

Piping plover foraging ecology in the Great Plains

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ABSTRACT

The Great Plains piping plover (*Charadrius melodus*) population was listed as threatened under the Endangered Species Act in 1986. The challenge for managers of this population is to increase the fledging rate and to ensure that there is sufficient habitat to support an increasing population. According to the revised recovery plan, there are insufficient quantitative data that relate habitat characteristics to reproductive success in riverine habitat. In particular, additional data are needed to determine if piping plover reproduction is limited by food abundance at breeding sites.

The goal of this research was to determine whether piping plover chick survival was limited by foraging site quality on the Missouri River. Productivity has historically varied among river reaches. The alkali wetlands, reported to be very productive, serve as an index to the upper limit of reproductive potential. We compared indices of foraging site quality, chick growth and survival among a reservoir, two river reaches and alkali wetland sites from 2001-2003. We compared piping plover use of protected shoreline and exposed shoreline to availability along two reaches of the Missouri River (Gavins and Garrison). We also examined piping plover chick diet. Chick weight gains were higher at alkali wetlands than Gavins and Garrison. Invertebrate numbers were higher at the alkali wetlands than the three river sites and lowest downstream of the cold water release dam. Invertebrate biomass was highest at the alkali wetlands and downstream of the warm water release dam and lowest downstream of the cold water release dam. Invertebrate biomass downstream of the cold water release dam was the lowest of all 4 sites. There was no relationship between chick daily survival rates and invertebrate biomass or predator presence. Although Diptera occurred more frequently (23% - 64%) at all sites (sticky traps), Coleoptera occurred most frequently in the fecal samples (fecal analysis; 69% to 89%). On the Missouri River, protected shorelines were important foraging sites for piping plovers during the breeding season. We also found that sandbars

with low-lying moist habitat are important to foraging chicks. Results are consistent with the prediction that foraging conditions downriver from cold water release dams are inferior to conditions in other habitats in the region. Differences in prey availability are reflected in chick growth rates, but not in survival rates. These results underscore the variability in different indices of habitat quality (invertebrate indices, predation, growth rates, survival rates) among the four sites, and the need for monitoring and management strategies that address each site individually. When managing or creating sandbars, ensuring the availability of protected shoreline will benefit piping plovers on the Missouri River.

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CHAPTER 1. FACTORS LIMITING PIPING PLOVER REPRODUCTIVE OUTPUT IN THE GREAT PLAINS

ABSTRACT

The Great Plains piping plover (*Charadrius melodus*) population was listed as threatened under the Endangered Species Act in 1986. The challenge for managers of this population is to increase the fledging rate and to ensure that there is sufficient habitat to support an increasing population. According to the revised recovery plan, there are insufficient quantitative data that relate habitat characteristics to reproductive success in riverine habitat. In particular, additional data are needed to determine if piping plover reproduction is limited by food abundance at breeding sites.

The goal of this research was to determine whether piping plover chick survival was limited by foraging site quality on the Missouri River. The hydrography on the Missouri River has changed due to dam construction, and dam management affects invertebrate species composition and abundance. Productivity has historically varied among river reaches. The alkali wetlands, reported to be very productive, serve as an index to the upper limit of reproductive potential. We compared indices of foraging site quality, chick growth and survival among a reservoir, two river reaches and alkali wetland sites from 2001-2003. Chick weight gains were higher at alkali wetlands than Gavins and Garrison. Invertebrate numbers were higher at the alkali wetlands (30.7 ± 6.6) than the three river sites and lowest downstream of the cold water release dam (5.9 ± 0.6). Invertebrate biomass was higher at the alkali wetlands (22.2 ± 6.1) and downstream of the warm water release dam (15.4 ± 2.3) than on the reservoir (8.3 ± 2.2) or downstream of the cold water release dam (4.1 ± 0.7). Invertebrate biomass downstream of the cold water release dam was the lowest of all 4 sites. Although chicks that survived to fledging were heavier at day 4 or 5 and days 8 or 9 than chicks that did not survive, there was no relationship between chick mass at these ages and invertebrate indices. There was no relationship between chick daily survival rates and invertebrate biomass or predator presence. The lack of a direct relationship between chick survival rates and chick growth rates or prey availability, and the lack of a relationship between mammalian

predator indices and chick survival rates indicate that another factor, perhaps avian predator presence, is affecting chick mortality.

Results are consistent with the prediction that foraging conditions downriver from cold water release dams are inferior to conditions in other habitats in the region. These differences in prey availability are reflected in chick growth rates, but not in survival rates. These results underscore the variability in different indices of habitat quality (invertebrate indices, predation, growth rates, survival rates) among the four sites, and the need for several monitoring and management strategies.

INTRODUCTION

The Great Plains piping plover (*Charadrius melodus*) was listed as threatened under the Endangered Species Act in 1986 (USFWS 1985). According to the 1994 draft recovery plan, for the plover to be considered for delisting, the U.S. Northern Great Plains population must equal or exceed 2,300 pairs for 15 years (in North Dakota, 150 pairs on the Missouri River and 600 pairs on the Missouri Coteau; in South Dakota, 400 pairs, with 300 shared with Nebraska on the Missouri River below Gavins Point; 75 pairs on other Missouri River sites; USFWS 1994). The 268 pairs of piping plovers on the Missouri River in 1999 represented only 51 percent of the recovery goal (USFWS 2000).

Specific measures to recover the species include meeting or exceeding a 1.13 chicks/pair fledging rate (USFWS 2000). Based on an estimated annual adult survival of 0.66, Prindiville Gaines and Ryan (1988) estimated that a fledging rate of at least 1.15 chicks per pair would maintain a stationary Great Plains piping plover population. The survival of adult Great Plains piping plovers has been most recently estimated at 0.74 (Larson et al. 2000). Simulations with this survival estimate have found that a population-wide mean of 1.10 fledglings/pair would maintain a stationary population (Larson et al. 2002). From 1995-2000, the estimated fledging rate on the Missouri River was 0.62 fledglings/pair, with annual rates ranging from 0 to 2.0 chicks/pair in different portions of the drainage (Niver 2000). The management challenges for this population are to increase the fledging rate and to ensure that there is sufficient habitat to support an increasing population.

In the Great Plains, productivity may be affected by predation, habitat loss, human disturbance, and water management (USFWS 1994). Along the Missouri River, piping plovers nest on rivers and reservoirs, along shores and on sandbars (Plissner and Haig 2000). According to the revised recovery plan, there are insufficient quantitative data that relate habitat characteristics to reproductive success in riverine habitats (USFWS 1994). In particular, additional data are needed to determine if piping plover reproduction is limited by food abundance or quality at breeding sites (USFWS 1994). Some actions needed for recovery include: determining habitat requirements and status, identifying prey resources, and preserving and enhancing piping plover habitat (USFWS

1994). In a supplemental biological opinion, USFWS adopted adaptive management of the river system to help produce variable and flexible river flows (USFWS 2003). Over the long-term, ensuring variable river flows and processes would provide the range of conditions necessary for piping plover habitat on the Missouri River (USFWS 2003).

Missouri River Operations

The flow dynamics on the Missouri River have been changed by dams. Prior to dam construction, scouring flows that created new sandbars occurred approximately every 1.5 years (Hesse and Mestl 1993; Niver 2000). Reservoirs now trap a large part of the sediment load, which leads to decreased creation of sandbar nesting habitat (USFWS 2000). In addition, the lack of high flows has reduced the scouring of sandbars, leading to increased encroachment by vegetation (USFWS 2000). Record flows occurred in 1996 and 1997 (Annual average: 40.0 and 52.3 Cfs, respectively, compared to an annual average of 23.8 Cfs from 1986 to 1995; U.S. Army Corps of Engineers 2004). The high flows deposited sand which created an abundance of sandbar complexes, and piping plover numbers and productivity increased on the Missouri River (Niver 2000).

The U. S. Fish and Wildlife Service recently concluded that the current operations of the Missouri River Main Stem System are likely to jeopardize the continued existence of the piping plover (USFWS 2000). Reasonable and Prudent Alternatives (RPA) were developed to avoid the likelihood of this jeopardy. These alternative measures include: (1) the implementation of flow enhancement, with a spring rise and summer decrease in water levels from Gavins Point Dam to maintain and develop sandbar habitat, and (2) habitat restoration, creation and enhancement. Managing the heights of the reservoirs on a three-year rotation is expected to increase habitat availability in reservoirs in drawdown years, create plover sandbar habitat in riverine segments in high release years, and increase sandbar habitat in years of steady or rising reservoir levels.

Relationship between post-hatching prey availability and fledging success

A positive relationship between foraging habitat, chick foraging rates and chick survival has been reported for piping plovers in other systems (Corn and Armbruster 1993; Loegering and Fraser 1995; Elias et al. 2000). Nordstrom and Ryan (1996) found

that food availability may limit the reestablishment of piping plovers at some Great Lakes beaches. Habitat quality can affect fledging rates: In Rhode Island, pairs whose chicks fed at mud flats had higher fledging success (3.0 fledglings/brood) than those feeding at ocean beachfront habitat (1.4 fledglings/brood; Goldin and Regosin 1998). In Maryland and New York, chicks on the bay beach and island interior were heavier and had higher daily survival rates than those on the ocean beach (Loefering and Fraser 1995; Elias et al. 2000).

Initially, precocial chicks such as piping plovers devote most of their energy to maintenance and survival (Ricklefs 1983). A lack of food resources may slow or limit development to the point that chicks that fail to gain mass above certain thresholds do not survive (Ricklefs 1983). At 10-25% of adult mass, the metabolic rate and energy demand are greatest (Ricklefs 1974); this corresponds to the piping plover chick masses of 5-13 g, the range of masses in chicks 4-5 days old (Loefering and Fraser 1995). Most piping plover chick mortality on Assateague Island occurred in the first 10 days of life (Loefering 1992). At 4 to 5 days of age, the weights of chicks that ultimately survived were greater than the weights of chicks that did not survive (Loefering and Fraser 1995). In captivity, Hawaiian stilt chicks that gained relatively more mass in the first 2 weeks after hatching tended to fledge at a heavier mass than chicks that gained less mass during their first two weeks (Reed et al. 1999). In warm weather, shorebird chicks may grow and survive equally in low and high quality habitats, but when bad weather limits the time available for foraging, the chicks in poorer habitats may starve (Beintema and Visser 1989).

Time budget strategies differ as territory quality varies (Maxson and Oring 1980). Adult semipalmated sandpipers spent more time foraging when food availability was lower: During all stages of the breeding cycle, foraging time showed a significant negative correlation with food abundance (Maxson and Oring 1980). Foraging time decreased as food increased and then leveled off as food became highly abundant (Maxson and Oring 1980). Peck rates were lower when food was low, indicating that prey was more widely dispersed (Maxson and Oring 1980).

Low food availability may affect survival directly due to starvation, or through increased exposure and predation risk. Increased food abundance allowed semipalmated

plovers to spend less time foraging; thus chicks had more time available for resting (Maxson and Oring 1980). When food was scarce, chicks spent more time foraging and were more visible to predators (Maxson and Oring 1980). At sites with higher invertebrate densities, chicks need to cover shorter distances in order to feed, leading to lower predation risk. At sites with higher invertebrate abundance, we would expect chick growth to be higher and predation risk to be lower, leading to higher brood fledging success rates.

Foraging rates can be a useful index of habitat quality (Loefering and Fraser 1995; Zonick 2000). Attack rates increase with prey density in Charadriidae (Baker and Baker 1973). Prey size can also influence peck rates: Foraging ringed (*Charadrius hiaticula*) and grey plovers appeared to select large prey when prey availability was high, in which case the time between pecks was greater (Pienkowski 1983). Ringed and grey plovers moved shorter distances after taking large prey than after taking small or no prey (Pienkowski 1983). Distance moved during foraging bouts could be an indication of patch quality and prey size.

Effect of female condition on egg size and chick survivorship

Juvenile growth rates may be influenced by date of hatch, and the age and pre-laying body weight of brood females (Quinn and Keppie 1981; Moss et al. 1993). Least sandpiper (*Calidris minutilla*) egg size was related directly to the size of the laying female in Nova Scotia, Canada (Miller 1979). Females with longer bills tended to lay longer and more voluminous eggs (Miller 1979). No paternal influences on egg dimensions were detected (Miller 1979). Spotted sandpiper mean egg mass varied significantly among females; some females consistently laid heavier eggs than others (Reed and Oring 1997). However, egg mass was not related to female mass in that study, in which food was abundant (Reed and Oring 1997). A condition index obtained as a ratio of weight:bill length is a good index of seasonal variation free from size variability, because bill length is significantly correlated with the bird's size and unaffected by metabolic rate (Ashkenazie and Safriel 1979).

Shorebirds may produce larger and more nutrient-rich eggs in response to increased food abundance (Miller 1979). Male and female semipalmated sandpipers

(*Calidris pusilla*) lose weight as the season advances: Late breeders weigh less than early breeders when they begin incubating (Ashkenazie and Safriel 1979). This could be due to a decrease in the food supply as the season progresses or because earlier breeders had more fat stored (Ashkenazie and Safriel 1979). Both sexes of spotted sandpipers tended to gain weight after arrival on breeding grounds, suggesting that fat reserves were depleted by the time they arrived (Maxson and Oring 1980). Female spotted sandpipers on Pelican Island, Minnesota, began laying as soon as the first peak of food abundance occurred, "suggesting that they were dependent on abundant food for production of the first clutch" (Maxson and Oring 1980).

Egg size may affect initial chick size, and chick survival. Larger eggs produce larger chicks (initially) with a higher proportion of egg yolk, which would give those chicks an advantage over other chicks (e.g. Martin 1987). King eider ducklings from large eggs "performed better" than small ducklings from small eggs: sprint speed, endurance and feeding rates were positively correlated with egg size and body size (Anderson and Alisauskas 2001). Ducklings from large eggs may have a survival advantage over those from small eggs, under conditions where predation and nutrition may constrain survival (Anderson and Alisauskas 2001). By measuring eggs we may be able to distinguish whether chicks have an initial advantage, and obtain information on the effect of egg size on chick survival when habitat quality varies. In addition, if adult female piping plovers arrive on the breeding grounds requiring energy for egg production, the pre-laying breeding site foraging quality may play a vital role in reproductive success.

Effect of adult attentiveness on chick survival

Adult attentiveness (vigilance, alarm calling, distance from young) can affect chick survival by decreasing predation risk and risk of chicks getting lost (Walters 1982). Adult-chick distances can be influenced by parental attentiveness, prey availability, and presence of predators. As food supply is sparser, young-adult distance increases, due to the increased movement of chicks (Walters 1984).

The amount of brooding required is determined by chick age, chick feeding efficiencies (which depend on food availability), and by weather (Ashkenazie and Safriel

1979; Maxson and Oring 1980; Beintema and Visser 1989). During the first week after hatching, young semipalmated sandpipers in Barrow, Alaska, were brooded about 50% of the time when weather and food were relatively favorable, and more often (83%) under unfavorable conditions (Ashkenazie and Safriel 1979). Male brooding of chicks in semipalmated sandpipers decreased as chick age increased: at 1-3 days, 35% of the male's time was spent brooding chicks (Maxson and Oring 1980). Brooding varied during the day, occurring most during the early morning and evening periods when temperatures were lowest (Maxson and Oring 1980).

Factors affecting invertebrate density in riverine habitats

Piping plover productivity varies along different sections of the Missouri River that are subject to different management regimes. Below the Garrison Dam, water height fluctuates daily. Water output over turbines is increased during peak energy demands (hydro-peaking) and this can affect invertebrate species composition and abundance in the riverine habitats below the dam. Diel fluctuations in discharges may lead to increased turbidity, differential stranding of certain macroinvertebrate taxa, higher invertebrate drift rates, and changes in invertebrate functional group composition (Troelstrup and Hergenrader 1990). On the Missouri River, invertebrate abundance and number of taxa were lower in a site with daily fluctuations than at a site with no fluctuation (Troelstrup and Hergenrader 1990). In addition, cold water releases downstream of dams may affect invertebrate abundance and composition (Hesse and Mestl 1993).

