 & 0 & 0 \\ 0 & s_2 & s_3 + \end{bmatrix}$$

In a Leslie matrix, fertilities (F_i) are always in the first row, and survival probabilities (s_i) on the subdiagonal. The F_i values represent the number of female offspring produced by an individual in age class i , and the s_i values are annual survival probabilities for birds in age class i . N_t is the population projection vector; where each element $n_i(t)$ indicates the number of birds in age class i in year t and the total population size in year t is equal to the sum of elements $n_i(t)$ (Hitchcock and Gratto-Trevor 1997).

$$N_t = \begin{bmatrix} n_1(t) \\ n_2(t) \\ n_3 + (t) \end{bmatrix}$$

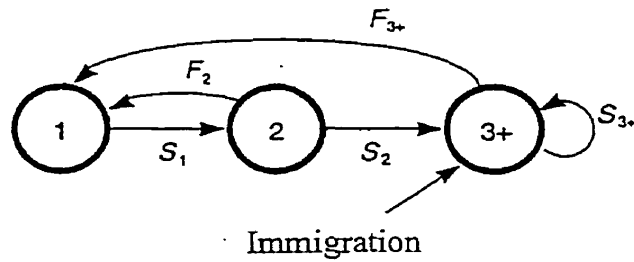


Figure 4.1 – Life-cycle graph for Semipalmated Plover stage-structured matrix population model. The model is a pre-breeding census, with three age classes (stages), and includes females only. The first age class consists of one-year old birds that hatched the previous year. The other two age classes are two-year old birds and birds three years of age and older (3+). Arrows denote transitions from one stage to another. The s_i are survival rates from stage i to stage $i+1$. The F_i are the average number of one-year old birds in year $t+1$ produced by each female in year t . This figure was modified from Hitchcock and Gratto-Trevor (1997).

Because I used a pre-breeding census model, the F_i values are affected both by the number of chicks hatched per female and first-year mortality (s_0) (Hitchcock and Gratto-Trevor 1997, Caswell 1989). The following formula was used to calculate F_i :

$$F_i = 0.5 \cdot \text{prbreed}_i \cdot \text{nhatch}_i \cdot s_{h \rightarrow f} \rightarrow f \cdot s_0$$

Prbreed_i is the probability of breeding at age i (breeding propensity), nhatch_i is the number of eggs hatched per nest by a female in age class i , $s_{h \rightarrow f}$ is pre-fledging survival rate, and s_0 is the probability of surviving from fledging to one year of age (juvenile survival). The equation was multiplied by 0.5 because I assumed an equal sex ratio, so only half of the hatched young will be female.

ESTIMATING DEMOGRAPHIC PARAMETERS

SURVIVAL PROBABILITIES (s_i)

Adult survival (s_1, s_2, s_{3+}). Adult survival rates were estimated from resightings of 152 colour-banded female Semipalmated Plovers from 1993-1998. Birds banded as nestlings were included in survival analyses when first observed as breeding adults. Survival analysis involved a two-step process following methodology outlined in Lebreton et al. (1992). RELEASE was first used to assess goodness-of-fit (GOF) to a Cormack-Jolly-Seber (CJS) model, in which survival and recapture probabilities vary between years (see Chapter 2 for more detail). Once a satisfactory starting model was identified, I then used SURGE for iterative model fitting. The model with the lowest Akaike's Information Criterion ($AIC = DEV + 2 \cdot NP$) was selected as the best fitting model because AIC provides an unbiased criterion for model selection (Burnham and Anderson 1992, Lebreton et al. 1992, Cooch et al. 1996, Chapter 2).

The best fitting female survival model contained constant survival rate over time (model: ϕ_c) (DEV=436.7, NP=2, AIC=440.7). Because female survival rates are not age specific, I assumed that survival rates of one and two year olds were equal to that of older birds (i.e., $s_1=s_2=s_{3+}$). Local survival rate for adult female Semipalmated Plovers (s_1, s_2, s_{3+}) obtained from model ϕ_c, p_c was 0.687220 (95% CI=0.60901-0.75605) (Table 4.1).

Juvenile survival (s_0). I was unable to estimate juvenile survival rate from my dataset, because of the small number of natal recruits in the population (<2% of Semipalmated Plovers banded as chicks returned in subsequent years). Natal philopatry is typically low for most shorebird species, so there are few estimates of juvenile survivorship available and most reported estimates are based on return rates, which tend to underestimate local survival (e.g., Page et al. 1983, Paton 1994, Pienkowski 1984, but see Sandercock and Gratto-Trevor 1997). In addition, few studies have measured fledging success, thus juvenile survivorship estimates are the product of pre-fledging and post-fledging survival. Shorebird mortality is highest in the first week of life, so juvenile survival estimates that include the pre-fledging period will be considerably lower than will post-fledging survival estimates (Evans and Pienkowski 1984). Juvenile post-fledging survival estimates were available for three plover species, and ranged from 65% to 87% that of adult conspecifics (Pienkowski 1984, Ryan et al. 1993, Paton 1994, USFWS 1996).

Based on return rates, juvenile Ringed Plover (*Charadrius hiaticula*), Snowy Plover and Piping Plover survival rates were 74%, 87% and 65% less than that of adults respectively (Ringed Plover: $s_0=0.59$, Pienkowski 1984; Snowy Plover: $s_0=0.64$, Page et al. 1983; Piping Plover: $s_0=0.48$, USFWS 1996).

Table 4.1 – Mean values of female Semipalmated Plover demographic parameters used in the matrix population model, sample sizes and sampling variance.

Demographic parameter	Mean	Variance	Sample Size
Breeding propensity of one year olds ($prbreed_1$)	0	0	general observations
Breeding propensity of two year olds ($prbreed_2$)	0.20000	0.04000	5
Breeding propensity of three year olds ($prbreed_{3+}$)	0.706964	0.00271	152
Number of eggs hatched per female ($nhatch_i$)	2.31970	0.18082	269
Pre-fledging survival ($s_{h \rightarrow f}$)	0.52743	0.01270	75
Juvenile post-fledging survival (s_0)	0.52229	0.00142	estimated from literature
One-year-old survival (s_1)	0.68722	0.00142	152
Two-year-old survival (s_2)	0.68722	0.00142	152
Survival of birds three years old and older (s_{3+})	0.68722	0.00142	152

Based on these values, I estimated that juvenile Semipalmated Plover survival was 76% (midpoint of 65% and 87%) that of adults ($s_0=0.52229$) (Table 4.1). I set the variance in juvenile post-fledging survival equal to that of adult Semipalmated Plovers (Table 4.1).

REPRODUCTIVE SUCCESS (F_i)

Breeding propensity ($prbreed_i$). Breeding propensity of two year olds ($prbreed_2$) was estimated from the small number of Semipalmated Plover chicks that hatched on the study area and returned to breed in subsequent years. One of five natal recruits returned to breed at age two, four returned at age three, and no birds returned to breed in their first year of life. Therefore, I estimated that the probability of a Semipalmated Plover breeding at age one was zero, and at age two was 0.2 (1/5) (Table 4.1).

Breeding propensity for a female Semipalmated Plover in age class 3+ ($prbreed_{3+}$) was estimated from the resighting rate generated from SURGE. Resighting rate is the product of detection rate and temporary emigration. A female that temporarily breeds elsewhere in a certain year, is not contributing to the local population. In fact, her reproductive contribution is equal to that of an individual that returns to the study area and fails to breed. Resighting rate provides a good estimate of female breeding propensity if detection rate is close to 100% (i.e., every female that breeds is resighted). Although search effort was consistently high in every year, because of the large study area, it is highly unlikely that every breeding female was resighted. Therefore, I used the upper 95% confidence interval for resighting rate as an estimate of breeding propensity. Of all resighting models tested, the most parsimonious model contained constant

resighting rate over time (ϕ_c, p_c). The maximum likelihood estimate of female resighting rate was 0.61099 (95% C.I 0.50556-0.70696), thus $prbreed3+$ was set at 0.70696.

Hatching success ($nhatch_i$). The number of eggs hatched per female was not influenced by female age (Chapter 3), so $nhatch_2$ was assumed equal to $nhatch_{3+}$. Hatching success was calculated from observations of 269 nesting attempts from 1992-1998. On average, females hatched 2.32 ± 0.11 eggs per nest, but number of eggs hatched per nest showed significant annual variation (Kruskal-Wallis: $\chi^2=18.23$, $df=6$, $P<0.01$), ranging from 1.83 ± 0.24 eggs/nest in 1997 to 2.98 ± 0.26 eggs/nest in 1994 (Chapter 3, Table 3.1).

Pre-fledging survival (s_{h-f}). The probability of survival from hatch to fledge was calculated from observations of 74 Semipalmated Plover broods from 1995-1998. There was no detectable annual variation in number of chicks fledged per brood (Kruskal-Wallis: $\chi^2=3.6$, $df=3$, $P=0.31$), and fledging success was not influenced by female age (Chapter 3, Tables 3.1 and 3.5). On average, Semipalmated Plovers fledged 1.74 ± 0.14 fledglings per brood, and pre-fledging survival was $0.527 \pm 0.089\%$ (Table 4.1).

IMMIGRATION

Like most shorebird species, adult Semipalmated Plover site fidelity is high, but few young birds return to their natal sites to breed. Thus, immigration can have an important influence on local population dynamics of shorebirds. Each year, most adult and young Semipalmated Plovers were banded, so the number of newly banded adults was used to estimate annual immigration rates. A small number of birds were banded in 1992, but intensive banding efforts began only in 1993. In early years most females were

newly banded and would thus be classified as immigrants. So, to avoid over-estimating immigration, only data from 1995-1998 were used.

POPULATION GROWTH RATE AND SENSITIVITY ANALYSIS

POPULATION GROWTH RATE

The dominant eigenvalue (λ) of matrix A defines population growth rate in the absence of immigration. When $\lambda < 1$, the population is decreasing, when $\lambda = 1$ the population is stable, and when $\lambda > 1$ the population is growing. The per capita rate of increase (r) gives the change in population size per individual per unit time, and is equal to the natural log of λ ($r = \ln\lambda$).

The right eigenvector of matrix A describes the stable age distribution (\mathbf{w}) of the population. The elements w_i of the right eigenvector give the proportion of the population in age class i once enough time has passed that fluctuations due to initial conditions have ended (McDonald and Caswell 1993). Any initial population age structure projected forward will eventually approach the stable age distribution, usually within a few generations (Crouse et al. 1987, McDonald and Caswell 1993). The left eigenvector (\mathbf{v}) is the reproductive value vector. Elements v_i of the reproductive vector represent the total number of progeny that an individual in age class i is expected to produce, including not only immediate offspring but all future descendants of that individual (Burgman et al. 1993).

SENSITIVITY

Sensitivity analysis provides an indication of which demographic parameter (i.e. matrix element) has the largest impact on population growth rate (Lande 1988, Hiraldo et al. 1996). A large sensitivity value indicates that a relatively small change in the value of the corresponding parameter will yield a relatively large change in population growth rate (Burgman et al. 1993). In addition to furthering our understanding of a species' demography, sensitivity analysis has many other useful conservation and management applications. First, it allows researchers to evaluate the effects of errors in estimation of demographic parameters, and to design sampling procedures that maximize precision of estimates with large sensitivities (Caswell 1989). A second use is planning conservation and management strategies (Caswell 1989, Burgman et al. 1993). By identifying the demographic parameter with the greatest influence on lambda, conservation or management activities can be directed at the appropriate life-stage (Caswell 1989, Burgman et al. 1993). For this reason, sensitivity analysis is often used to evaluate strategies to protect endangered species (Simons 1984, Crouse et al. 1987, Lande 1988, Heppell et al. 1994, Hiraldo 1996) or to control pest species (Smith and Trout 1994). Finally, because the coefficients of a sensitivity matrix are equivalent to selection gradients (McDonald and Caswell 1993), sensitivity analysis is commonly used by quantitative genetists to predict life-history trait combinations that should be favored by natural selection (Caswell 1989).