On the Mississippi River, areas with sand substrates had lowest benthic macroinvertebrate density and diversity (Anderson and Day 1986). Macroinvertebrate density in the water was highest in areas with silt-sand substrates, but they had low diversity (Anderson and Day 1986). High macroinvertebrate diversity was found in areas with coarse substrates and macrophytic vegetation (Anderson and Day 1986). High silt areas were found in areas with slow water velocity (Anderson and Day 1986). Changes in invertebrate abundance and taxa could impact piping plover clutch size and chick survival on the river.

Our goal was to determine the factors limiting piping plover reproductive output on the Missouri River. Understanding which systems on the river have higher

reproductive success can aid managers in selecting potential sites for habitat enhancement or protection. Our objectives were: 1) to determine whether reproductive output and invertebrate indices varied among sites with different management schemes; 2) to examine the relationship between habitat variables and invertebrate indices; 3) to examine the relationship between invertebrates on reproductive success; 4) to test the relationship between parental quality and reproductive success; 5) to examine the relationship between predation and chick survival.

STUDY AREA

Along the upper Missouri River, piping plovers nest from southeast South Dakota to Fort Peck Lake in northeast Montana (Niver 2000). We studied piping plovers on three stretches of the Missouri River (two riverine and one reservoir) and in the alkali wetlands of North Dakota (Figure 1.1). Study sites on the Missouri River included the Gavins Reach in South Dakota, downstream of the Gavins Point Dam (Gavins); the Garrison Reach downstream of the Garrison Dam (Garrison) and Lake Sakakawea upstream of the Garrison Dam in North Dakota (Appendix 1.1). In the alkali wetlands, we observed broods on the Williams Nature Conservancy Preserve, and on private land monitored by the Audubon National Wildlife Refuge.

On the river reaches (Gavins and Garrison) we studied plovers nesting on sandbars. Sandbars varied in size from 0.04 to 224 hectares. On Lake Sakakawea, we studied plovers nesting along the edge of the lake. Vegetation on the sandbars and along the shore of the lake consisted of cottonwood (*Populus spp.*) and willow (*Salix spp.*) saplings up to 2 m in height in the dry, middle parts of the islands. Later in the summer at Gavins and Sakakawea, annual vegetation grew in the moist and saturated habitat. Vegetation did not grow along the shoreline at Garrison. Vegetation increased in density at Gavins over the course of the 3 years of the study, probably due to the lack of long periods of flooding.

Temperature and precipitation

The mean monthly temperature in Yankton, South Dakota, during the breeding season ranged from 10° C in April to 26° C in August (NOAA 2004, Figure 1.2). In Washburn, North Dakota, the mean monthly temperature in April were 5° C and reached a high of 23° C in July and August (NOAA 2004, Figure 1.2). Total precipitation was lowest in 2002 in Yankton, South Dakota, and lowest in 2001 in Washburn, North Dakota (NOAA 2004, Figure 1.2).

Water levels

Water levels at Lake Sakakawea were highest in 2001 and lowest in 2003 (Table 1.1, U.S. Army Corps of Engineers 2004). At Gavins Point, average daily outflow was higher in 2003 than in 2001 and 2002. At Garrison, average daily outflow was lower in 2001 than in the following two years.

METHODS

Analytical design

Variation in site quality

We compared reproductive output and invertebrate abundance on rivers and reservoirs on the Missouri River to “high quality” alkali wetland sites. We compared chick size, chick growth rates and invertebrate abundance as an index of foraging quality within rivers, reservoirs and alkali wetlands. Alkali wetlands are reported to be very productive (Nordstrom and Ryan 1996). Therefore chick growth rates at the alkali wetlands were used as an index of the potential daily growth rates on the river.

We compared Gavins Reach, downstream of a warm-water release dam with minimal daily fluctuation in water levels, Garrison Reach, downstream of a cold-water release dam with daily fluctuations in water levels, and Lake Sakakawea, a deep, cold water reservoir with minimal daily change in water levels (Figure 1.1). We tested the predictions that egg size, chick growth, invertebrate abundance and reproductive success would be lower on the Missouri River than in the alkali wetlands; egg size, chick growth,

invertebrate abundance and reproductive success would be lower on reservoirs than rivers; and that egg size, chick growth rates, invertebrate abundance and reproductive success would be lower on Garrison Reach than Gavins Reach.

Factors affecting invertebrate indices

We predicted that in addition to soil substrate type, variation in soil moisture could impact invertebrate indices. We modeled the relationship between habitat characteristics (proportion of saturated and moist substrate, percent sand in substrate, and shoreline type (protected or exposed)) and invertebrate biomass.

Factors affecting reproductive output

To determine factors limiting piping plover reproductive output in the Great Plains, we examined the relationship between invertebrate availability, chick foraging rates, chick growth rates, adult condition and attentiveness, and predators, and chick survival.

We modeled brood success (success = at least one fledged chick) based on the predictor variables: invertebrate biomass, proportion of saturated and moist habitat, predator tracks, adult attentiveness and site. We modeled chick daily survival rates (brood as the sampling unit) based on invertebrate biomass, predator presence (tracks present or not), adult attentiveness, site and year.

Field methods

At the beginning of the breeding season, we monitored sandbars downstream of Garrison and Gavins dams to locate breeding territories. On Lake Sakakawea and the Alkali wetlands we monitored selected shoreline based on proximity to our field base. We walked along shoreline until we located breeding pairs. We observed adults and searched for nests at four-day intervals at all sites where pairs were identified. Invertebrate sampling began when pairs were identified at sites. We collected data from 0600 to 1400, and rotated the timing of visits to ensure that all sites were monitored at different times of the day.

Substrate arthropods

To evaluate invertebrate abundance below the substrate surface, we collected soil cores twice a month at each foraging site, in the saturated zone. Soil cores were 4-cm in diameter and 2-cm deep. Samples were preserved in 95% ethanol until invertebrates were counted, within 3 months of collection.

Surface invertebrates

We sampled relative invertebrate abundance at pre-hatching and post-hatching breeding stages. We collected data on invertebrate abundance every 15 days prior to chick hatching, and every eight days post-hatching. We measured windspeed and temperature at the start of collection time. We placed paint stirrers coated with Tanglefoot Insect Trap Coating (The Tanglefoot Company, Grand Rapids, MI 49504) in each habitat along transects on each territory. Sticks were placed along one transect each sampling period, based on the center of foraging activity from the foraging observation period immediately preceding sampling. Transects were 50 m long and perpendicular to the water's edge. Stirrers were placed in pairs, one vertically in the sand (with tanglefoot on both sides) and one horizontally on the ground (tanglefoot on upward side), 5 cm apart, for 30 min. The catch area for the traps was 64.5 cm² (21.5 cm x 3 cm) for the horizontal stick and 129 cm² for the vertical stick. We sampled invertebrates in saturated, moist, dry and vegetated habitats. We placed chicken wire cages (diameter = 0.5 m, height = 0.6 m, mesh size = 2.5 cm) around each set of traps to prevent bird injury. Cages may influence capture rate and complicate comparisons with previous studies. We counted, measured and identified invertebrates to order. We calculated invertebrate catch rates (number of invertebrates/half hour), and estimated biomass (mg dry weight/half hour). We used invertebrate length measurements to calculate biomass based on an equation developed with data from a range of invertebrate orders (Dry Weight (mg) = 0.0305 x Length (mm)^{2.62}; Rogers et al. 1976). We estimated the invertebrate biomass consumed by chicks (mg/min) at each site (estimated biomass consumed = individual invertebrate biomass (mg) x foraging rate during 2-min intervals (# pecks / min)).

Egg size

We measured the length and width (mm) at the widest point of all of the eggs in a clutch with calipers after clutch completion. We calculated an index to egg volume with a formula used for least sandpiper (*Calidris minutilla*) eggs (length x breadth²; Miller 1979). We calculated the clutch volume as the sum of volumes of all eggs in a clutch.

Chick condition and survival

We attempted to observe chicks every four days until they were 22 days old or were seen flying. Chicks were considered fledged if they were seen at 18 days or older, based on the youngest chicks seen flying. We systematically searched nesting islands for adults and chicks by walking the shoreline and the interior. We considered chicks younger than 18 days of age dead if we failed to find them on two consecutive visits.

We attempted to catch chicks every four days, by chasing them with butterfly nets. We weighed and measured chicks (wing chord (± 1 mm), tail (± 1 mm), exposed culmen (± 1 mm), weight (± 0.1 g)), beginning on the day of hatching (Scale: Ohaus CS-200, Ohaus Corporation, 29 Hanover Road, Florham NJ 07932-0900; Calipers: Swiss Precision Instruments, dial metric calipers, 1555 Mittel Blvd Ste F, Wood Dale IL 60191-1046; Wing rule: Avinet Inc., POB 1103, Dryden NY 13053-1103). Chicks were temporarily color-banded with one Darvic band on the tarsus to identify individual chicks during time budget and foraging observations. We spent up to 10 min attempting to capture a brood, and returned another day if we were unsuccessful. We calculated condition indices as body weight/exposed culmen (Beintema 1994). We estimated daily survival rates for chicks with a variation of the Mayfield method, modified for dependence within broods (Flint et al. 1995).

Chick foraging behavior

Habitat use

Every four days, we conducted 2-min behavioral observations on each chick within a brood, recording habitat use and chick behavior at the start of the observation period, and then at 10-sec intervals. We calculated the proportion of observations in which chicks were foraging in different habitats (water, saturated soil, moist soil, dry soil,

vegetation). Saturated habitats were adjacent to the water's edge and retained a wet sheen. Water appeared at the surface when pressure was applied. Moist habitats were identified by dark but not saturated sand. Dry sand was at higher elevations and not exposed to river water. The vegetated habitat consisted of dry sand with 10% or more plant cover.

We recorded time budget data on focal chicks in each brood at 10-sec intervals during 2-min foraging observations. Behavior was characterized as: foraging, disturbed (crouch, stand or run, often while peeping), resting (stand, sit, preen), alert, brooded, locomotion (Loefering and Fraser 1995). Disturbed behavior was based on a change in behavior that appeared related to an outside source. If the chick disappeared from view during an observation, the clock was stopped. The observation was resumed when the chick was spotted if the time elapsed was less than five minutes. After 5 min, if the chick was not spotted, the observation was deleted.

Foraging rates

We recorded individual chick foraging rates (pecks/min) during a 2-min interval, noting each habitat in which the chick foraged. We recorded the total peck rate in each habitat during the 2-min interval and the peck rate during the time that the chick was actively foraging. We considered a chick to be foraging if it was standing or walking between pecks.

Foraging distance

In 2002 and 2003, we estimated the distance chicks traveled in a 2-min observation period. Estimates were ground-truthed at the beginning of the season by comparing estimates to paced distances. We compared the distance moved while actively foraging (observations where proportion of time spent foraging was 1.00) among years and sites.

Chick behavioral observations (foraging rate, proportion of time spent foraging, distance moved, distance from adult) were analyzed by age class (3 to 10 days, 11 to fledging) based on the age at which brooding is no longer necessary and because mortality may be higher in the younger chicks (3 to 10 days).

Adult condition and behavior

Adult measurements

To determine whether adult condition influenced egg size and adult attentiveness, we trapped, measured and weighed adults on the nest. We captured incubating adults on the Missouri River in 2002 and 2003 with drop door traps placed on completed nests. We did not capture adults at Alkali sites. We attempted to capture both adults. We recorded weight, exposed culmen, proportion of orange on culmen, wing chord, and width of black on the forehead at the widest point.

Adult behavior

In 2002 and 2003, at the start of each observation period, we noted the number of adults present and distance of nearest adult to chick, for each individual chick observed. We compared the mean distance of foraging chicks in a brood (observations where the proportion of time spent foraging was 1.00) to the nearest adult among years and sites. To measure adult attentiveness, we conducted 2-min behavioral observations on focal adults within a brood, recording the proportion of time spent in activities at 10-sec intervals. We considered an adult attentive when it stood near the brood and was not involved in other activities (foraging).

Predator abundance

We counted predator signs (tracks, scat) within foraging territories every 15 days. In 2001, we walked 50-m transects perpendicular to the shoreline, starting at the approximate center of chick foraging activity. In 2002 and 2003 we changed the protocol to increase the likelihood of finding tracks. Tracks were clearer in the moist zone close to the shoreline and a greater number of animals followed the shoreline. In 2002 and 2003, we walked along a 200-m transect on the edge of the shoreline and counted tracks within two meters of the water's edge (an animal trail was considered one set of tracks). We started transects at the point we first saw chicks, and alternated the direction we walked in for each sampling event. We noted track presence of any potential chick predators: gull (*Larus sp.*), coyote (*Canis latrans*), dog (*Canis familiaris*), mink (*Mustela vison*), raccoon (*Procyon lotor*) and great blue heron (*Ardea herodias*).

Statistical Analyses

We compared invertebrate indices among sites and years with a two-way ANOVA on ranks, followed by a pair-wise comparison with Fisher's LSD if significant differences were found (Akritas et al. 1997). When significant differences were found among years and sites, or significant interaction effects were found, we analyzed the effects of year and site separately.

We used a two-way ANOVA to compare egg length, width, and volume among years and sites. If significant differences were found, we conducted a pair-wise comparison with Fisher's LSD. Variables were evaluated for normality (Shapiro-Wilks test) and we examined residuals (plotted residuals against the predicted values) to determine that they were randomly distributed and that variance was homogeneous.

We calculated brood mean morphometrics (weight, wing, exposed culmen) for chicks (day 0, age 4 to 5 days and age 8 to 9 days) and compared chick size among sites and years with a two-way ANOVA. We calculated chick growth rates for each site using a regression of log-transformed measurements on age (days). The brood was the sampling unit. We compared the slopes of the growth rates (weight, wing chord, exposed culmen, condition index (weight / culmen)) among sites with a regression with indicator variables for the sites. We compared daily survival rates among sites and years with a two-way ANOVA. We compared predator indices among sites with a likelihood ratio Chi-Square test.

We examined the relationship of chick survival to chick size (weight, wing), invertebrate numbers and biomass, foraging rates, and adult attentiveness with logistic regression. We used logistic regression to identify relationships between successful broods (broods where at least one chick survived) and invertebrate abundance and biomass. We examined the relationship between chick daily survival rates and invertebrate indices (invertebrate numbers, invertebrate biomass, estimated biomass consumed (mg/min), Coleoptera biomass) with a Spearman rank correlation.

We examined the relationship between chick size at age 4-5 days and age 8-9 days and invertebrate indices, foraging rates and proportion of time foraging with a Spearman rank correlation.

We assessed the relationship between invertebrate indices and female condition, and the relationship between female condition (weight / culmen) and total clutch volume with regression analyses. We plotted residuals against the predicted values to determine that they were randomly distributed and that variance was homogeneous.

We compared chick daily survival rates at sites with and without predator tracks with an ANOVA. The brood was the sampling unit for invertebrate indices, adult-chick distance and predator tracks. We used the statistical analysis software (SAS) for analyses (SAS 2004).

We used logistic regression to model piping plover brood success (success = at least one chick survived to fledging) based on invertebrate biomass, proportion of saturated and moist substrate, predator indices, and adult attentiveness. We modeled the relationship between chick daily survival rates and invertebrate biomass, predator presence, and adult attentiveness using multiple linear regression.

RESULTS

Site quality

Invertebrates

Sampling began on 30 April and 15 May in 2001, and 28 April and 13 May in 2002 at Gavins and the other sites respectively. In 2003, we began sampling on 1 May at Gavins, 9 May at Alkali, 21 May at Sakakawea, 30 May at Garrison.

Substrate arthropods

Invertebrate numbers in the soil samples did not differ among years (ANOVA on ranks, year: $F_{2,91} = 2.3$, $P = 0.11$). When the three years were pooled, substrate invertebrate numbers were highest in the Alkali wetlands and lowest in Sakakawea (ANOVA on ranks, $F_{3,91} = 5.9$, $P = 0.0009$, Table 1.2).