Sensitivity was calculated according to the following equation (Caswell 1989):

$$\frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i, w_j}{(w, v)} ,$$

where \mathbf{v} and \mathbf{w} are the left and right eigenvectors of \mathbf{A} and (\mathbf{w}, \mathbf{v}) is the scalar product of the vectors. Sensitivity of λ to changes in lower level parameters (e.g., prbreed_i , $s_{h \rightarrow t}$) was calculated using simple chain rule differentiation where matrix elements (a_{ij}) are functions of x (Caswell 1989):

$$\frac{\partial \lambda}{\partial x} = \sum \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial x}$$

ELASTICITY

Elasticity analysis was used to assess the proportional contributions of the matrix elements to λ (Brault and Caswell 1993). Because elasticities sum to one, the relative contributions of matrix elements (e.g., survival rates and fertilities) can be compared (Crouse et al. 1987). Elasticity (e_{ij}) was calculated by multiplying the matrix coefficient (a_{ij}) by its corresponding sensitivity value and dividing it by λ (Hitchcock and Gratto-Trevor 1997):

$$e_{ij} = \frac{a_{ij}}{\lambda} \left(\frac{\partial \lambda}{\partial a_{ij}} \right)$$

$$= \frac{a_{ij} s_{ij}}{\lambda}$$

STANDARD ERROR OF λ

There is no simple formula to calculate variance of λ as a function of variances of the matrix elements, but the following formula approximates variance of λ (Lande 1988):

$$\sigma_{\lambda}^2 = \sum (\partial \lambda / \partial a_{\pi})^2 \sigma_{\pi}^2 ,$$

where π represents each of the parameters in the model (s_i , $prbreed_i$, $s_{h \rightarrow i}$, $nhatch_i$), σ_π^2 is the sampling variance of π estimated from N_π individuals in the population and the expression in parentheses is the sensitivity (Tables 4.1 and 4.2). The standard error of λ is equal to the square root of the sampling variance. This formula only approximates standard error because it does not consider covariance between sample statistics (Lande 1988).

RESULTS

Despite small annual fluctuations in number of breeding pairs, and a population increase in 1997, there has been little overall change in the number of Semipalmated Plover pairs at Churchill, Manitoba. The population size showed no signs of increase or decrease from 1992-1998 (linear regression: $df=5$, $F=0.021$, $P=0.89$) (Figure 4.2).

MODEL RESULTS

The following population projection matrix was derived from mean values for all demographic parameters:

$$A = \begin{bmatrix} 0 & 0.06390 & 0.22588 \\ 0.68722 & 0 & 0 \\ 0 & 0.68722 & 0.68722 \end{bmatrix}$$

According to this projection matrix, the growth rate of the Semipalmated Plover population was $\lambda=0.84600$ and the intrinsic rate of increase was $r=-0.16723$.

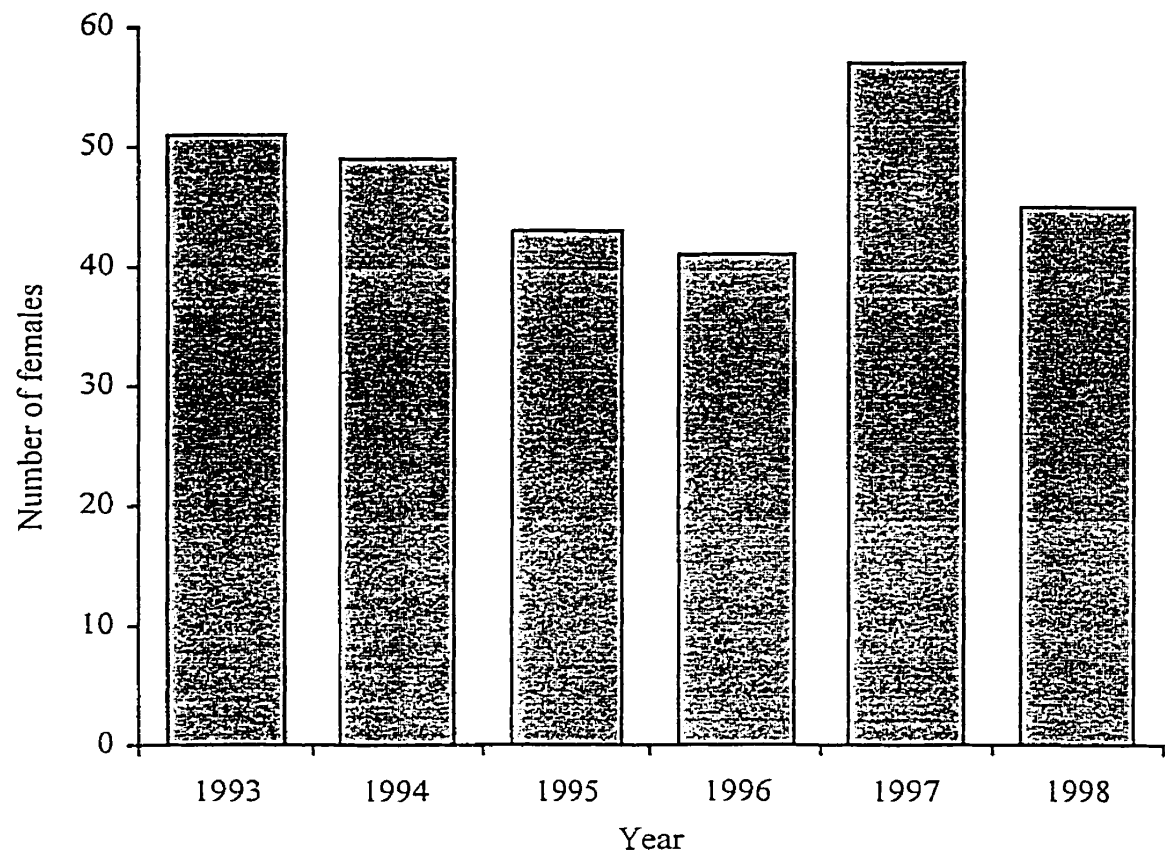


Figure 4.2 - Number of female Semipalmated Plovers breeding on the study area at Churchill, Manitoba from 1993 to 1998.

The standard error of lambda (0.04651) and the 95% confidence interval (0.75484-0.93717) indicated that lambda was significantly different from that of a stable population ($\lambda=1$) (Table 4.2). So, without immigration, the Semipalmated Plover population would have decreased annually by 15.4% (range: 6.3%-24.6%). The stable age distribution (w) and reproductive value (v) vectors were:

$$w = \begin{bmatrix} 0.26707 \\ 0.21694 \\ 0.93894 \end{bmatrix} \quad v = \begin{bmatrix} 1.00000 \\ 1.23105 \\ 1.42252 \end{bmatrix}$$

The stable age distribution was dominated by individuals in age class 3+ (age1: 18.8% age 2: 15.2% age 3+: 66.0%), and reproductive values were lowest for one year olds and highest for individuals in age class 3+.

SENSITIVITY AND ELASTICITY ANALYSES

The sensitivity matrix for the Semipalmated Plover population (with only sensitivities to non-zero transitions shown) was:

$$\left[\frac{\partial \lambda}{\partial a_{ij}} \right] = \begin{bmatrix} \dots & 0.11603 & 0.50216 \\ 0.17865 & \dots & \dots \\ \dots & 0.16505 & 0.71433 \end{bmatrix}$$

and the elasticity matrix was:

$$[e_{ij}] = \begin{bmatrix} 0 & 0.00876 & 0.13407 \\ 0.14284 & 0 & 0 \\ 0 & 0.13407 & 0.57985 \end{bmatrix}$$

Table 4.2 – Sensitivity of λ to changes in each demographic parameter in the matrix population model and the contribution of each parameter to variance of λ . Parameters are listed in order of decreasing sensitivity.

Demographic parameter	Sensitivity	Contribution to σ_λ^2
s_{3+}	0.71433	7.24458×10^{-4}
s_0	0.23137	0.76015×10^{-4}
$s_{h \rightarrow f}$	0.22911	6.66641×10^{-4}
s_1	0.17583	0.43901×10^{-4}
s_2	0.16505	0.38659×10^{-4}
prbreed_{3+}	0.16044	0.69758×10^{-4}
Nhatch	0.05209	4.90631×10^{-4}
prbreed_2	0.03707	0.54967×10^{-4}
Total (σ_λ^2) = 2.16515×10^{-3}		

The sensitivity of lambda to changes in lower level parameters is shown in Table 4.2. In descending order, λ was most sensitive to survival of birds in age class 3+, juvenile survival, and pre-fledging survival. Survival of one and two year olds and probability of breeding at age 3+ had very similar sensitivity values; number of eggs hatched per female and probability of breeding at age 2 had the lowest sensitivities (Table 4.2).

Results of sensitivity and elasticity analyses differed slightly. Fertility of females in age class 3+ had the second highest sensitivity coefficient, but had the third ranked elasticity value, indicating that a proportional change in fertility will have little impact on population growth rate. In the elasticity analysis, survival of females in age class 3+ remained most important, followed by survival of birds to age one. Proportional changes in second year survival and age class 3+ fertility had identical impacts on λ ($e_{3,2}$ and $e_{1,3}=0.13407$). Fertility of two-year-old females had the smallest proportional impact on λ ($e_{1,2}=0.00876$) because few individuals (20%) in this age class are breeders.

To further investigate the effects of changes in life-history parameters on population growth rate, I simulated a 25% reduction and a 25% increase in survival and fecundity while holding the remaining matrix components constant (Figures 4.3a and b). As expected from the sensitivity analysis, a 25% increase in age class 3+ survival had the greatest impact on population growth rate (15.4% increase in λ). Twenty-five percent changes in age class one survival and age class 3+ fertility had equally small effects on population growth rate (3.4% and 3.2% change in λ respectively). Changes in age class 2 survival had a slightly weaker impact on λ (2.7% change) and age class 2 fertility had only a minute impact on λ (0.22%).