Surface Invertebrates

Because chicks spent a greater percent of their time foraging in the saturated and moist substrates than in the dry substrate or vegetation (Chapter 2) and because most

invertebrates were caught in the saturated and moist zones (Table 1.3), we pooled invertebrate indices in the saturated and moist habitats for analyses. Data for all habitats are in Appendices 1.2 and 1.3.

Invertebrates pre-hatching

Pre-hatching invertebrate biomass varied among sites, and there was a site by year interaction (Table 1.4). In 2001, invertebrate biomass was higher at Gavins than at Garrison and Alkali, and higher at Sakakawea than at Alkali (Table 1.4). In 2002, invertebrate biomass was higher at Alkali and Gavins than at Garrison and Sakakawea (Table 1.4). In 2003, there was no difference in pre-hatching invertebrate biomass among sites (Table 1.4). Across all years (years pooled), pre-hatching invertebrate biomass was higher at Alkali and Gavins than at Garrison and Sakakawea (Table 1.4).

Pre-hatching invertebrate biomass at Alkali was higher in 2002 than 2001 (Table 1.4). There was no difference among years in pre-hatching invertebrate biomass at Garrison and Gavins (Table 1.4). Pre-hatching invertebrate biomass at Sakakawea was higher in 2001 than 2002 (Table 1.4). When all sites were pooled, there was no difference among years in pre-hatching invertebrate biomass (Table 1.4).

Pre-hatching invertebrate numbers varied among sites, years, and there was a year by site interaction (Table 1.4). In 2001, pre-hatching invertebrate numbers were lower at Garrison than at Gavins (Table 1.4). In 2002, pre-hatching invertebrate numbers were higher at Alkali and Gavins than at Garrison and Sakakawea (Table 1.4). In 2003, there was no difference among sites in pre-hatching invertebrate numbers (Table 1.4). Across all years (years pooled), pre-hatching invertebrate numbers were lower at Garrison than at the other three sites, and invertebrate numbers were higher at Gavins than at Sakakawea (Table 1.4).

Pre-hatching invertebrate numbers at Alkali were higher in 2002 and 2003 than 2001 (Table 1.4). There was no difference among years in pre-hatching invertebrate numbers at Garrison and Sakakawea (Table 1.4). When all sites were pooled, there was no difference among years in pre-hatching invertebrate numbers (Table 1.4).

Invertebrates during chick-rearing

Invertebrate biomass during the chick-rearing period varied among sites and years (Table 1.5). In 2001 and 2002, invertebrate biomass was higher at Alkali and Gavins than at Garrison and Sakakawea (Table 1.5). In 2003, invertebrate biomass was higher at Alkali and Gavins than at Garrison (Table 1.5). Across all years pooled, invertebrate biomass was higher at Alkali and Gavins than at Sakakawea and Garrison (Table 1.5). Invertebrate biomass was lower at Garrison than at any of the other sites (Table 1.5). There was no difference among years in invertebrate biomass at Alkali and Garrison (Table 1.5). Invertebrate biomass at Gavins was higher in 2001 and 2002 than 2003 (Table 1.5). Invertebrate biomass at Sakakawea was higher in 2001 than 2002 and 2003 (Table 1.5). When all sites were pooled, invertebrate biomass was higher in 2001 than 2002 and 2003 (Table 1.5).

Invertebrate numbers during the chick-rearing period varied among sites and years, and there was a site by year interaction (Table 1.5). In 2001 and 2002, invertebrate numbers were highest at Alkali and lowest at Garrison (Table 1.5). In 2001 and 2002, invertebrate numbers at Gavins and Sakakawea did not differ (Table 1.5). In 2003, there was no difference in invertebrate numbers among sites (Table 1.5). Across all years (years pooled), invertebrate numbers were highest at Alkali, and higher at Gavins than at Garrison (Table 1.5).

Coleoptera biomass varied among sites and years (Table 1.5). In 2001, 2002, and all years pooled, Coleoptera biomass was higher at Gavins than at the other sites (Table 1.5). In 2003, Coleoptera biomass did not differ among sites (Table 1.5). Coleoptera biomass differed among years only at Gavins, where biomass was lower in 2003 (Table 1.5).

Coleoptera numbers varied among sites, but not among years (Table 1.5). In 2001, Coleoptera numbers were highest at Gavins and lowest at Garrison (Table 1.5). In 2002, numbers were higher at Gavins (Table 1.5). There were no differences in Coleoptera numbers among sites in 2003 (Table 1.5). Across all years, Coleoptera numbers were higher at Gavins than at the other sites (Table 1.5).

Individual invertebrate biomass varied among sites and years (Table 1.5). In 2001, individual invertebrate biomass did not differ among sites (Table 1.5). In 2002,

individual invertebrate biomass was highest at Gavins, with no differences among the other three sites (Table 1.5). In 2003, individual invertebrate biomass was higher at Alkali and Gavins than at Garrison (Table 1.5). Across all years, individual invertebrate biomass was higher at Gavins than at the other three sites (Table 1.5). Individual invertebrate biomass at Alkali was higher in 2001 than 2002 (Table 1.5). There was no difference among years in individual invertebrate biomass at Garrison (Table 1.5). At Gavins, individual invertebrate biomass was higher in 2001 than 2003 (Table 1.5). At Sakakawea, individual invertebrate biomass was higher in 2001 than 2002 and 2003 (Table 1.5). When all sites were pooled, individual invertebrate biomass was higher in 2001 than the other years (Table 1.5).

Egg and clutch size

Clutch size did not vary among years or sites, and there was no year by site interaction (Table 1.6). Egg measurements (length, width, egg volume index, clutch volume index) did not differ among years (Table 1.7). When years were pooled, egg length and egg volume indices were lower at Gavins than at the other 3 sites (Table 1.7). When years were pooled, egg width and clutch volume indices did not differ among sites (Table 1.7).

Chick survival

We observed 94 broods from 2001-2003 at Gavins (29), Garrison (22), Lake Sakakawea (20), and Alkali (23).

Chick daily survival rates differed among sites, but did not differ among years and there was no site by year interaction (Table 1.8). Chick daily survival rates for the three years pooled were higher at Garrison than at Gavins (Table 1.8). Daily survival rates among the other sites did not differ (Table 1.8). We found no differences among sites when each year was examined separately (Table 1.8).

Chick growth rates

Within all years, chick weight gains were higher at Alkali than at Gavins and Garrison (Table 1.9, Figure 1.3). Wing growth rates were higher at Alkali and Garrison

than Gavins (Table 1.9, Figure 1.4). Exposed culmen growth rates were higher at Sakakawea and Garrison than at Alkali (Table 1.9, Figure 1.5). Condition indices (weight/culmen) as a function of age were higher at Alkali than at the three Missouri River sites (Table 1.9, Figure 1.6).

Because invertebrate indices varied among years, we compared chick growth rates among sites for each year separately. In 2001, mass growth rates were higher at Gavins than Garrison and Sakakawea (Table 1.9, Figure 1.3). In 2002, mass growth rates were higher at Gavins than Garrison (Table 1.9, Figure 1.3). In 2003, mass growth rates were highest at Alkali and lowest at Gavins (Table 1.3). In 2001, wing growth rates were highest at Gavins, but in 2003 they were lowest at Gavins (Table 1.9, Figure 1.4). In 2002, wing growth rates did not differ among sites (Table 1.9). Culmen growth rates were highest at Garrison in 2002 and 2003, but highest at Gavins in 2001 (Table 1.9, Figure 1.5). In all years, the slope for condition indices (mass / culmen) was lowest at Garrison (Table 1.9, Figure 1.6). The slope for condition indices (mass / culmen) was higher at Alkali in 2001 and 2003 than 2002 (Table 1.9).

Chick size at different age intervals

Chick weights did not vary among years or sites at any of the age intervals (0, 4-5, 8-9; Table 1.10). Chick culmen length and condition indices at day 0, 4 to 5 days and 8 to 9 days did not differ among years or sites (Table 1.10). Chick wing length did not differ among years or sites at any of the age intervals (Table 1.10).

Chick foraging behavior

Chick foraging rates (pecks/min) during the full 2-min observation time (total foraging rate (pecks/minute) differed among sites, but did not differ among years and there was no site by year interaction for chicks age 3 to 10 days or 11 to fledging (Table 1.11). Foraging rates for chicks age 3 to 10 were higher at Garrison than at the other sites (Table 1.11). Chicks aged 11 to fledging foraged at higher rates at Garrison than at the other sites (Table 1.11).

The peck rate (pecks/min) while actively foraging (foraging peck rate) for chicks age 3 to 10 days differed among sites, but did not differ among years and there was no

site by year interaction (Table 1.11). Chicks age 3 to 10 days foraged at a higher rate at Garrison and Alkali than at Gavins (Table 1.11). The peck rate while actively foraging for chicks age 11 days and older did not vary among sites, or years, and there was no site by year interaction.

The proportion of time chicks spent foraging differed among sites, but did not differ among years and there was no site by year interaction for the two age groups (Table 1.11). Chicks 3 to 10 days old spent less time foraging at Alkali sites (0.43) compared to the other sites (0.64 – 0.78) (Table 1.11). The proportion of time spent foraging was higher at Garrison and Gavins for chicks aged 11 to fledging (Table 1.11).

Chick distance to the nearest adult at age 3 to 10 days varied among sites, but did not vary among years (2002 and 2003) (Table 1.11). Chicks aged 3 to 10 foraged farther from the adult at Gavins than at the other sites (Table 1.11). Chick distance to the nearest adult at age 11 to fledging did not vary among sites, or years, and there was no site by year interaction (Table 1.11). We did not include brooded chicks in the analyses.

The distance chicks moved while actively foraging did not vary among sites, years, and there was no site by year interaction for any of the age groups (2002 and 2003) (Table 1.11).

The estimated biomass consumed by chicks (estimated biomass consumed = individual invertebrate biomass x foraging rate during the 2-min interval) of both age groups varied among sites and years, but there was no site by year interaction (Table 1.11). When all years were pooled, estimated biomass consumed was lower for chicks age 3 to 10 days at Alkali than at Gavins and Garrison. In 2001, the estimated biomass consumed by chicks age 3 to 10 days was lower at Alkali than at Garrison and Gavins (Table 1.11). In 2002 and 2003, the estimated biomass consumed by chicks age 3 to 10 days did not differ among sites. Estimated biomass consumed by chicks age 3 to 10 days did not differ among years at any of the sites, except Sakakawea, where estimated biomass consumed was higher in 2001 than in other years.

When all years were pooled, the estimated biomass consumed was lower for chicks age 11 to fledging at Alkali and Sakakawea than at Gavins and Garrison (Table 1.11). In 2001, the estimated biomass consumed by chicks age 11 to fledging did not differ among sites. In 2002, the estimated biomass consumed by chicks age 11 to

fledging was lower at Garrison and Gavins than at Alkali (Table 1.11). In 2003, the estimated biomass consumed was higher at Gavins than at the other sites. There was no difference among years at any of the sites, except at Sakakawea, where the estimated biomass consumed was higher in 2001 than in other years.

Adult foraging behavior

We began observing adults on the breeding grounds in mid-April in South Dakota and the last week in April in North Dakota, 2001-2003. Adult peck rates while actively foraging (foraging peck rate) during the pre-hatching period varied among sites and years, and there was no site by year interaction (Table 1.12). There was no difference among sites in 2001 and 2002 (Table 1.12). In 2003, the foraging peck rate was higher at Garrison than at the other sites (Table 1.12). When all years were pooled, the foraging peck rate was higher at Garrison than at Alkali and Gavins (Table 1.12). Foraging peck rates did not differ among years at Alkali, Garrison and Sakakawea (Table 1.12). Foraging peck rates at Gavins were higher in 2003 than 2001 and 2002. When all sites were pooled, foraging peck rates were higher in 2003, followed by 2001 and 2002 (Table 1.12).

Adult peck rates during the 2-min observation period (total peck rate) differed among sites and years, and there was a site by year interaction (Table 1.12). There was no difference among sites in 2001. In 2002 and 2003, and when all sites were pooled, Gavins had higher total peck rates than the other sites. Gavins was the only site with differences among years. Total peck rates were higher in 2003 than in the other years. When all sites were pooled, total peck rates were higher in 2001 than 2002.

The proportion of time adults spent foraging differed among years and sites (Table 1.12). When years were pooled, the proportion of time adults spent foraging was highest at Gavins, followed by Alkali and Sakakawea, and lowest at Garrison (Table 1.12). When all sites were pooled, the proportion of time adults spent foraging was higher in 2001 than in the other two years (Table 1.12). We did not compare each year separately, due to small and uneven sample sizes.

During the chick-rearing period, adults at Gavins spent less time attentive to chicks than at the other three sites (Table 1.13). Adults at Gavins spent more time

foraging than at Garrison and Sakakawea (Table 1.13). There were no differences in the time spent in other activities (Table 1.13). We did not analyze each year separately because of low and uneven sample sizes.

Adult measurements

We trapped 35 adult plovers at the nest in 2002 (20 females and 15 males) and 21 adults in 2003 (11 females and 10 males) at Garrison, Gavins and Sakakawea. Female and male weights were higher at Sakakawea than at the other two river sites (ANOVA, Females, $F_{2,30} = 7.61$, $P = 0.002$; Males, $F_{2,24} = 9.35$, $P = 0.001$, Table 1.14). Female culmen lengths did not differ among sites, but male culmens were longer at Garrison than at Gavins (ANOVA, Females, $F_{2,30} = 0.4$, $P = 0.67$; Males, $F_{2,24} = 3.7$, $P = 0.04$, Table 1.14). (Female condition indices (weight/culmen) did not differ among sites (ANOVA, $F_{2,30} = 2.47$, $P = 0.11$). Male condition indices were higher at Sakakawea and Gavins than at Garrison (ANOVA, $F_{2,24} = 4.47$, $P = 0.002$). Adult wing length did not vary among sites (ANOVA, Females, $F_{2,30} = 2.86$, $P = 0.07$; Males, $F_{2,24} = 0.21$, $P = 0.8$).

Predator tracks

In 2001, Garrison had a higher percent (83%) of brood locations at which predator tracks were found than the other sites, and there were no predator tracks at Gavins (Table 1.15). In 2002 there was no difference in predator track frequency among sites (Table 1.15). In 2003, predator track frequency was higher at Alkali (100%) and Gavins (56%) than at Sakakawea (25%) (Table 1.15). When 2002 and 2003 were pooled, there was no difference in the frequency of brood locations at which predator tracks were found (Table 1.15).

In 2001, mammalian predator tracks occurred more often at Garrison (67%), and no tracks occurred at Gavins and Sakakawea (Table 1.15). In 2002 and 2003, mammalian tracks occurred most often at Alkali (83% in 2002; 100% in 2003), and least often at Garrison (22% in 2002; 0% in 2003). When 2002 and 2003 were pooled, mammalian predator track frequency was highest at Alkali (93%), and lowest at Garrison (13%) (Table 1.15). The frequency of individual predator species at each site is in Appendix 1.4.

In 2001, gull occurrence did not vary among sites (Table 1.15). In 2002, gull occurrence was highest at Garrison (67%) and lowest at Gavins (0%). In 2003, gull occurrence was highest at Alkali (50%) and Garrison (50%). When 2002 and 2003 were pooled, gull frequency was highest at Garrison (60%) and lowest at Gavins (0%).

Factors affecting invertebrate abundance

Since invertebrate biomass differed among sites on the Missouri River (Table 1.5), we developed individual models for each site to determine whether there was a relationship between any physical variables (proportion of saturated and moist substrate, percent sand, and location (exposed or protected shoreline)) and invertebrate biomass. At Sakakawea, we included only the variables proportion of saturated and moist, and percent sand in the model, because we did not have data on location type. The global model was not significant at any of the sites (Table 1.16).

Factors affecting reproductive output

Effect of prey availability on reproductive output

Adult fitness

There was no relationship between invertebrate biomass or numbers and female condition indices (Spearman rank-order correlation, biomass: $r_s = -0.02$, $P = 0.9$, $n = 26$; numbers: $r_s = 0.04$, $P = 0.8$, $n = 26$).