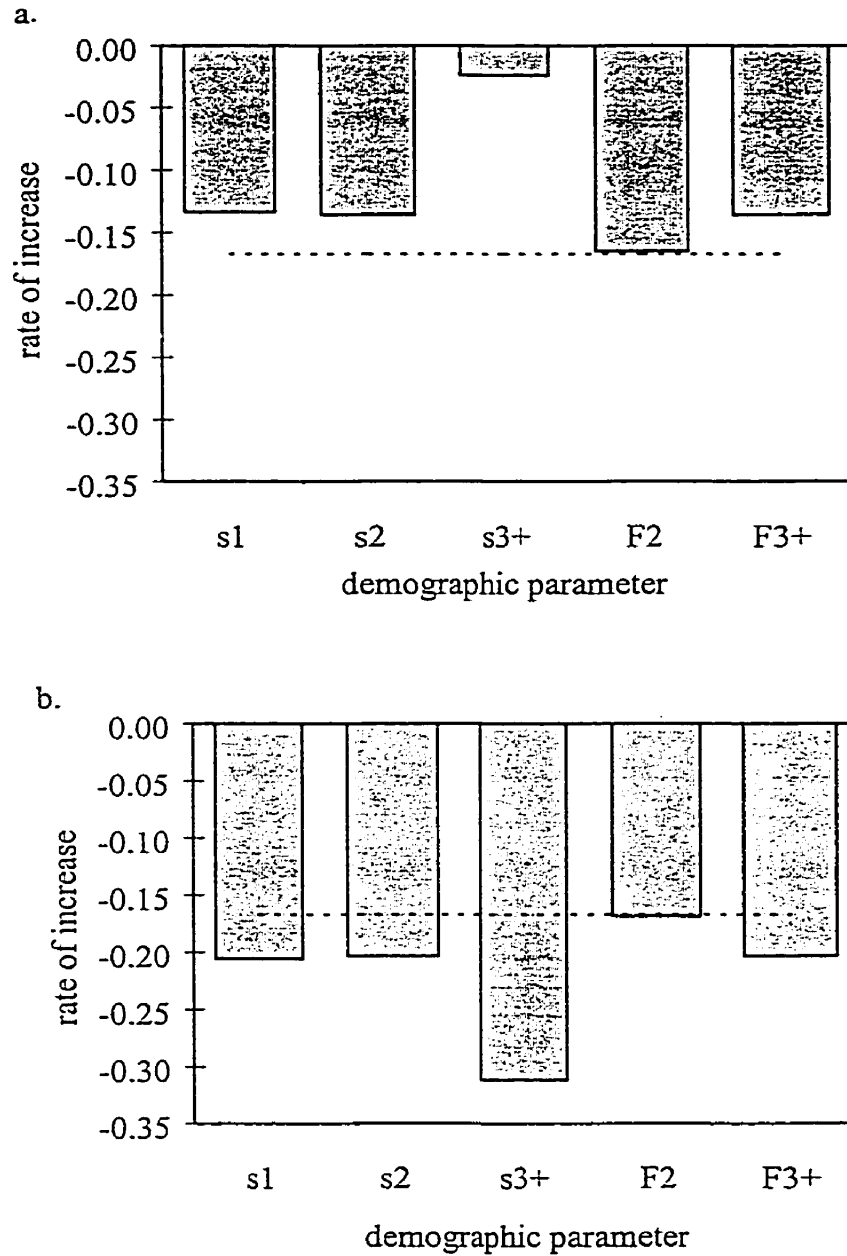


Figure 4.3 – Changes in rate of increase (r) resulting from a simulated 25% increase (a) and a 25% decrease (b) in survival and reproductive success of Semipalmated Plovers in age class 2 and age class 3. The dashed line indicates the rate of increase for the Semipalmated Plover population based on mean demographic parameters ($r = -0.16724$) (Table 4.1).

To stabilize the population (to $\lambda=1$) required a 22% increase in survival (from 0.6722 to 0.83841) of individuals in all age classes (s_1, s_2, s_{3+}) or a 160% increase in age 2 and age 3+ fertility. Because there was much uncertainty associated with my estimate of $prbreed_2$, I also investigated the effect of errors in estimation of this parameter on λ . Setting $prbreed_2$ (and thus F_2) equal to $prbreed_{3+}$ (0.706964) increased λ to 0.86638 (a 2.4% increase).

IMMIGRATION

Immigration was an important component of Semipalmated Plover demography. From 1995-1998, over 50% of the female population was comprised of immigrant females (i.e., newly banded birds) and in 1996 and 1997, 66% of the females were immigrants (Table 4.3).

DISCUSSION

Annual population censuses showed no change in population size, but, according to the model, rates of survival and fecundity were insufficient to maintain a stable population. The model predicted an annual population decline of more than 15%. So, why is this model poorly describing Semipalmated Plover population dynamics? There are two possible explanations.

First, the main assumption of matrix modelling (that the balance between emigration and immigration is zero) may have been violated such that in each year, the number of immigrants entering the population was much greater than the number of birds emigrating.

Table 4.3 – Number of newly banded and previously banded female Semipalmated Plovers in the population each year. The number of newly banded adults represents the number of immigrant females entering the population that year.

Year	Previously banded females	Newly banded females	Percentage of immigrants in the population
1995	20	23	54%
1996	20	21	49%
1997	23	34	62%
1998	14	27	66%

High rates of immigration are a common feature of shorebird populations (e.g., Evans and Pienkowski 1984, Hitchcock and Gratto-Trevor 1997) and the large number of newly banded female Semipalmated Plovers in the study population each year suggests high immigration. Therefore it is likely that the negative population growth rate was compensated by immigration. For most shorebird species, birds disperse away from their natal site early in life, but once settled on a breeding site, typically remain faithful to the site for many years (Hitchcock and Gratto-Trevor 1997). Semipalmated Plovers are no exception; adult site fidelity is high, whereas rates of natal philopatry are among the lowest reported for shorebirds (Flynn et al. 1999). Because population growth rate is often most sensitive to adult survival, and permanent emigration and mortality have identical effects on local population dynamics, emigration can have a strong influence on population demography (Danchin and Monnat 1992). Estimates of local survival generated from SURGE are the product of true survival and permanent emigration, but it is not possible to determine the relative importance of each factor. Colour-marked Churchill Semipalmated Plovers have never been sighted at other breeding sites, so I was unable to estimate rates of adult emigration. However, the relative stability of population size over time suggests that adult emigration is low and is more than compensated by an influx of immigrant birds. If emigration rates were high, a population decline would have occurred (e.g., Danchin and Monnat 1992, Hitchcock and Gratto-Trevor 1997).

The second possible reason for the discrepancy between observed and calculated population growth could be errors in estimation of demographic parameters. I feel confident of my annual survival estimates because estimates were based on six years of capture-resighting data, resighting rates were high, and survival rates were comparable to

those of other shorebirds (Root et al. 1992, Thompson and Hale 1993, Paton 1994, USFWS 1996, Insley et al. 1997, Warnock et al. 1997, Chapter 2). Similarly, eggs hatched per female and pre-fledging survival were calculated from observations of breeding birds from 1992-1998 and 1995-1998 respectively, thus, sample sizes were sufficiently large to obtain accurate estimates of these parameters. The main weakness of this model, and a common problem of shorebird population studies was a lack of age-specific data. Estimates of age at first breeding and breeding propensity of two year olds were highly uncertain because the five natal recruits from which these parameters were estimated may not be representative of the Semipalmated Plover population as a whole. Delayed age at first breeding is fairly uncommon among plovers. Ringed, Snowy, Piping, Mountain, American Golden and Pacific Golden plovers all breed as one year olds (Pienkowski 1984, Haig 1992, Warriner and Paton 1995, Knopf 1996, Johnson and Connors 1996), but Black-bellied Plover may delay breeding until two or three years of age (Paulson 1995). So, although uncommon, it is possible that Semipalmated Plovers may also delay breeding.