Adult condition indices were negatively correlated with pre-hatching foraging rates (total peck rate and foraging peck rate), but not with the proportion of time spent foraging (Table 1.17).

Adult attentiveness, measured as proportion of time spent brooding chicks, proportion of time alert, and distance from chicks, was not related to average invertebrate abundance or biomass at the foraging site (Table 1.18). Chicks age 0 to 10 days were brooded longer when they were younger and when temperatures were lower (Multiple regression: $P < 0.0001$, $R^2 = 0.38$, Table 1.19).

Egg and clutch size

There was no relationship between egg volume (sum of egg volume for the clutch) and invertebrate indices on each territory (Spearman rank correlation, biomass: $r_s = 0.04$, $P = 0.7$, $n = 98$; numbers: $r_s = -0.06$, $P = 0.58$, $n = 98$), or mean egg volume in a clutch and invertebrate indices on each territory (Spearman rank correlation, biomass: $r_s = -0.12$, $P = 0.22$, $n = 98$; numbers: $r_s = -0.19$, $P = 0.06$, $n = 98$).

Chick size

There was no evidence of a relationship between chick weight, wing chord, or condition index at age 4 to 5 days or 8 to 9 days and invertebrate indices or foraging indices (Table 1.20).

Chicks that survived to age day 4 did not weigh more at hatching (Mean = 6.6 ± 0.03 (SE), $n = 196$) than those that did not survive to age day 4 (Mean = 6.5 ± 0.08 (SE), $n = 47$) (ANOVA on ranks, $F_{242} = 0.62$, $P = 0.43$).

Chicks that survived to fledging had greater mass at age 4 to 5 days and 8 to 9 days than chicks that did not fledge (Table 1.21). Wing length at age 8 to 9 days was not related to fledging (Table 1.21).

Chick survival

There was no relationship between chick daily survival rates and invertebrate numbers or biomass, Coleoptera biomass or biomass consumed (mg/minute) (Spearman rank correlation, invertebrate numbers: $r_s = -0.09$, $P = 0.4$, $n = 90$; invertebrate biomass: $r_s = -0.15$, $P = 0.16$, $n = 90$; Coleoptera biomass: $r_s = -0.05$, $P = 0.61$, $n = 90$; estimated biomass consumed: $r_s = 0.1$, $P = 0.4$, $n = 67$).

There was no relationship between brood success (probability of a brood fledging at least one chick) and invertebrate biomass or proportion of saturated and moist substrate (Table 1.22).

Effect of adult fitness on reproductive output

There was no relationship between the total egg volume in a clutch (clutches of 3, 4 and 5 eggs included) and female condition indices (Linear regression, condition index =

weight/culmen; $F_{25} = 0.15$, $P = 0.7$, $R^2 = 0.006$). There was no relationship between mean egg volume for 4-egg clutches and female condition indices (Linear regression, $F_{22} = 3.7$, $P = 0.07$, $R^2 = 0.15$). There was no relationship between brood success and adult attentiveness (Table 1.23).

Effect of predator abundance on reproductive output

Daily survival rates did not vary between brood locations with and without predators (at least one track found at a brood location) for all predator tracks, mammalian tracks and gull tracks in 2002 and 2003 (Table 1.24). There was no relationship between brood survival (probability of fledging at least one chick) and predator tracks (Table 1.25).

Chick Daily Survival Rate model

There was no relationship between chick daily survival rates (brood as the sampling unit) and invertebrate biomass, predator tracks, adult attentiveness, site or year when interaction effects were included ($F_{37} = 0.41$, $P = 0.97$), without interaction effects ($F_{37} = 0.65$, $P = 0.73$), or with site and year were pooled ($F_{37} = 2.6$, $P = 0.06$, Adj. $R^2 = 0.1$).

DISCUSSION

Variation in perceived site quality

When years were pooled (2001-2003), the sites hypothesized *a priori* to have higher invertebrate indices (Alkali and Gavins) had higher biomass during the chick-rearing period than the two cold water river sites (Garrison is downstream of a cold water release dam and Sakakawea is a deep reservoir). The higher invertebrate biomass indices at Alkali and Gavins were due to higher invertebrate numbers and higher individual invertebrate size, respectively. For 2001 to 2003 (years pooled), invertebrate biomass during the chick-rearing period was lower at Garrison, which has fluctuating water levels, than at Sakakawea, which fluctuates less. Overall, invertebrate indices (biomass and

numbers) were higher at Alkali and Gavins than at Garrison, the cold water, hydro-peaking site.

There were annual differences as well as site differences in invertebrate indices. The lower invertebrate indices at Gavins in 2003 than in the previous years were most likely due to the lower Coleoptera biomass in 2003. This decline could be due to lower summer temperatures (June and July) in South Dakota in 2003, or to lower nutrient availability over time, as time since the high winter flows (1996 and 1997) increases. At Sakakawea, higher invertebrate indices in 2001 than in the following years coincided with lower reservoir levels and lower precipitation in July.

During the pre-chick period, adults at Gavins spent more time foraging and their foraging rate was higher than at Garrison and Sakakawea, indicating that it might be taking them longer to obtain required energy. However, the adult peck rate while actively foraging was lower at Gavins, the site with higher invertebrate biomass and numbers than the other two river sites. Adults at Gavins may have been selecting invertebrates with higher handling times (Coleoptera rather than Diptera).

Chick foraging rates differed among sites, reflecting differences in invertebrate indices. The higher total foraging rate for chicks age 3 to 10 days and 11 to fledging at Garrison compared to the other sites, could be due to differences in prey selection at Garrison. Prey size and mobility (fast moving, smaller, Diptera vs slower, larger, Coleoptera), as well as digestibility, nutritive value, and handling time, may affect foraging rates and chick growth rates. Larger invertebrates (Coleoptera) may have a higher energy return for the amount of energy exerted in capture, and a longer handling time due to their larger size (compared to Diptera). Coleoptera numbers, Coleoptera biomass and individual invertebrate size were higher at Gavins than at the other sites, but the estimated biomass consumed at Garrison was similar to Gavins. In New York, piping plover chick foraging rates (day 3 to 25) were higher at the sites with highest invertebrate numbers (ephemeral pools: 10.4 – 15.5 pecks/min; Elias et al. 2000). The peck rate at the lowest quality site in New York (3.7 pecks/min) was lower than any Great Plains sites. In Assateague, Maryland, chick peck rates at the higher quality bay beach and island interior (3 to 10 days: 10.8 – 13.3 pecks/min; 11 to 20 days: 15.6 – 17.4 pecks/min; Loegering and Fraser 1995) were higher than at the Great Plains sites. Lower foraging

rates in the Great Plains could be due to chicks foraging on larger prey (Coleoptera) compared to Eastern beaches where Diptera are more frequent (% abundance of diptera on sticky stix in Long Island: 61.4 – 90.1 %; Cohen 2005).

In the Great Plains, chicks appear to use different foraging strategies relative to prey availability and characteristics. Previous studies on piping plovers have found that chicks spent more time foraging at sites with higher prey availability (Loefering and Fraser 1995; Goldin and Regosin 1998; Elias et al. 2000). Spotted sandpipers in Minnesota spent less time (30% of time) foraging when prey numbers were high compared to times with low prey availability (65% of time foraging) (Maxson and Oring 1980). Foraging time decreased as food increased to a certain level, then leveled off even if prey abundance continued to increase (Maxson and Oring 1980). In North and South Dakota, chicks age 3 to 10 days, an important age for growth and survival, spent less time foraging at Alkali, where invertebrate abundance was high. At Gavins, peck rates were low, but proportion of time foraging was high, and estimated biomass consumed was high. At Garrison, with low invertebrate indices, foraging rates and the proportion of time foraging were high, and so estimated biomass consumed was similar to Gavins, higher than Alkali, a site with high invertebrate indices. At Sakakawea, where peck rates were average, proportion of time foraging was high. Chicks “adjusted” to lower invertebrate numbers by foraging at higher rates or increasing the amount of time spent foraging.

Factors affecting reproductive output

Prey availability hypothesis

Clutch size

Clutch size, which tends to be fixed in shorebirds, remained near 4 eggs per clutch, and did not vary among sites. Since clutch size in shorebirds is limited, any change in energy allocation for eggs is most likely to appear as a change in egg size or nutritive value (Vaisanen et al. 1972). Egg volume and egg length of 4-egg clutches were lower at Gavins, a site with high pre-hatching invertebrate indices, indicating that a factor other than prey abundance was influencing energy availability for egg laying, or that the

prey index did not adequately reflect differences among sites. Migratory shorebirds have high energy requirements and most arrive at breeding sites with little stored energy (Howe 1983). Recent studies have determined that arctic-breeding waders are income, rather than capital breeders (i.e. egg nutrients are obtained from recently ingested nutrients, not from body stores; Klaassen et al. 2001). However, piping plovers are relatively short distance migrants, and their energetic costs for migration may be lower than arctic breeders. Since larger bird species may be able to depend more on endogenous resources, the impact of differences in invertebrates may not be apparent in certain species (Martin 1987). On Pelican Island, Minnesota, spotted sandpiper egg production was not affected by food availability, and invertebrate availability had no effect on egg mass (Lank et al. 1985).

We may have missed differences in prey availability at the sites by only measuring prey availability on territories. Adults in the Great Plains may fly to other areas to feed during the pre-chick hatching period. At our sites, both adults were not always present. Unattending semipalmated sandpiper adults in Barrow, Alaska, foraged away from the territory (Ashkenazie and Safriel 1979). On the East Coast, piping plover adults may fly up to 2 km from their territories to forage (Cohen 2005).

Piping plovers may not be limited by food for egg production: Ettinger and King (1980) hypothesized that clutch sizes (and perhaps their egg sizes) may be based on periods of low food availability, and that therefore, time spent foraging does not reflect prey availability. Adults could increase the number of surviving young by allocating more energy to eggs, but this would decrease adults' available energy, and could reduce their long-term survival, and therefore their residual reproductive value (Martin 1987).

Heredity and female condition also may affect egg size. Although we did not find a relationship between female condition indices and invertebrate indices, mean egg volume was larger for females with higher condition indices. We did not individually mark eggs to determine if larger eggs lead to higher chick survival, but we did not find a relationship between chick mass at hatching (day 0) and chick survival to fledging.

Chick survival and growth rates

Chicks in the Great Plains grew faster than on the East Coast. Chick mass and wing growth rates for 2001 to 2003 were higher in the Great Plains (mass: slope = 0.08; wing: slope = 0.09) than on Long Island, New York (mass: slope = 0.07; wing: slope = 0.08) (Cohen 2005). The lowest wing growth rate for all sites and years in the Great Plains was 0.08. The lowest mass growth rate in the Great Plains (Gavins, 2003, slope = 0.07) was equivalent to the Long Island mean.

Growth rate differences among sites reflected trends in invertebrate numbers: Chick growth rates were higher at Alkali, where invertebrate biomass was greatest. In 2001 and 2002, chicks at Alkali and Gavins, sites with high invertebrate biomass, had high growth rates for weight and condition indices (mass / exposed culmen). In 2003, this pattern was present at Alkali, but not at Gavins, which had high invertebrate indices, and the lowest chick growth rates for mass and wing length of all of the sites. However, in 2003, rates of condition indices (mass / exposed culmen) were higher at Gavins than at Garrison.

Studies on the East Coast piping plover population have found that 75% of chick mortality occurred before age six days (Loefering 1992) and 79% occurred before age 10 days (Patterson 1988). In the Great Plains, chicks that were larger at these early stages (age 4 to 5 days, and 8 to 9 days) were more likely to survive to fledging. Larger chicks are less likely to die of exposure or predation than smaller chicks. In king eider (*Somaterias spectabilis*) chicks, swimming speed and endurance were related to body size (Anderson and Alisauskas 2001). In our study, chick size at 4 to 5 days and 8 to 9 days did not vary among sites, and thus did not explain differential survival among sites. However, chick weights at age 4 to 5 days were higher in the Great Plains than Assateague Island National Seashore, Maryland for both chicks that fledged (Great Plains: fledged: 9.5 g; Assateague: fledged 8.0 g) and those that did not fledge (Great Plains: 8.3 g; Assateague: 6.8 g; Loefering and Fraser 1995). Even though chicks were heavier at the Great Plains sites, daily survival rates were lower than at Assateague Island National Seashore, Maryland (0.96) at all of our study sites (0.92-0.93) except Garrison (0.99) (Loefering and Fraser 1995). This indicates that something other than growth rates may be driving the differences in chick survival. The Great Plains chick daily

survival rates were lower than those on New York barrier islands, even at the poor quality habitats (no pools or tidal flats) in New York (high quality: 0.97 – 0.98; poor quality: 0.96; Elias et al. 2000).

We found no direct relationship between chick size or chick daily survival rates and invertebrate indices. Brood survival was lower at the site with high invertebrate indices (Gavins), and highest at the site with the lowest invertebrate indices (Garrison).

Parental quality hypothesis

Pre-hatching foraging rates were higher at sites where adults had lower condition indices, but the proportion of time spent foraging was not correlated with condition indices. Female and male mass, and male condition indices were higher at Garrison, the site with lower invertebrate indices. Early in the season, perhaps adults were feeding away from their territories.

There was no relationship between adult attentiveness and invertebrate indices or chick survival. Adults at Gavins spent less time attentive to chicks and more time foraging than at other sites. Chick survival was lower at Gavins, where chicks age 3 to 10 foraged further from the adult than chick than at other sites. Higher adult – chick distances can lead to higher chick predation (Walters 1984). Chick – adult distance may increase regardless of adult behavior if prey is scarce (Walters 1984); however, invertebrate indices were higher at Gavins, and the distance chicks moved while actively foraging did not vary among sites and years. Differences in chick – adult distances among sites could be related to habitat characteristics: the length and width of available shoreline was greater at Gavins than at Alkali, Garrison and Sakakawea (personal observation).

Predation hypothesis

Predation is a possible factor differentially affecting chick survival. However, sites with higher frequencies of predator tracks did not have lower chick survival. Other studies have indicated that the main predators on Great Plains piping plovers are avian, and except for gulls, we did not quantify avian predator presence (Kruse et al. 2001; Knetter et al. 2002). In the Alkali wetlands, fences to keep out mammalian predators did

not increase fledging rates more than nest exclosures alone (Knetter et al. 2002). American kestrels (*Falco sparverius*) and great horned owls (*Bubo virginianus*) caused the majority of chick mortalities in the Alkali wetlands and on the Missouri River (Kruse et al. 2001; Knetter et al. 2002). Kruse et al. (2001) attributed high predation rates at Gavins to habitat changes, particularly the fact that islands were small and isolated. In addition, due to the limited amount of available habitat, the same habitat was used year after year, increasing predators' ability to key into them from year to year (Kruse et al. 2001). Thus, creating dynamic sandbar complexes that change in size and location and that increase the area of unused habitat, could decrease predator efficiency (Kruse et al. 2001).

The lack of a direct relationship between chick survival rates and chick growth rates or prey availability, and the lack of a relationship between mammalian predator indices and chick survival rates indicate that another factor is affecting chick mortality. Knetter et al. (2002) suggested that in the alkali wetlands, avian predators may have a greater impact on piping plover chick survival than mammalian predators. Differences in survival rates among sites are most likely caused by differences in avian predator numbers, which we did not measure. At Gavins in 2002 and 2003, adult plovers were found dead in a manner consistent with avian (great horned owl) predation (decapitated, wings clipped). In addition, predation rates may have been exacerbated in years when chick growth rates were lower, or when chicks spent more time foraging due to lower prey availability.

MANAGEMENT IMPLICATIONS

Prey availability plays a role in chick survival (heavier chicks were more likely to survive to fledging). In addition, chicks that fledge at a heavier weight may be more likely to survive during migration and into the following year (Sagar and Horning 1990; Keedwell 2003). However, other factors in addition to prey availability, such as predation pressures, also play a role in reproductive output in the Great Plains population. Managing vegetation along the shoreline to decrease piping plover vulnerability to

mammalian predators and managing the surrounding landscape to minimize elevated perches for avian predators may increase chick survival rates.