A further complication in determining age at first breeding was the paucity of information on Semipalmated Plovers moult patterns and plumages (for review see Nol and Blanken 1999). Yearling breeders may be distinguishable from older birds by the presence of worn Juvenal primaries and wing coverts (Prater et al. 1977) but, unless researchers were actively looking for this trait, it would have easily been overlooked. So, some first-time breeders may have been yearlings and breeding propensity of two year olds may be greater than 20%.

To improve the accuracy of this model, future field studies should focus on acquiring more age-specific data. Studies of shorebird natal dispersal have found that most dispersing birds settle within 8 km of their natal site (Jackson 1994), so, it may be advantageous to conduct an extensive search for neighbouring Semipalmated Plover populations at and near Churchill. If source population(s) of immigrant Semipalmated Plovers could be identified, then chicks at that site could be banded in the hope of their emigrating to the Churchill population, and thus increasing the number of known age individuals (Hitchcock and Gratto-Trevor 1997). A summer survey of wintering and staging areas could also be conducted to determine whether Semipalmated Plovers typically delay breeding and over-summer in their first two years. For example, Paulson (1995) found that one-year-old Black-bellied Plovers were common south of their breeding range but that older birds were not. It would be interesting to conduct a similar survey of Semipalmated Plovers, but again this depends on being able to accurately age birds based on plumage characteristics. Despite the uncertainty associated with age at first breeding and breeding propensity of two year-olds, these parameters had little influence on population growth rate. In fact, when pr_{breed_2} was set equal to $pr_{breed_{3+}}$, λ increased by only 2.4%. Thus, it seems likely that high rates of immigration were mostly responsible for the difference between the predicted negative growth rate and the observed stable population.

Semipalmated Plover population growth rate was most sensitive to changes in adult survival. Life-history theory predicts that sensitivity of adult survival will be high for birds with long generation times and low for birds with short generation times (Lebreton and Clobert 1991). This concurs with several other studies of relatively long-

lived species including raptors (Hiraldo et al. 1996, Wootton and Bell 1992, Lande 1988), seabirds (Simons 1984), waterfowl (Brault et al. 1994, Goudie et al. 1994, Schmutz et al. 1997), and shorebirds (Hitchcock and Gratto-Trevor 1997) that found that adult survival had the highest sensitivity. Following adult survival (s_{3+}), population growth rate was most sensitive to changes in juvenile survival, fledging success, 1-year old survival and 2-year old survival. With the exception of fledging success (which was not measured for Semipalmated Sandpipers), Hitchcock and Gratto-Trevor (1997) found the same sequence of sensitivity values for a breeding Semipalmated Sandpiper population at La Pérouse Bay, Manitoba. Both studies also found that survival probabilities had the highest elasticities and fertilities had the lowest.

When designing sampling procedures for future Semipalmated Plover research, sensitivities of demographic parameters should be considered. Lande (1988) suggested that sampling effort to measure a certain demographic parameter should be proportional to its contribution to sampling variance of λ . Based on my results, future studies should concentrate most sampling effort on adult survival (s_{3+}), because this parameter contributed most to sampling variance of λ . With more years of capture-resighting data, the precision of annual survival estimates will increase, provided that banding and resighting efforts remain high. Pre-fledging survival ($s_{h \rightarrow f}$), and eggs hatched per female ($nhatch_i$) had the second and third highest contributions to sampling variance of λ . Much of the variation in these parameters can be attributed to among year variation in reproductive success and the inclusion of data from two breeding seasons with higher than average predation rates ($> 50\%$ nests depredated) (Chapter 3). The Churchill Semipalmated Plover research is part of a long-term population study, so with more years

of data, the inclusion of ‘bad’ years will have less influence on mean values and will help to identify factors affecting among and within year variation in adult survival and fecundity.

There are several assumptions and limitations associated with the deterministic, density-independent approach used in this study. First, a deterministic model (as opposed to a stochastic model) deals only with average demographic parameters but does not account for temporal fluctuations in fecundity and survival. When a demographic parameter is highly influential on population growth rate (i.e., has a high elasticity), the amount of annual variability in that parameter can also be highly influential (Hitchcock and Gratto-Trevor 1997). Although sensitivity analysis quantifies the population’s response to a change in a given demographic parameter, it fails to address how frequently such a change may occur (Schmutz et al. 1997). Thus, it is important to consider the amount of variation in demographic parameters when interpreting results of sensitivity analyses. If adult survival has the highest sensitivity but reproductive parameters are significantly more variable than are survival rates, then reproductive success could potentially contribute more to population change (Schmutz et al. 1997). Killer Whale (*Orcinus orca*) demography clearly illustrates this. Adult survival had the highest elasticity value, but variation in adult fecundity was more strongly correlated to annual variation in population size than was any other demographic parameter (Brault and Caswell 1993).

Random variation in fecundity and survival rates can have a very large impact on population growth rate. Annual variability in demographic parameters resulting from environmental and demographic stochasticity tends to reduce long-term population

growth rate relative to a theoretical population with no variability (Boyce 1977, Burgman et al, 1993, Hitchcock and Gratto-Trevor 1997). Thus, estimates of λ derived from deterministic matrices that do not incorporate variability (even if calculated from long-term data) tend to overestimate population growth (Burgman et al. 1993). Simulations of Semipalmated Sandpiper population growth found that population growth rate was depressed by annual variability in adult survival (Hitchcock and Gratto-Trevor 1997). Conversely, Lande (1988) found that substantial annual fluctuations in Northern Spotted Owl demographic parameters (adult and juvenile survival, reproductive success) caused only a small decrease in population growth rate because long life expectancy (17.5 years) diminished the effect of annual variation.