This study underscores the variability in different indices among the four sites we studied in the Great Plains. The fact that invertebrate indices, predation pressures, chick growth rates and chick survival varied among the sites, suggests the need for different management strategies at each site. In addition, these factors may vary from year to year. The Great Plains, and particularly the Missouri River, are a dynamic system, in which piping plovers move among different habitat types from year to year depending on conditions (weather, hydrological conditions and cycles, management impacts) (Haig and Oring 1988a; Haig and Oring 1988b; Knetter et al. 2002; USFWS 2003; Haig et al. 2005). Decreasing predation pressure at Alkali and Gavins may increase productivity at these sites. At Garrison and Sakakawea, lower predation pressure appears to compensate for lower prey availability. However, the cold water river sites (Garrison and Sakakawea), with a lower prey base, may ultimately be able to support lower densities of plovers. Sandbars at Garrison and Sakakawea may not have sufficient invertebrate numbers to support the same densities of plover breeding sites as equivalent sized sandbars on Gavins. Plover nesting densities on East Coast beaches were higher at sites with higher prey abundance (Elias et al. 2000).

Maintaining, creating and evaluating foraging sites on sandbars and along reservoirs should be an important part of piping plover management in the Great Plains (USFWS 2003). The importance of maintaining a variety of suitable habitat along the Missouri River has been reinforced by the results of the 2001 census, documenting decreased numbers in Prairie Canada (due to habitat loss, including drought and flooding) along with an increase on the Missouri River (Montana, North Dakota, South Dakota; Haig et al. 2005). A combination of lower summer flows that expose more shoreline, spring flows that help create new nutrient-rich sandbar habitat, and creation of new habitat are all positive options for maintaining or creating critical piping plover habitat. Adaptive management and further studies on the long-term relative value of each of these processes needs to be evaluated.

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Table 1.1. Average daily elevation (feet above mean sea level) for Lake Sakakawea, and average daily outflow for Gavins Point and Garrison (in 1,000 CFS), for April through August 2001-2003.

Site	Year	April	May	June	July	August
Garrison						
	2001	13	12	14	14	14
	2002	11	13	21	21	21
	2003	19	19	21	21	21
Gavins						
	2001	11	16	19	23	25
	2002	23	23	25	26	28
	2003	25	26	26	26	25
Sakakawea						
	2001	1831	1831	1833	1834	1834
	2002	1827	1828	1830	1832	1830
	2003	1822	1822	1825	1827	1825

Table 1.2. Invertebrate numbers in core samples \pm SE, in North and South Dakota 2001-2003 (all years pooled). Results of Analysis of Variance on ranks, followed by Fisher's LSD for effects with significant P values. Sites with the same letters are not significantly different ($\alpha = 0.05$)^a. Brood territories are the sampling unit.

Site	2001 to 2003				2001		2002		2003				
	<i>n</i>	Mean \pm SE			<i>n</i>	Mean \pm SE		<i>n</i>	Mean \pm SE				
Alkali	26	5.5	\pm 1.5	A	7	10.7	\pm 3.9	10	3.5	\pm 2.2	9	3.6	\pm 1.5
Garrison	24	1.6	\pm 0.9	BC	5	0.3	\pm 0.2	9	2.4	\pm 2.4	10	1.6	\pm 0.6
Gavins	31	2.0	\pm 0.6	AB	9	0.2	\pm 0.1	11	3.5	\pm 1.4	11	2.0	\pm 0.6
Sakakawea	22	0.5	\pm 0.2	C	8	0.5	\pm 0.2	8	0.1	\pm 0.1	6	1.1	\pm 0.7

^aTwo-way ANOVA: Reach: $F_{3,91} = 5.9$, $P = 0.0009$; Year: $F_{2,91} = 2.3$, $P = 0.11$; Reach x Year: $F_{6,91} = 3.1$, $P = 0.008$

Table 1.3. Mean invertebrate abundance and biomass (mg dry weight) \pm SE by habitat. Invertebrates were collected in North and South Dakota, 2001-2003, on paint stirrers covered with Tanglefoot insect coating and placed for 30 min. Results of Analysis of Variance on ranks, followed by Fisher's LSD for effects with significant *P* values. Habitats with the same letters are not significantly different ($\alpha = 0.05$).

Habitat	<i>n</i>	Numbers			Biomass		
		Mean \pm SE			Mean \pm SE		
Saturated	96	22.2	\pm 4.8	A	25.5	\pm 6.5	A
Moist	95	9.1	\pm 1.1	B	8.2	\pm 1.4	B
Vegetation	85	4.4	\pm 0.4	C	4.5	\pm 0.6	C
Dry	71	2.9	\pm 0.3	D	3.9	\pm 1.2	D

Table 1.4. Mean invertebrate numbers and biomass (mg dry weight) \pm SE per set of sticky traps in saturated and moist habitats by site and year during the pre-hatching period. Invertebrates were collected in North and South Dakota, 2001-2003, on paint st

Site	2001			2002			2003			2001-2003		
	<i>n</i>	Mean \pm SE		<i>n</i>	Mean \pm SE		<i>n</i>	Mean \pm SE		<i>n</i>	Mean \pm SE	
Invertebrate biomass ^a												
Alkali	10	1.4 \pm 0.4	C ^b b ^c	9	7.2 \pm 1.8	A a	5	5.2 \pm 2.4	ab	24	4.4 \pm 1.0	A
Garrison	12	1.8 \pm 0.6	BC	10	1.7 \pm 0.7	B	4	1.8 \pm 1.2		26	1.8 \pm 0.4	B
Gavins	15	5.2 \pm 1.2	A	9	4.8 \pm 0.8	A	8	3.2 \pm 0.5		32	4.6 \pm 0.6	A
Sakakawea	5	4.3 \pm 2.5	AB a	8	0.7 \pm 0.2	B, b	5	2.0 \pm 0.9	ab	18	2.1 \pm 0.8	B
Sites pooled	42	3.2 \pm 3.2		36	3.6 \pm 3.6		22	3.1 \pm 3.1				
Invertebrate numbers ^d												
Alkali	10	1.5 \pm 0.3	AB b	9	10.4 \pm 4.0	A a	5	11.9 \pm 7.4	a	24	7.4 \pm 2.3	AB
Garrison	12	1.4 \pm 0.5	B	10	0.7 \pm 0.2	B	4	4.5 \pm 3.7		26	1.6 \pm 0.6	C
Gavins	15	4.7 \pm 1.5	A b	9	11.1 \pm 2.2	A a	8	3.2 \pm 0.7	b	32	6.2 \pm 1.1	A
Sakakawea	5	3.3 \pm 1.9	AB	8	1.5 \pm 0.3	B	5	4.3 \pm 2.2		18	2.8 \pm 0.8	B
Sites pooled	42	2.9 \pm 0.6		36	6.2 \pm 1.4		22	5.7 \pm 1.9				

^aANOVA on ranks: Site: $F_{3,99} = 9.12, P < 0.0001$, Year: $F_{2,99} = 0.14, P = 0.87$, Site X Year: $F_{6,99} = 4.2, P = 0.0009$

^bSite means with the same upper case letter within columns are not significantly different, $\alpha = 0.05$

^cSite means with the same lower case letter within rows are not significantly different, $\alpha = 0.05$

^dANOVA on ranks: Site: $F_{3,99} = 7.3, P = 0.0002$, Year: $F_{2,99} = 3.1, P = 0.05$, Site X Year: $F_{6,99} = 4.2, P = 0.0002$

Table 1.5. Mean invertebrate biomass (mg dry weight), invertebrate numbers, Coleoptera biomass (mg), Coleoptera numbers \pm SE per set of sticky traps, and individual invertebrate biomass (mg) in saturated and moist habitats during the chick rearing period. Invertebrates were collected in North and South Dakota, 2001-2003, on paint stirrers covered with Tanglefoot insect coating and placed for 30 min. If global model was significant, main effects are shown.

Site	2001				2002				2003				2001-2003			
	<i>n</i>	Mean \pm SE			<i>n</i>	Mean \pm SE			<i>n</i>	Mean \pm SE			<i>n</i>	Mean \pm SE		
Invertebrate biomass (mg) ^a																
Alkali	7	35.9	\pm 17.4	A ^b	8	40	\pm 12.9	A	8	9.5	\pm 2.4	A	23	22.2	\pm 6.1	A
Garrison	6	5.3	\pm 1.4	B	10	4.5	\pm 1.4	B	8	2.9	\pm 0.3	B	24	4.1	\pm 0.7	C
Gavins	8	24.9	\pm 4.9	A a ^c	11	17.2	\pm 3.7	A a	9	6	\pm 1.2	A b	28	15.4	\pm 2.3	A
Sakakawea	7	15.7	\pm 5.4	B a	10	4.8	\pm 1.3	B b	4	4	\pm 1.3	AB b	21	8.3	\pm 2.2	B
Sites pooled	28	21.1	\pm 5	a	39	11.7	\pm 2.1	b	29	5.8	\pm 0.9	b				
Invertebrate numbers ^d																
Alkali	7	29.3	\pm 7.3	A ab	8	49.8	\pm 15.5	A a	8	12.9	\pm 3.7	b	23	30.7	\pm 6.6	A
Garrison	6	4.5	\pm 0.8	C	10	5.9	\pm 1	C	8	7	\pm 1.2		24	5.9	\pm 0.6	C
Gavins	8	11.9	\pm 1.4	AB a	11	13.8	\pm 3.6	B a	9	5.1	\pm 0.7	b	28	10.5	\pm 1.6	B
Sakakawea	7	10.7	\pm 2.7	B a	10	8.2	\pm 1.4	BC b	4	7.6	\pm 3	b	21	8.9	\pm 1.2	BC
Sites pooled	28	14.4	\pm 2.6		39	17.7	\pm 4.2		29	8.1	\pm 1.3					
Coleoptera biomass (mg) ^e																
Alkali	7	0.4	\pm 0.2	B	8	0.1	\pm 0	B	8	0	\pm 0		23	0.2	\pm 0.1	B
Garrison	6	0.7	\pm 0.6	B	10	1.2	\pm 1.1	B	8	0.2	\pm 0.1		24	0.8	\pm 0.5	B
Gavins	8	12.8	\pm 4.4	A a	11	10.5	\pm 3.5	A a	9	1.5	\pm 0.5	b	28	8.3	\pm 2.1	A
Sakakawea	7	2	\pm 1.6	B	10	0.5	\pm 0.5	B	4	0.1	\pm 0		21	0.9	\pm 0.6	B
Sites pooled	28	4.4	\pm 1.6		39	3.4	\pm 1.2		29	0.5	\pm 0.2					

Site	2001				2002				2003				2001-2003							
	<i>n</i>	Mean ± SE			<i>n</i>	Mean ± SE			<i>n</i>	Mean ± SE			<i>n</i>	Mean ± SE						
Coleoptera numbers ^f																				
Alkali	7	0.2	±	0.1	BC	8	0.1	±	0.1	B	8	0.1	±	0.1	23	0.2	±	0	B	
Garrison	6	0.1	±	0	C	10	0.1	±	0.1	B	8	0.1	±	0	24	0.1	±	0	B	
Gavins	8	2.3	±	0.6	A a	11	1.1	±	0.3	A ab	9	0.7	±	0.3	b	28	1.3	±	0.3	A
Sakakawea	7	1.6	±	1.1	B	10	0.2	±	0.1	B	4	0.3	±	0.2	21	0.7	±	0.4	B	
Sites pooled	28	1.1	±	0.4		39	0.4	±	0.1		29	0.3	±	0.1						
Individual invertebrate biomass (mg) ^g																				
Alkali	7	1.1	±	0.3	a	8	0.5	±	0.1	B b	8	1	±	0.3	AB ab	23	0.9	±	0.2	B
Garrison	6	1.3	±	0.3		10	1	±	0.4	B	8	0.5	±	0.1	C	24	0.9	±	0.2	B
Gavins	8	2	±	0.2	a	11	1.6	±	0.4	A ab	9	1.2	±	0.2	A b BC	28	1.6	±	0.2	A
Sakakawea	7	1.5	±	0.2	a	10	0.6	±	0.1	B b	4	0.7	±	0.3	b	21	0.9	±	0.1	B
Sites pooled	28	1.5	±	0.1	a	39	0.9	±	0.2	b	29	0.9	±	0.1	b					

^aANOVA on ranks: Site: $F_{3,95} = 19.9, P < 0.0001$, Year: $F_{2,95} = 15.2, P < 0.0001$, Site X Year: $F_{6,95} = 1.4, P = 0.21$

^bSite means with the same letter within columns are not significantly different, $\alpha = 0.05$

^cSite means with the same letter within rows are not significantly different, $\alpha = 0.05$

^dANOVA on ranks: Site: $F_{3,95} = 13.1, P < 0.0001$, Year: $F_{2,95} = 2.9, P = 0.06$, Site X Year: $F_{6,95} = 2.7, P = 0.02$

^eANOVA on ranks: Site: $F_{3,95} = 17.5, P < 0.0001$, Year: $F_{2,95} = 3.3, P = 0.04$, Site X Year: $F_{6,95} = 0.66, P = 0.7$

^fANOVA on ranks: Site: $F_{3,95} = 20.3, P < 0.0001$, Year: $F_{2,95} = 2.1, P = 1.3$, Site X Year: $F_{6,95} = 1.1, P = 0.36$

^gANOVA on ranks: Site: $F_{3,95} = 13.9, P < 0.0001$, Year: $F_{2,95} = 14.5, P < 0.0001$, Site X Year: $F_{6,95} = 1.6, P = 0.15$

Table 1.6. Mean piping plover clutch size for each site and year in North and South Dakota, 2001-2003. Data are for first clutches. Results of Analysis of Variance on ranks, followed by Fisher's LSD for effects with significant P values ($\alpha = 0.05$).

Site	Year	2001				2002				2003				2001 - 2003			
		n	Mean	\pm	SE	n	Mean	\pm	SE	n	Mean	\pm	SE	n	Mean	\pm	SE
Alkali		14	3.9	\pm	0.07	9	4.0	\pm	0.00	10	3.9	\pm	0.10	33	3.9	\pm	0.04
Garrison		7	3.7	\pm	0.18	10	3.9	\pm	0.10	6	4.0	\pm	0.00	23	3.9	\pm	0.07
Gavins		11	3.8	\pm	0.12	15	3.8	\pm	0.11	10	4.0	\pm	0.00	36	3.9	\pm	0.06
Sakakawea		10	3.9	\pm	0.10	11	3.8	\pm	0.12	4	3.8	\pm	0.25	25	3.8	\pm	0.07
Sites pooled		42	3.9	\pm	0.05	45	3.9	\pm	0.05	30	3.9	\pm	0.05				

^aANOVA on ranks: Year: $F_{2,116} = 0.4, P = 0.7$; Site: $F_{3,116} = 0.6, P = 0.6$; Year x Site: $F_{6,116} = 0.8, P = 0.5$

Table 1.7. Piping plover mean egg length (mm), width (mm) and volume index (mm)³, and clutch volume index (mm)³ ± SE for North and South Dakota, 2001-2003. If global model was significant, main effects are shown.