Estimating the standard error of λ provided some indication of variation in Semipalmated Plover mean demographic parameters. The 95% confidence intervals on λ were wide, indicating high annual variability in Semipalmated Plover survival and fecundity. Like most shorebirds, Semipalmated Plover reproductive success fluctuated greatly among years in response to weather conditions and fluctuations in predator abundance (Chapter 3). Survival rates also varied annually, but to a lesser extent than did reproductive success. Over the course of the study, hatching success varied by 63% and survival rates varied by 30%.

It is important to note that sensitivities and elasticities are dependent on the values of all model parameters, and even when all other parameters remain constant, the sensitivity of one parameter responds in a non-linear way to the actual value of the parameter (Hitchcock and Gratto-Trevor 1997). For example, Hitchcock and Gratto-Trevor (1997) found that simulated increase in survival from 0.45 to 0.56 (a 25%

increase) had little effect, whereas an increase from 0.76 to 0.86 (a 13% increase) had a dramatic impact on Semipalmated Sandpiper population size. So, it is important to consider whether any of the model parameters may have low sensitivities because the value of the demographic parameter is depressed relative to those of a 'healthy' population (Green and Hirons 1991, Hiraldo et al. 1996). There were no other monitored Semipalmated Plover populations for comparison, but hatching success, pre-fledging and adult survival rates in the Churchill population were comparable to or higher than that of several other plover species (Pienkowski 1984, Bergstrom 1988, Prindiville-Gaines and Ryan 1988, Root et al. 1992, Thompson and Hale 1993, Paton 1994, Warriner and Paton 1995, Knopf 1996, USFWS 1996, Yogeve et al. 1996, Insley et al. 1997, Warnock et al. 1997). This suggests that fecundity and survival rates are not depressed.

The model used in this study also did not consider the effects of density-dependence. I assumed the population was not regulated by density-dependent factors operating on the breeding grounds (i.e., survival and reproductive success were independent of breeding density). There is little evidence of density-dependent mortality or restriction of reproductive output for breeding shorebirds (see review in Evans and Pienkowski 1984). Shorebird population size is more likely influenced by density-independent factors such as unfavourable weather conditions, which increase wintering ground mortality, and suppress or prevent reproduction on breeding grounds (Evans and Pienkowski 1984). Thus, it did not seem appropriate to include density-dependence in the model.

Finally, when calculating the variance of λ , I assumed that life-history parameters varied between years independently (i.e., there was no covariance). This

assumption is likely invalid because survival analyses have shown that Semipalmated Plover hatching success and survival rates are correlated (Chapter 2). Survival rates are lower in years with lower than average hatching success, likely because conditions that result in low hatching success also cause higher emigration and/or mortality.

Although sensitivity analysis provided some insight into Semipalmated Plover demography, I recommend that future demographic studies use life stage simulation analysis (LSA) (Wisdom and Mills 1997, Wisdom et al. 2000). LSA considers the influence of variation, covariation, and uncertainty in demographic parameters and can be used to test whether rank orders of elasticities change with real-world variation in demographic parameters (Wisdom et al. 2000). The simple model used in this study should be considered a starting point for future matrix modeling and demographic analyses. This model was used to gain insight into factors affecting Semipalmated Plover population size and to highlight future research needs. As more data are collected, the validity and accuracy of the model will improve, which will allow for more sophisticated analyses such as stochastic models, life-stage analyses and population projections.

The fact that population growth rate was most sensitive to adult survival in Semipalmated Plovers (this study) and in Semipalmated Sandpipers (Hitchcock and Gratto-Trevor 1997) has important implications for shorebird conservation. Small changes in adult survival can have a large influence on shorebird population size, and increases in fecundity appear to be insufficient at increasing population growth rate (Hitchcock and Gratto-Trevor 1997). In addition, most shorebirds are constrained by a four-egg clutch, so they have less latitude to increase fecundity than do other bird species. Fecundity of arctic and sub arctic nesting shorebirds is further limited because they can

hatch only one clutch per year. High adult survival and high immigration compensate for low fecundity, but as a result, shorebird populations are slow to recover from population decreases. This study also demonstrated the importance of immigration and emigration on shorebird demography. The Churchill Semipalmated Plover population is reliant on a constant influx of birds from other, perhaps neighbouring populations, and it is likely that successful juveniles from the Churchill population are feeding nearby populations. This suggests that the local Churchill Semipalmated Plover population is part of a larger metapopulation, which means that changes in the demography of these populations will also affect the Churchill population.

CHAPTER 5

GENERAL DISCUSSION

The picture of Semipalmated Plover demography revealed by my analyses is that of a population with low fecundity, which is balanced by high adult survival and high immigration rates. Local survival as well as clutch size, hatching success, and egg hatchability showed significant annual variation. Annual variation in local survival was unrelated to weather conditions on the breeding grounds, but was correlated with hatching success. In years with high predation rates (and thus low hatching success), birds are more likely to permanently emigrate from the study area. Local ecological conditions such as individual nesting success, success of conspecifics or predator abundance may serve as indicators of a poor nesting site thereby encouraging birds to emigrate to a 'safer' nesting area.

Female Semipalmated Plover resighting rates were lower than that of males, which suggests that like most shorebirds, female Semipalmated Plovers are less site tenacious and more dispersive than are males. Females were more likely to be absent during a breeding season, and then return to the Churchill study area in subsequent years. Females may be reducing risk of death caused by stress of breeding by avoiding nesting in years when they may be unable to meet the energetic demands of breeding. For long-lived species, one breeding season represents only a small contribution to lifetime reproductive success (Coulson 1984).

Furthermore, nesting under conditions where cost of breeding is likely to negatively influence survival and consequently the number of future breeding opportunities is a strategy against which there would be strong selection (Coulson 1994). Further research is needed to determine the extent to which non-breeding occurs among Semipalmated Plovers, because this could have important effects on the population dynamics of this species. Future studies should focus on ascertaining whether females are skipping breeding seasons and over-summering at lower latitudes, or are temporarily emigrating to other areas to breed.