Site	2001				2002				2003				2001 - 2003				
	<i>n</i>	Mean	±	SE	<i>n</i>	Mean	±	SE	<i>n</i>	Mean	±	SE	<i>n</i>	Mean	±	SE	
Length (mm) ^a																	
Alkali	14	31.7	±	0.2	9	31.8	±	0.3	10	31.8	±	0.3	33	31.8	±	0.1	A ^b
Garrison	7	32.2	±	0.3	10	32.2	±	0.3	6	31.6	±	0.2	23	32.1	±	0.2	A
Gavins	11	31.3	±	0.2	15	31.3	±	0.2	10	31	±	0.2	36	31.2	±	0.1	B
Sakakawea	10	31.8	±	0.2	11	32.2	±	0.2	4	32.3	±	0.4	25	32.1	±	0.1	A
Sites pooled	42	31.7	±	0.1	45	31.8	±	0.1	30	31.6	±	0.2					
Width (mm) ^c																	
Alkali	14	24.2	±	0.1	9	24.1	±	0.2	10	24.1	±	0.2	33	24.1	±	0.1	
Garrison	7	24.1	±	0.2	10	24.4	±	0.1	6	23.9	±	0.2	23	24.2	±	0.1	
Gavins	11	24.1	±	0.1	15	23.8	±	0.1	10	23.9	±	0.1	36	24	±	0.1	
Sakakawea	10	24.2	±	0.1	11	24.2	±	0.2	4	24.5	±	0.4	25	24.2	±	0.1	
Sites pooled	42	24.1	±	0.1	45	24.1	±	0.1	30	24.1	±	0.1					
Egg volume index (mm) ³ ^d																	
Alkali	14	18.5	±	0.3	9	18.5	±	0.4	10	18.6	±	0.4	33	18.5	±	0.2	A
Garrison	7	18.7	±	0.3	10	19.2	±	0.3	6	18.1	±	0.4	23	18.7	±	0.2	A
Gavins	11	18.2	±	0.3	15	17.8	±	0.2	10	17.8	±	0.2	36	18	±	0.1	B
Sakakawea	10	18.6	±	0.2	11	18.8	±	0.3	4	19.4	±	0.7	25	18.8	±	0.2	A
Sites pooled	42	18.4	±	0.1	45	18.5	±	0.2	30	18.3	±	0.2					

Site	2001				2002				2003				2001 - 2003			
	<i>n</i>	Mean	±	SE	<i>n</i>	Mean	±	SE	<i>n</i>	Mean	±	SE	<i>n</i>	Mean	±	SE
Clutch volume index (mm) ³ ^e																
Alkali	14	74.1	±	2	9	75.9	±	3	10	72.4	±	2	33	74.1	±	1.3
Garrison	7	69.2	±	3.4	10	72.7	±	3.9	6	72.4	±	1.6	23	71.6	±	2
Gavins	11	71.3	±	3.2	15	67.6	±	2.2	10	71.1	±	0.9	36	69.8	±	1.4
Sakakawea	10	72.5	±	2	11	72	±	2.8	4	72.5	±	3.8	25	72.3	±	1.5
Sites pooled	42	72.1	±	1.2	45	72	±	1.4	30	72.2	±	0.8				

^aANOVA: Site: $F_{3,116} = 8.8$, $P < 0.0001$, Year: $F_{2,116} = 0.6$, $P = 0.6$, Site X Year: $F_{6,116} = 0.6$, $P = 0.7$

^bSite means with the same letter within columns are not significantly different, $\alpha = 0.05$

^cANOVA: Site: $F_{3,116} = 1.9$, $P = 0.1$, Year: $F_{2,116} = 0.03$, $P = 0.9$, Site X Year: $F_{6,116} = 1.5$, $P = 0.2$

^dANOVA: Site: $F_{3,116} = 5.4$, $P = 0.002$, Year: $F_{2,116} = 0.06$, $P = 0.9$, Site X Year: $F_{6,116} = 1.4$, $P = 0.2$

^eANOVA: Site: $F_{3,116} = 1.4$, $P = 0.3$, Year: $F_{2,116} = 0.02$, $P = 0.9$, Site X Year: $F_{6,116} = 0.6$, $P = 0.8$

Table 1.8. Piping plover mean chick daily survival rates (DSR) \pm SE in North and South Dakota, 2001-2003. Results of two-way ANOVA comparing daily survival rates among sites^a. Sites with the same letters are not significantly different ($\alpha = 0.05$). Sample size is the number of broods.

Site	2001		2002		2003		2001-2003		
	<i>n</i>	Mean \pm SE	<i>n</i>	Mean \pm SE	<i>n</i>	Mean \pm SE	<i>n</i>	Mean \pm SE	
Alkali	6	0.971 \pm 0.017	9	0.892 \pm 0.058	8	0.950 \pm 0.018	23	0.932 ^b \pm 0.024	AB
Garrison	6	0.988 \pm 0.010	10	0.978 \pm 0.010	6	0.996 \pm 0.003	22	0.985 \pm 0.005	A
Gavins	8	0.904 \pm 0.076	12	0.849 \pm 0.066	9	0.814 \pm 0.083	29	0.853 \pm 0.042	B
Sakakawea	7	0.845 \pm 0.056	9	0.975 \pm 0.012	4	0.944 \pm 0.044	20	0.923 \pm 0.025	AB
Sites pooled	27	0.922 \pm 0.028	40	0.919 \pm 0.025	27	0.914 \pm 0.031			

^aANOVA: Site: $F_{3,94} = 3.25$, $P = 0.03$, Year: $F_{2,94} = 0.01$, $P = 0.99$, Site x Year: $F_{6,94} = 0.97$, $P = 0.45$.

^bSites with the same letter are not significantly different, $\alpha = 0.05$.

Table 1.9. Results of regression with indicator variables to compare slopes for growth rates at 4 sites in North and South Dakota, in 2001-2003. Individual points in the regression were mean brood measurements for each chick age. Variables were body mass, wing chord, exposed culmen, and condition index (mass / culmen). Sites with the same letter are not significantly different ($\alpha = 0.05$).

Year	Site	Mass			Wing			Culmen			Condition index (mass / culmen)		
		Slope \pm SE			Slope \pm SE			Slope \pm SE			Slope \pm SE		
2001-2003 ^a													
	Alkali	0.081	\pm 0.002	A	0.09	\pm 0.002	A	0.026	\pm 0	A	0.04	\pm 0.001	A
	Garrison	0.076	\pm 0.001	B	0.09	\pm 0.001	A	0.029	\pm 0	B	0.03	\pm 0.001	B
	Gavins	0.077	\pm 0.001	B	0.086	\pm 0.001	B	0.028	\pm 0	AB	0.03	\pm 0.001	B
	Sakakawea	0.078	\pm 0.002	AB	0.088	\pm 0.002	AB	0.028	\pm 0	B	0.03	\pm 0.001	B
2001 ^b													
	Alkali	0.086	\pm 0.004	AB	0.081	\pm 0	BC	0.03	\pm 0	B	0.04	\pm 0.002	A
	Garrison	0.078	\pm 0.003	B	0.085	\pm 0	B	0.029	\pm 0	B	0.03	\pm 0.001	B
	Gavins	0.092	\pm 0.003	A	0.093	\pm 0	A	0.035	\pm 0	A	0.04	\pm 0.001	A
	Sakakawea	0.08	\pm 0.005	B	0.075	\pm 0	C	0.03	\pm 0	B	0.03	\pm 0.002	B
2002 ^c													
	Alkali	0.079	\pm 0.002	AB	0.094	\pm 0		0.025	\pm 0	B	0.04	\pm 0.001	A
	Garrison	0.076	\pm 0.002	B	0.092	\pm 0		0.028	\pm 0	A	0.03	\pm 0.001	B
	Gavins	0.081	\pm 0.002	A	0.093	\pm 0		0.024	\pm 0	B	0.03	\pm 0.002	A
	Sakakawea	0.078	\pm 0.002	AB	0.094	\pm 0		0.028	\pm 0	A	0.03	\pm 0.001	A

Year	Site	Mass			Wing			Culmen			Condition index (mass / culmen)						
		Slope ± SE			Slope ± SE			Slope ± SE			Slope ± SE						
2003 ^d																	
	Alkali	0.083	±	0.002	A	0.092	±	0	A	0.026	±	0	AB	0.04	±	0.001	A
	Garrison	0.077	±	0.002	B	0.091	±	0	B	0.028	±	0	A	0.03	±	0.001	D
	Gavins	0.067	±	0.002	C	0.077	±	0	C	0.025	±	0	B	0.03	±	0.001	C
	Sakakawea	0.075	±	0.003	B	0.086	±	0	B	0.025	±	0	B	0.03	±	0.002	B

^aMass: $F_{3,581} = 1641, P < 0.0001$; Wing: $F_{3,584} = 223, P < 0.0001$; Culmen: $F_{3,525} = 773, P < 0.0001$; Condition index: $F_{3,522} = 944, P < 0.0001$

^bMass: $F_{3,148} = 481, P < 0.0001$; Wing: $F_{3,150} = 576, P < 0.0001$; Culmen: $F_{3,150} = 215, P < 0.0001$; Condition index: $F_{3,148} = 298, P < 0.0001$

^cMass: $F_{3,237} = 738, P < 0.0001$; Wing: $F_{3,237} = 1073, P < 0.0001$; Culmen: $F_{3,178} = 271, P < 0.0001$; Condition index: $F_{3,178} = 378, P < 0.0001$

^dMass: $F_{3,196} = 747, P < 0.0001$; Wing: $F_{3,197} = 1086, P < 0.0001$; Culmen: $F_{3,197} = 416, P < 0.0001$; Condition index: $F_{3,196} = 413, P < 0.0001$

Table 1.10. Mean values by site and results of ANOVA comparing sites for piping plover chick mass (g), wing chord (mm), culmen (mm), and condition index (weight/culmen) at day 0, day 4-5 and day 8-9, in North and South Dakota, 2001-2003. Results of ANOVA for years pooled ($\alpha = 0.05$). Only years pooled analyzed due to small sample size.

Age	Site	2001 - 2003			2001			2002			2003		
		<i>n</i>	Mean	± SE	<i>n</i>	Mean	± SE	<i>n</i>	Mean	± SE	<i>n</i>	Mean	± SE
Day 0 ^a													
	Mass (g)												
	Alkali	18	6.7	± 0.1	3	6.6	± 0.2	8	6.5	± 0.2	7	6.8	± 0.2
	Garrison	22	6.6	± 0.1	6	6.6	± 0.2	9	6.7	± 0.1	7	6.6	± 0.2
	Gavins	25	6.5	± 0.1	6	6.5	± 0.1	11	6.5	± 0.1	8	6.5	± 0.1
	Sakakawea	21	6.7	± 0.1	8	6.6	± 0.1	9	6.7	± 0.1	4	7	± 0.5
Day 4-5 ^b													
	Mass (g)												
	Alkali	14	9.4	± 0.5	4	9	± 1.4	5	8.7	± 0.3	5	10.3	± 0.8
	Garrison	15	8.9	± 0.4	2	8.7	± 0.7	8	9	± 0.6	5	9	± 0.7
	Gavins	20	9.2	± 0.4	6	9.6	± 0.6	9	9.2	± 0.5	5	8.5	± 0.9
	Sakakawea	13	8.7	± 0.3	5	8.2	± 0.5	4	9.2	± 0.5	4	8.8	± 0.3
	Exposed culmen (mm)												
	Alkali	14	7.5	± 0.2	4	7.3	± 0.4	5	7.6	± 0.4	5	7.4	± 0.1
	Garrison	15	7.9	± 0.1	2	7.6	± 0	8	7.9	± 0.2	5	7.9	± 0.2
	Gavins	11	7.4	± 0.2	6	7.6	± 0.2	9	.	± .	5	7.2	± 0.3
	Sakakawea	13	7.4	± 0.2	5	7.2	± 0.3	4	7.9	± 0.2	4	7.2	± 0.2

Age	Site	2001 - 2003				2001				2002				2003			
		<i>n</i>	Mean	±	SE	<i>n</i>	Mean	±	SE	<i>n</i>	Mean	±	SE	<i>n</i>	Mean	±	SE
Condition Index																	
	Alkali	14	1.3	±	0.2	4	1.2	±	0.1	5	1.2	±	0.1	5	1.4	±	0.1
	Garrison	15	1.1	±	0.1	2	1.1	±	0.1	8	1.1	±	0.1	5	1.1	±	0.1
	Gavins	11	1.2	±	0.2	6	1.3	±	0.1	9	.	±	.	5	1.2	±	0.1
	Sakakawea	13	1.2	±	0.1	5	1.1	±	0.1	4	1.2	±	0.1	4	1.2	±	0
Wing (mm)																	
	Alkali	14	15.3	±	0.3	4	16.6	±	0.4	5	14.7	±	0.3	5	14.8	±	0.2
	Garrison	15	15.1	±	0.4	2	16.3	±	1.7	8	14.4	±	0.4	5	15.8	±	0.6
	Gavins	20	14.9	±	0.4	6	16	±	0.5	9	14.1	±	0.5	5	13.8	±	0.3
	Sakakawea	13	15.5	±	0.3	5	15.7	±	0.2	4	15.3	±	0.5	4	15.6	±	0.5
Day 8-9 ^c																	
Mass (g)																	
	Alkali	8	16.1	±	1.1	2	17	±	1.2	3	14.2	±	2.3	3	17.3	±	1.7
	Garrison	14	15.3	±	0.6	2	16	±	1.1	6	14.9	±	1.2	6	15.6	±	0.8
	Gavins	17	15.5	±	0.8	6	17.7	±	1.1	6	15.5	±	1.3	5	12.9	±	0.8
	Sakakawea	5	15.4	±	0.4	1	15.6	±	.	2	14.9	±	0.7	2	15.7	±	1
Exposed culmen (mm)																	
	Alkali	8	8.9	±	0.2	2	8.8	±	0.7	3	9.2	±	0.4	3	8.7	±	0.3
	Garrison	14	9.1	±	0.1	2	8.9	±	0.1	6	9.4	±	0.3	6	8.9	±	0.1
	Gavins	11	9.1	±	0.2	6	9.4	±	0.3	6	.	±	.	5	8.7	±	0.3
	Sakakawea	5	9.1	±	0.2	1	9	±	.	2	9.5	±	0	2	8.9	±	0.4

Age	Site	2001 - 2003				2001				2002				2003			
		<i>n</i>	Mean	±	SE	<i>n</i>	Mean	±	SE	<i>n</i>	Mean	±	SE	<i>n</i>	Mean	±	SE
Condition index																	
	Alkali	8	1.8	±	0.1	2	2	±	0	3	1.5	±	0.2	3	2	±	0.3
	Garrison	14	1.7	±	0.1	2	1.8	±	0.1	6	1.6	±	0.1	6	1.8	±	0.1
	Gavins	11	1.7	±	0.1	6	1.9	±	0.1	6	.	±	.	5	1.5	±	0.1
	Sakakawea	5	1.7	±	0.1	1	1.7	±	.	2	1.6	±	0.1	2	1.8	±	0
Wing (mm)																	
	Alkali	8	25.3	±	1.9	2	26.5	±	1.2	3	22.3	±	4.3	3	27.3	±	2.9
	Garrison	14	24.8	±	0.9	2	25.3	±	2.7	6	23.6	±	1.8	6	25.8	±	1.2
	Gavins	17	23.7	±	1.4	6	28.9	±	1.8	6	22.7	±	1.4	5	18.5	±	1.7
	Sakakawea	5	24.3	±	0.7	1	25	±	.	2	24.8	±	1.8	2	23.5	±	0.5

^aANOVA: Weight: $F_{3,84} = 1.4, P = 0.26$; Culmen: $F_{3,73} = 1.6, P = 0.19$; Condition Inex: $F_{3,71} = 0.99, P = 0.4$; Wing: $F_{3,84} = 2.5, P = 0.06$

^bANOVA: Weight: $F_{3,60} = 0.44, P = 0.7$; Culmen: $F_{3,52} = 2.1, P = 0.12$; Condition index: $F_{3,52} = 1.2, P = 0.34$; Wing: $F_{3,60} = 1.7, P = 0.19$

^cANOVA: Weight: $F_{3,43} = 0.13, P = 0.9$; Culmen: $F_{3,37} = 2.1, P = 0.89$; Condition index: $F_{3,37} = 0.44, P = 0.72$; Wing: $F_{3,43} = 0.27, P = 0.85$

Table 1.11. Mean foraging rates (pecks/min), proportion of time foraging, distance to nearest adult (m), distance moved while foraging (m) and estimated biomass consumed (mg/min) \pm SE for piping plover chicks aged day 3-10 and 11 to fledging, in North and South Dakota, 2001-2003. If global model was significant, main effects are shown.

Site	2001		2002		2003		2001-2003				
	<i>n</i>	Mean \pm SE	<i>n</i>	Mean \pm SE	<i>n</i>	Mean \pm SE	<i>n</i>	Mean \pm SE			
Total peck rate (pecks / min) ^a											
Day 3 - 10											
Alkali	7	4.9 \pm 1.8	7	5.6 \pm 1.6	7	6.9 \pm 1.6	21	5.8 \pm 0.9	B ^b		
Garrison	4	10.6 \pm 3.3	6	12 \pm 3.5	6	9.8 \pm 3.3	16	10.8 \pm 1.9	A		
Gavins	9	6.8 \pm 0.8	7	7 \pm 1.7	5	6 \pm 1.6	21	6.7 \pm 0.7	B		
Sakakawea	4	6.7 \pm 3.9	7	7.9 \pm 1.1	2	5.8 \pm 2.3	13	7.2 \pm 1.3	B		
Sites pooled	23	7.5 \pm 1.5	26	8.4 \pm 1.1	19	7.5 \pm 1.3					
Day 11 - fledge											
Alkali	7	9.9 \pm 3.1	6	6.9 \pm 2.1	6	1.9 \pm 0.9	15	6.5 \pm 1.5	B		
Garrison	3	15.8 \pm 3.3	4	13.9 \pm 0.8	5	13.5 \pm 2.2	11	14.2 \pm 1.3	A		
Gavins	8	8.7 \pm 0.8	4	9.7 \pm 1.4	2	10.5 \pm 2.8	14	9.2 \pm 0.7	B		
Sakakawea	1	13.2 \pm .	2	9.3 \pm 9.3	2	5 \pm 2.5	4	8.4 \pm 3.4	B		
Sites pooled	19	10.5 \pm 1.3	16	9.4 \pm 1.4	15	7.3 \pm 1.6					
Foraging peck rate (pecks / min) ^c											
Day 3 - 10											
Alkali	7	15.4 \pm 3.1	7	12.7 \pm 1.8	7	11.1 \pm 1.8	19	14.4 \pm 1.7	A		
Garrison	4	17 \pm 3.5	6	13.4 \pm 3	6	13.5 \pm 2.7	15	12.9 \pm 1.3	A		
Gavins	9	7.5 \pm 0.6	7	10.1 \pm 1.6	5	6.7 \pm 1.4	20	8.1 \pm 0.7	B		
Sakakawea	4	14.5 \pm 7.2	7	9.6 \pm 0.7	2	10.9 \pm 0.9	13	11.3 \pm 2.1	AB		
Sites pooled	23	12.4 \pm 1.9	26	11.6 \pm 1	19	10.6 \pm 1.2					

Site	2001				2002				2003				2001-2003				
	<i>n</i>	Mean	±	SE	<i>n</i>	Mean	±	SE	<i>n</i>	Mean	±	SE	<i>n</i>	Mean	±	SE	
Day 11 - fledge																	
Alkali	7	18.4	±	2	6	9.7	±	1.6	6	10	±	4	19	13.3	±	1.7	
Garrison	3	17.9	±	4	4	21	±	2.2	5	15.2	±	2	11	17.5	±	1.6	
Gavins	8	8.8	±	0.8	4	12.1	±	1.4	2	21.2	±	6.6	14	11.5	±	1.5	
Sakakawea	1	14.4	±	.	2	18.5	±	.	2	11.4	±	2.3	4	13.9	±	1.9	
Sites pooled	19	13.8	±	1.4	16	13.7	±	1.6	15	13.9	±	1.9					
Proportion of time foraging ^d																	
Day 3 - 10																	
Alkali	7	0.27	±	0.09	7	0.44	±	0.13	7	0.59	±	0.08	21	0.43	±	0.06	B
Garrison	4	0.59	±	0.12	6	0.77	±	0.1	6	0.67	±	0.15	16	0.69	±	0.07	A
Gavins	9	0.82	±	0.05	7	0.67	±	0.15	5	0.85	±	0.1	21	0.78	±	0.06	A
Sakakawea	4	0.39	±	0.06	7	0.8	±	0.1	2	0.55	±	0.26	13	0.64	±	0.08	A
Sites pooled	23	0.6	±	0.1	26	0.7	±	0.1	19	0.7	±	0.1					
Day 11 - fledge																	
Alkali	7	0.46	±	0.14	6	0.7	±	0.16	6	0.38	±	0.15	19	0.51	±	0.09	B
Garrison	3	0.9	±	0.09	4	0.66	±	0.09	5	0.87	±	0.06	12	0.82	±	0.05	A
Gavins	8	0.87	±	0.04	4	0.8	±	0.12	2	0.76	±	0.12	14	0.83	±	0.04	A
Sakakawea	1	0.87	±	.	2	0.5	±	0.5	2	0.4	±	0.12	5	0.53	±	0.18	B
Sites pooled	19	0.7	±	0.1	16	0.7	±	0.1	15	0.6	±	0.1					

Site	2001		2002		2003		2001-2003			
	<i>n</i>	Mean ± SE	<i>n</i>	Mean ± SE	<i>n</i>	Mean ± SE	<i>n</i>	Mean ± SE		
Distance to nearest adult (m), while actively foraging, 2002 and 2003 ^e										
Day 3 - 10										
Alkali			6	4.6 ± 1.9	5	4.4 ± 1.2	9	4.4 ± 1.2	1.2	B
Garrison			5	8.4 ± 1.8	5	7.4 ± 2.6	9	8.1 ± 1.4	1.4	B
Gavins			4	12 ± 2	4	17.4 ± 10.7	5	15.2 ± 6.1	6.1	A
Sakakawea			6	4.4 ± 1.1	1	2.5 ± .	7	4.2 ± 0.9	0.9	B
Sites pooled			19	6.5 ± 1.2	14	8.7 ± 2.9				
Day 11 - fledge										
Alkali			5	7.6 ± 2.7	2	8 ± .	5	7.7 ± 2.1	2.1	
Garrison			2	2.5 ± .	4	12.7 ± 6.1	5	10.7 ± 5.1	5.1	
Gavins			3	21.6 ± 1.6	2	6.7 ± 1.7	4	14.2 ± 4.4	4.4	
Sakakawea			
Sites pooled			11	10.1 ± 2.9	8	10.3 ± 3.5				
Distance moved (m) while foraging, 2002 and 2003 ^f										
Day 3 - 10										
Alkali			6	9.5 ± 3.1	5	6.7 ± 1	10	8.2 ± 1.9	1.9	
Garrison			5	8.6 ± 1.9	5	5.1 ± 0.9	10	6.9 ± 1.1	1.1	
Gavins			4	8 ± 3.3	4	7.1 ± 1.1	7	7.6 ± 1.8	1.8	
Sakakawea			6	4.1 ± 0.7	1	5 ± .	7	4.1 ± 0.6	0.6	
Sites pooled			19	7.3 ± 1.4	14	6.3 ± 0.6				

Site	2001		2002		2003		2001-2003	
	<i>n</i>	Mean ± SE	<i>n</i>	Mean ± SE	<i>n</i>	Mean ± SE	<i>n</i>	Mean ± SE
Day 11 - fledge								
Alkali			5	10.6 ± 4.4	2	3.5 ± 2.5	7	8.6 ± 3.4
Garrison			2	8.5 ± 0.2	4	7.5 ± 0.3	6	7.8 ± 0.3
Gavins			3	9.3 ± 1.2	2	15.8 ± 4.2	5	12 ± 2.2
Sakakawea		
Sites pooled			11	9.9 ± 1.9	8	8.6 ± 1.9		
Biomass consumption index (mg / minute) ^g								
Day 3 - 10								
Alkali	7	5.6 ± 1.3	7	2.6 ± 0.7	7	7.1 ± 2.3	21	5 ± 1 C
Garrison	4	13.4 ± 3.2	6	11.7 ± 4.5	6	4.5 ± 0.6	16	9.7 ± 2.1 AB
Gavins	9	13.4 ± 1.4	7	11 ± 2.7	5	7.5 ± 1.2	21	10.6 ± 1.2 A
Sakakawea	4	9.8 ± 1.4	7	4.6 ± 0.8	2	3.9 ± 1.5	13	6.2 ± 0.9 BC
Sites pooled	24	10.5 ± 1.1 a ^h	27	7.8 ± 1.5 ab	20	6 ± 0.8 b		
Day 11 - fledge								
Alkali	7	11.3 ± 2.6	6	3.2 ± 0.8	6	3 ± 1	15	5.6 ± 1.2 B
Garrison	3	19.9 ± 4.7	4	13.5 ± 5.3	5	6.2 ± 0.8	11	12.7 ± 2.6 A
Gavins	8	17.2 ± 1.8	4	15.3 ± 3.7	2	13.1 ± 2.1	14	15.1 ± 1.7 A
Sakakawea	1	19.3 ± 2.7	2	5.4 ± 1	2	3.4 ± 1.3	4	9.6 ± 1.8 B
Sites pooled	19	16.8 ± 1.5 a	16	9.8 ± 1.9 b	15	7.1 ± 1.1 b		

^a ANOVA on ranks: Day 3 to 10: Site: $F_{3,70} = 3.3, P = 0.02$; Year: $F_{2,70} = 5.7, P = 0.18$; Site x Year: $F_{6,70} = 0.8, P = 0.55$; Day 11 to fledge: Site: $F_{3,43} = 5.1, P = 0.004$; Year: $F_{2,43} = 0.2, P = 0.8$; Site x Year: $F_{6,43} = 0.2, P = 0.98$

^b Site means with the same letter within columns are not significantly different, $\alpha = 0.05$

^c ANOVA on ranks: Day 3 to 10: Site: $F_{3,66} = 4.0, P = 0.01$; Year: $F_{2,66} = 0.09, P = 0.9$; Site x Year: $F_{6,66} = 1.5, P = 0.16$; Day 11 to fledge: Site: $F_{3,47} = 7.0, P = 0.07$; Year: $F_{2,47} = 1.3, P = 0.3$; Site x Year: $F_{6,47} = 0.5, P = 0.8$

^dANOVA on ranks: Day 3 to 10: Site: $F_{3,70} = 5.4, P = 0.002$; Year: $F_{2,70} = 0.9, P = 0.4$; Site x Year: $F_{6,70} = 1.0, P = 0.4$; Day 11 to fledge: Site: $F_{3,49} = 4.7, P = 0.007$; Year: $F_{2,49} = 2.1, P = 0.13$; Site x Year: $F_{6,49} = 1.6, P = 0.15$

^eANOVA on ranks: Day 3 to 10: Site: $F_{3,49} = 4.1, P = 0.02$; Year: $F_{2,49} = 2.1, P = 0.13$; 0.84; Site x Year: $F_{3,29} = 0.3, P = 0.82$; Day 11 to fledge: Site: $F_{3,17} = 0.59, P = 0.56$; Year: $F_{1,17} = 0.08, P = 0.8$; Site x Year: $F_{2,17} = 2.1, P = 0.2$. Brooded chicks excluded.

^fANOVA on ranks: Day 3 to 10: Site: $F_{3,33} = 1.3, P = 0.3$; year: $F_{1,33} = 0.8, P = 0.4$; site *year: $F_{3,33} = 0.3, P = 0.8$; Day 11 to fledge: Site: $F_{3,17} = 0.67, P = 0.5$; year: $F_{1,17} = 0.03, P = 0.9$; site*year: $F_{2,17} = 1.6, P = 0.2$

^g Biomass consumption index = average invertebrate individual biomass x peck rate; ANOVA on ranks: Day 3 to 10: Site: $F_{3,70} = 3.9, P = 0.001$; Year: $F_{2,70} = 3.8, P = 0.03$; Site x Year: $F_{6,70} = 1.4, P = 0.2$; Day 11 to fledge: Site: $F_{3,43} = 5.9, P = 0.001$; Year: $F_{2,43} = 10.8, P = < 0.0001$; Site x Year: $F_{6,43} = 1.2, P = 0.3$

^hSite means with the same letter within rows are not significantly different, $\alpha = 0.05$

Table 1.12. Adult piping plover foraging rates (pecks/min) and proportion of time foraging during the pre-chick period in North and South Dakota, 2001-2003. If global model was significant, main effects are shown.

Site	2001			2002			2003			2001-2003		
	<i>n</i>	Mean ± SE		<i>n</i>	Mean ± SE		<i>n</i>	Mean ± SE		<i>n</i>	Mean ± SE	
Foraging peck rate ^a												
Alkali	10	19.9 ± 3.1		4	17.5 ± 6.6		8	19.0 ± 1.6	B ^b	22	19.2 ± 1.8	B
Garrison	2	22.7 ± 10.7		5	13.5 ± .		9	28.3 ± 2.8	A	16	25.7 ± 2.9	A
Gavins	9	15.3 ± 2.4	b ^c	12	11.4 ± 1.2	b	11	22.3 ± 1.7	B a	32	15.9 ± 1.3	B
Sakakawea	5	19.7 ± 3.2		1	. ± .		8	21.5 ± 1.8	B	14	20.8 ± 1.6	AB
Sites pooled	26	18.5 ± 1.7	b	22	12.7 ± 1.5	c	36	22.7 ± 1.2	a	84	19.1 ± 0.9	
Total peck rate ^d												
Alkali	10	14.8 ± 3.7		4	3.8 ± 1.5	B	8	7.1 ± 1.6	B	22	10.0 ± 2	B
Garrison	2	18.0 ± 15.5		5	2.7 ± 2.7	B	9	9.1 ± 2.9	B	16	8.7 ± 2.7	B
Gavins	9	14.7 ± 2.5	b	12	16.5 ± 1.3	A b	11	25.7 ± 1.8	A a	32	18.7 ± 1.3	A
Sakakawea	5	16.5 ± 4.2		1	0.0 ± .	B	8	9.9 ± 2.6	B	14	11.5 ± 2.3	B
Sites pooled	26	15.4 ± 2.0	a	22	10.3 ± 1.7	b	36	13.2 ± 1.7	ab	84	13.3 ± 1.1	
Proportion of time foraging ^e												
Alkali	10	66 ± 7	AB a	4	28 ± 13	AB b	8	38 ± 9	B b	22	49 ± 6	B
Garrison	2	61 ± 40	B	5	20 ± 20	AB	9	29 ± 9	B	16	32 ± 9	C
Gavins	9	94 ± 4	A	12	68 ± 7	A	11	84 ± 3	A a	32	81 ± 4	A
Sakakawea	5	82 ± 9	a	1	0 ± .	B	8	41 ± 8	B ab	14	53 ± 9	B
Sites pooled	26	78 ± 5	AB a	22	47 ± 8	b	36	48 ± 5	b	84	58 ± 4	

^aANOVA: Site: $F_{3,83} = 5.5$, $P < 0.002$, Year: $F_{2,83} = 6.4$, $P = 0.003$, Site X Year: $F_{6,83} = 0.9$, $P = 0.4$

^bSite means with the same letter within columns are not significantly different, $\alpha = 0.05$

^cSite means with the same letter within rows are not significantly different, $\alpha = 0.05$

^dANOVA: Site: $F_{3,83} = 8.6$, $P < 0.0001$, Year: $F_{2,83} = 4.8$, $P = 0.01$, Site X Year: $F_{6,83} = 3.1$, $P = 0.01$

^eANOVA on ranks: Site: $F_{3,83} = 17.1$, $P < 0.0001$, Year: $F_{2,83} = 14.5$, $P < 0.0001$, Site X Year: $F_{6,83} = 0.9$, $P = 0.5$

Table 1.13. Percent time in each activity for piping plover adults with chicks less than 11 days old, in North and South Dakota, 2001-2003. Results of ANOVA on ranks, followed by Fisher's LSD for significant effects. Sites within the same rows with the same letters are not significantly different ($\alpha = 0.05$). Only years pooled were analyzed statistically due to low sample sizes.