The effects of age on local survival and reproductive success were equivocal. Age does not seem to affect Semipalmated Plover survival, because older, previously banded birds had higher local survival rates than did newly banded birds in only one year. In most years there was no difference between the age classes. Age had a greater effect on reproductive success, but the effects varied annually, and between the sexes. Furthermore, age influenced fledging success, but not hatching success. Male parental breeding experience had a greater effect on Semipalmated Plover reproductive success than did female experience, probably because males remain with the brood longer than do females. Pairs containing an experienced male were more likely to fledge chicks than were inexperienced pairs or pairs with an experienced female. Many factors may be responsible for the increase in reproductive success with male experience. Experienced males may choose safer brood-rearing areas, or may be more vigilant and better able to defend the brood against predators and/or conspecifics. More research is needed to determine why experienced males are better parents.

Juvenile survival remains the missing link in this and most other shorebird population studies. For most shorebird species, rates of natal philopatry are low, and most juveniles presumably disperse to new areas to breed (Evans and Pienkowski 1984, Flynn et al. 1999). As in the present study, this creates a gap in the understanding of population dynamics. I was able to estimate Semipalmated Plover pre-fledging survival probabilities, which is an improvement over most studies, but the fate of chicks once they departed the breeding grounds is unknown. Future, advancements in the field of satellite telemetry will likely result in a transmitter that is sufficiently small for use on shorebirds, and thus allow researchers to track the shorebird movements throughout their migratory route. For the time being, a study of juvenile Semipalmated Plover over-winter survival rates would result in a better estimate of this critical demographic parameter.

Adult survival is the limiting demographic component on the population dynamics of Semipalmated Plovers - the survival of adult birds has a much greater influence on population growth rate than does reproductive success. The market hunting of shorebirds throughout the 1800s clearly demonstrates the vulnerability of shorebird populations to reductions in adult mortality. Hunting reduced the once abundant Eskimo Curlew population to near extinction just after the turn of the century and this species may now be extinct (Hayman et al. 1986). Several other shorebird populations including Hudsonian Godwit (*Limosa haemastica*) and Lesser Golden Plover (*Pluvialis dominica*) suffered similar declines, and have not yet returned to their historic population size (Senner and Howe 1984). Because of low fecundity, and for larger shorebirds, a delayed age at first breeding, shorebird populations are slow to recover from population declines.

These characteristics of shorebird demography revealed by this thesis highlight the need for conservation of appropriate habitat throughout shorebirds migration range. Many North American shorebird populations are in decline, and three plover species have been listed as species of concern. As a result, there has been some recent attention and effort focused on the conservation of shorebirds. A major shorebird conservation priority should be to protect the quality of habitats used by shorebirds throughout their annual cycle (Evans 1991). For arctic-nesting shorebirds, in particular, a protected network of staging areas is critical, because if shorebirds are delayed by poor conditions at a staging area, they may be unable to reach their breeding grounds with sufficient time to complete their breeding cycle (Evans 1991). It is my hope that shorebird conservation initiatives will focus on protecting appropriate habitat so that adult shorebirds can maintain high survival rates, and thus stable populations.

CONCLUSIONS

Long-term longitudinal studies such as this one are critical in understanding population dynamics of birds. This thesis demonstrated that Semipalmated Plovers, have high adult survival rates, and low fecundity, both of which show significant annual variation. Local survival rates are not sex specific, and are not influenced by weather conditions on the breeding grounds. Hatching success is a good predictor of adult survival likely because poor nesting success encourages birds to permanently emigrate.

With the exception of fledging success, all reproductive parameters, including clutch size showed significant annual variation, and a wide range of factors are likely responsible for this variation. In years following El Niño events, local survival rates, and reproductive success were lower, and changes in lemming abundance may be related to

high rates of predation. Semipalmated Plover reproductive success is influenced by male, but not female breeding experience. Pairs with an experienced male are more successful than are inexperienced pairs.

Adult survival has the greatest influence on population growth rate, and despite large annual variation in survival and reproductive success, the Churchill study population remained stable. High rates of immigration are probably responsible for the stability of the population. The Churchill population is reliant on a large influx of immigrants, and is therefore part of a larger metapopulation. The maintenance of high adult survival rates is critical to the stability of shorebird populations.

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Appendix 1 – Capture or resighting matrix for colour-banded adult male and female Semipalmated Plovers at Churchill, Manitoba from 1992-1998. The first '1' from the left represents the initial banding occasion, and each subsequent digit represents one breeding season from 1992-1998 during which resightings and recaptures occurred. A zero in the capture history indicates that the bird was either dead, or alive and not resighted that year. Birds banded as nestlings were included in the capture history when they were first observed as a breeding adult.

Capture/Resighting History	Number of Individuals	
	Females	Males
0000010	20	13
0000011	10	9
0000100	7	3
0000101	2	0
0000110	7	10
0000111	4	7
0001000	12	3
0001010	1	0
0001011	0	1
0001100	3	3
0001101	1	0
0001110	2	6
0001111	0	1
0010000	15	14
0010010	0	1
0010110	2	0
0010111	1	0
0011000	4	8
0011010	1	0
0011100	2	0

Appendix 1 continued.

Capture/Resighting History	Number of Individuals	
	Females	Males
0011101	0	1
0011110	2	2
0011111	1	2
0100000	10	8
0100100	1	0
0100110	2	0
0101000	1	0
0101011	1	0
0101100	1	0
0101111	0	1
0110000	3	3
0111000	4	6
0111001	2	0
0111100	1	1
0111101	1	2
0111110	1	2
0111111	1	3
1000000	5	7
1001000	0	1
1001110	0	1
1011000	2	0
1110000	0	1
1110010	0	1
1110111	1	0
1111000	0	1
Total	134	122