Year	Alkali			Garrison			Gavins			Sakakawea			All sites								
Activity	<i>n</i>	Mean	SE	<i>n</i>	Mean	SE	<i>n</i>	Mean	SE	<i>n</i>	Mean	SE	<i>n</i>	Mean	SE	<i>F</i>	<i>P</i>				
2001 - 2003																					
Attentive	21	61	6	a	14	57	10	a	20	23	7	b	6	72	10	a	61	49	5	16.1	0.001
Disturbed	21	2	1		14	2	1		20	4	2		6	0	0		61	2	1	2.7	0.44
Foraging	21	19	5	ab	14	21	8	b	20	44	7	a	6	18	10	b	61	27	4	9.8	0.02
Other	21	5	2		14	9	4		20	3	1		6	2	2		61	5	1	1.6	0.66
Resting	21	14	5		14	11	7		20	22	6		6	7	6		61	15	3	4.1	0.25
2001																					
Attentive	7	42	10		4	56	16		8	18	7		3	57	9						
Foraging	7	5	1		4	0	0		8	9	2		3		0						
Disturbed	7	21	5		4	11	8		8	32	8		3	14	4						
Resting	7	11	2		4	21	11		8	5	2		3								
Other	7	21	4		4	12	5		8	36	6		3	29	12						
2002																					
Attentive	7	46	6		6	44	14		7	13	7		2	67	16						
Foraging	7	0	0		6	11	1		7	13	5		2								
Disturbed	7	32	11		6	17	14		7	38	12		2	33	25						
Resting	7	9	2		6	17	4		7	19	5		2								
Other	7	14	4		6	11	5		7	19	6		2								

Year	Alkali			Garrison			Gavins			Sakakawea		
2003												
Attentive	7	30	6	5	33	9	5	53	14	1	50	.
Foraging	7	20	2	5	11	4	5	13	7	1		.
Disturbed	7	20	7	5	22	18	5	27	12	1	50	.
Resting	7	15	4	5	11	7	5	0	0	1		.
Other	7	15	12	5	22	19	5	7	2	1		.

Table 1.14. Female and male adult piping plover wing chord (mm), mass (g), exposed culmen (mm) and condition indices (mass / culmen) on the Missouri River in North and South Dakota, 2002-2003. Results of ANOVA comparing sites. Sites with the same letters are not significantly different ($\alpha = 0.05$).

Measurement	Site	Female			Male		
		<i>n</i>	Mean \pm SE		<i>n</i>	Mean \pm SE	
Mass (g)							
	Garrison	7	50.2 \pm 0.9	B	8	50.6 \pm 0.4	B
	Gavins	14	50.8 \pm 0.6	B	12	51.6 \pm 0.7	B
	Sakakawea	10	54.6 \pm 1.1	A	5	54.9 \pm 0.6	A
Wing (mm)							
	Garrison	7	117.4 \pm 1.3		8	121.1 \pm 1.0	
	Gavins	14	116.8 \pm 0.7		12	120.7 \pm 0.8	
	Sakakawea	10	119.2 \pm 0.4		5	120 \pm 1.7	
Exposed culmen (mm)							
	Garrison	7	12.6 \pm 0.2		8	13.4 \pm 0.3	A
	Gavins	14	12.8 \pm 0.2		12	12.5 \pm 0.1	B
	Sakakawea	10	12.9 \pm 0.3		5	12.9 \pm 0.4	AB
Condition Index (Mass / Culmen)							
	Garrison	7	4.0 \pm 0.1		8	3.8 \pm 0.1	B
	Gavins	14	4.0 \pm 0.1		12	4.1 \pm 0.1	A
	Sakakawea	10	4.2 \pm 0.1		5	4.3 \pm 0.2	A

Table 1.15. Percent and number of piping plover brood locations at each site with predator tracks, in North and South Dakota, 2001-2003. Results Likelihood Ratio Chi-Square (G test) comparing presence of predator tracks among sites. Sample size (*n*) represents the number of brood locations at each site.

Predator type	Alkali		Garrison		Gavins		Sakakawea		<i>P</i>	<i>G</i>
	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>		
All predators										
2001	33	6	83	6	0	6	17	6	0.007	12.1
2002	83	6	78	9	64	11	78	9	0.8	1
2003	100	8	83	6	56	9	25	4	0.01	10.5
2002 & 2003 ¹	93	14	80	15	60	20	62	13	0.09	6.4
Mammalian predators										
2001	17	6	67	6	0	6	0	6	0.01	11.5
2002	83	6	22	9	64	11	78	9	0.04	8.2
2003	100	8	0	6	56	9	25	4	0.0001	20.5
2002 & 2003 ¹	93	14	13	15	60	20	62	13	< 0.0001	21.7
Gulls										
2001	33	6	33	6	0	6	17	6	0.3	3.9
2002	17	6	67	9	0	11	33	9	0.004	13.6
2003	50	8	50	6	0	9	25	4	0.03	8.9
2002 & 2003 ¹	36	14	60	15	0	20	31	13	0.0002	20.2

¹Only 2002 and 2003 pooled, because methods were different in 2001

Table 1.16. Regression analysis used to predict total invertebrate biomass on the Missouri River, North and South Dakota, 2001-2003. Variables in the model are proportion of saturated and moist substrate, percent sand in substrate, and location (protected, exposed). Each site was modeled separately. Variables at Sakakawea were proportion of saturated and moist substrate, and percent sand.

Site	df	<i>F</i>	<i>P</i>	R ²
Garrison	3,17	0.98	0.43	-0.004
Gavins	3,17	0.51	0.68	-0.08
Sakakawea	2,6	1.17	0.37	0.04

Table 1.17. Spearman correlation analysis between piping plover adult condition indices (weight/culmen) and foraging indices on the Missouri River, North and South Dakota, 2002 - 2003.

Variables	r_s	P	n
Total pecks (per min)	-0.65	0.002	21
Foraging pecks (per min)	-0.63	0.004	21
Proportion time foraging	-0.30	0.90	21

Table 1.18. Spearman correlation analysis of piping plover parental attention (for chicks aged 10 or less) and invertebrate indices (mean biomass and mean numbers) during chick rearing period, in North and South Dakota, 2001-2003.

Parameter	<i>n</i>	Invertebrate biomass		Invertebrate numbers	
		<i>P</i>	<i>r_s</i>	<i>P</i>	<i>r_s</i>
Distance to chicks	31	0.5	0.12	0.66	-0.08
Percent time attentive (brooding or alert)	58	0.4	-0.11	0.33	-0.13
Percent time brooding	57	0.95	-0.009	0.53	-0.08
Percent time alert	58	0.11	-0.21	0.67	-0.06

Table 1.19. Results of multiple regression analysis of temperature (°C) and chick age (chicks aged 0-10 days) on percent of time spent brooded, in North and South Dakota, 2001-2003.

Variable	Parameter	SE	t	<i>P</i>
Intercept	127.91	12.58	10.17	< 0.0001
Temperature	-3.78	0.48	-7.91	< 0.0001
Age	-3.40	0.97	-3.50	0.0007

Table 1.20. Results of regression analyses of chick size in North and South Dakota, 2001-2003, at day 4-5 and 8-9 with invertebrate and foraging indices. Brood means were used in the analyses.

Age	Weight			Wing			Condition index (Weight / culmen)		
	<i>n</i>	R ²	<i>P</i>	<i>n</i>	R ²	<i>P</i>	<i>n</i>	R ²	<i>P</i>
Day 4-5									
Mean invertebrate number	62	0.01	0.9	61	0.02	0.3	52	0.01	0.6
Mean invertebrate biomass	62	0.09	0.1	61	0.05	0.1	52	0.01	0.4
Estimated biomass consumed ^a	51	0.01	0.8	61	0.03	0.2	53	0.03	0.2
Foraging peck rate	51	0.04	0.2	48	0.01	0.6	42	0.04	0.2
Total peck rate	51	0.02	0.3	50	0.01	0.8	44	0.01	0.7
Proportion time foraging	51	0.01	0.8	50	0.05	0.1	44	0.01	0.5
Day 8-9									
Mean invertebrate number	43	0.01	0.9	43	0.01	0.7	37	0.01	0.8
Mean invertebrate biomass	43	0.01	0.7	43	0.01	0.6	37	0.02	0.4
Estimated biomass consumed ^a	37	0.01	0.9	37	0.01	0.7	37	0.02	0.4
Foraging peck rate	37	0.01	0.7	37	0.01	0.9	32	0.01	0.6
Total peck rate	37	0.01	1.0	37	0.01	0.8	32	0.01	0.8
Proportion time foraging	37	0.04	0.2	37	0.04	0.2	32	0.03	0.3

^aEstimated biomass consumed: Mean biomass of single invertebrate x peck rate

Table 1.21. Mass and wing measurements \pm SE for piping plover chicks age 4 to 5 and 8 to 9 days old surviving to fledging and those that did not, in North and South Dakota, 2001-2003. Results of ANOVA comparing body sizes ($\alpha = 0.05$).

Age (days)	<i>n</i>	Fledged		Didn't Fledge		<i>F</i>	<i>P</i>
		Mean \pm SE	<i>n</i>	Mean \pm SE	<i>n</i>		
Mass (g)							
4 to 5	85	9.5 \pm 0.2	43	8.3 \pm 0.2	15.4	0.0001	
8 to 9	68	16.0 \pm 0.3	13	14.2 \pm 0.64	4.9	0.03	
Wing length (mm)							
4 to 5	85	15.2 \pm 0.2	43	15.0 \pm 0.2	0.6	0.45	
8 to 9	68	25.1 \pm 0.6	13	22.4 \pm 0.2	3.8	0.056	

Table 1.22. Logistic regression modeling results for probability of piping plovers fledging at least one chick as a function of invertebrate biomass and proportion of saturated and moist substrate in North and South Dakota, 2001 - 2003.

Site	<i>n</i>	Intercept	±	SE	β_1	±	SE	Wald χ^2	<i>P</i>
Invertebrate biomass									
Sites pooled	89	1.6	±	0.3	-0.02	±	0.01	2.77	0.10
Alkali	22	1.7	±	0.7	-0.01	±	0.01	1.48	0.22
Garrison	21	13.1	±	21.6	-1.1	±	1.9	0.32	0.57
Gavins	26	0.6	±	0.8	0.03	±	0.05	0.37	0.54
Sakakawea	20	1.9	±	1.0	-0.1	±	0.1	1.51	0.22
Proportion saturated and moist substrate									
Sites pooled	84	0.1	±	0.47	0.5	±	0.9	0.33	0.56
Alkali	22	1.9	±	1	-2.4	±	2.9	0.69	0.40
Garrison	22	-1.4	±	1.9	8.1	±	5.3	2.33	0.13
Gavins	24	0.7	±	1.1	-0.02	±	1.6	0.00	0.99
Sakakawea	16	1.1	±	1	-0.02	±	3.2	0.01	0.96

Table 1.23. Logistic regression modeling results for probability of piping plovers fledging at least one chick as a function of parental attentiveness (proportion of time spent brooding chicks and proportion of time alert), in North and South Dakota, 2001 - 2003.

Site	<i>n</i>	Intercept	± SE	β_1	± SE	Wald χ^2	<i>P</i>
Adult attentiveness							
Sites pooled	51	2.3	± 0.7	-0.01	± 0.02	0.28	0.60
Alkali	20	0.7	± 0.9	0.02	± 0.03	0.28	0.60
Garrison ^a							
Gavins	15	7.3	± 5.8	-0.1	± 0.1	1.33	0.25
Sakakakawea ^a							

^aInestimable: All observations have the same response

Table 1.24. Piping plover chick mean daily survival rates (DSR) \pm SE for sites with predators and without predators, in North and South Dakota, 2002-2003. Results of ANOVA comparing DSR for sites with and without predator tracks ($\alpha = 0.05$).

	No predator tracks		Predator tracks		$F_{3,61}$	P
	Mean DSR \pm SE	n	Mean DSR \pm SE	n		
All predators	0.925 \pm 0.029	17	0.926 \pm 0.023	45	0.02	0.9
Mammals	0.949 \pm 0.019	27	0.908 \pm 0.029	35	0.96	0.33
Gulls	0.905 \pm 0.026	44	0.978 \pm 0.009	18	3	0.09

Table 1.25. Logistic regression modeling results for probability of piping plovers fledging at least one chick as a function of predator track occurrence (at least one track found at brood location) in North and South Dakota, 2001 - 2003.

Site	<i>n</i>	Intercept	±	SE	β_1	±	SE	Wald χ^2	<i>P</i>
Predator tracks									
Sites pooled	86	0.1	±	0.5	0.5	±	0.9	0.33	0.56
Alkali	20	2.0	±	1.0	-1.2	±	1.0	1.70	0.19
Garrison ^a	21								
Gavins	26	1.3	±	0.6	-2.5	±	1.4	3.22	0.08
Sakakawea	19	0.3	±	0.6	1.6	±	1.5	1.09	0.30

^aInestimable: Only one brood not successful

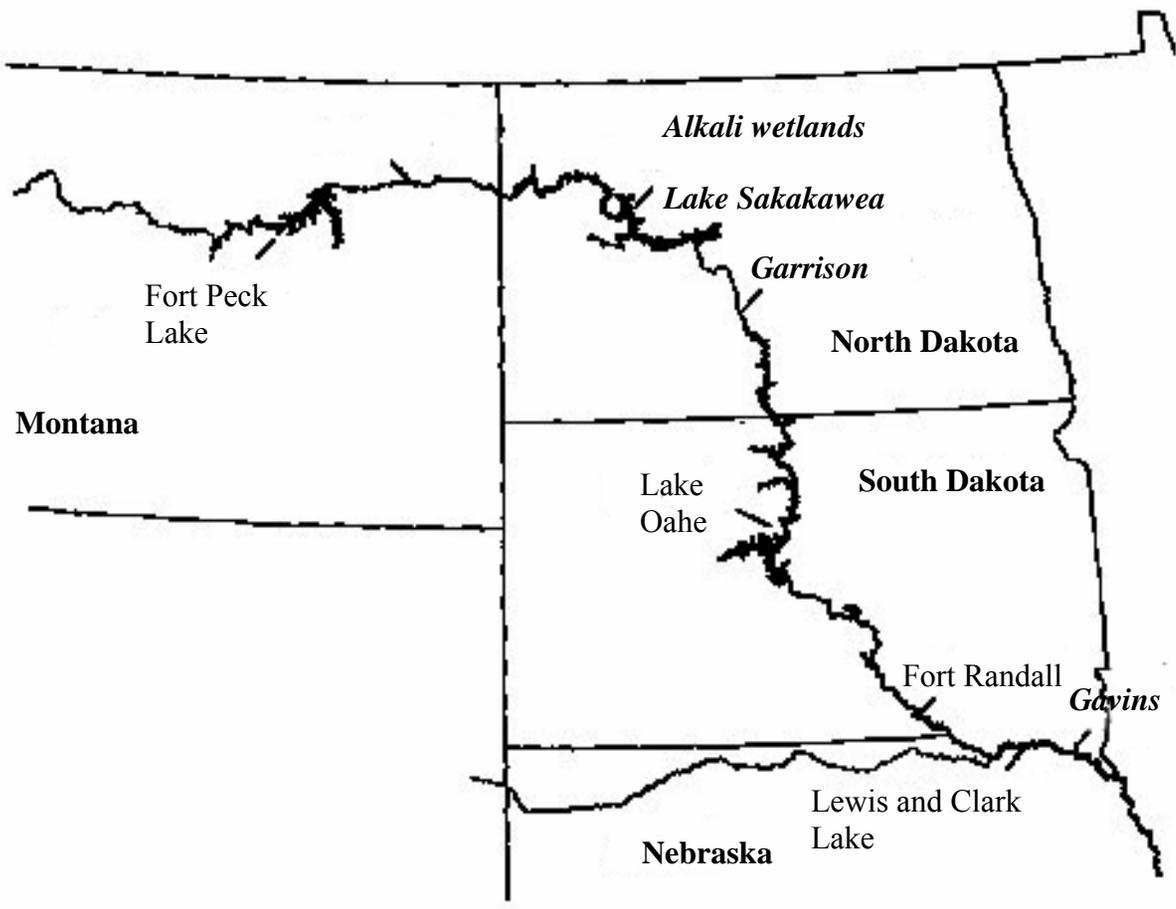


Figure 1.1. Missouri River reaches and study sites in North Dakota and South Dakota in 2001-2003. Study sites are in bold italics.

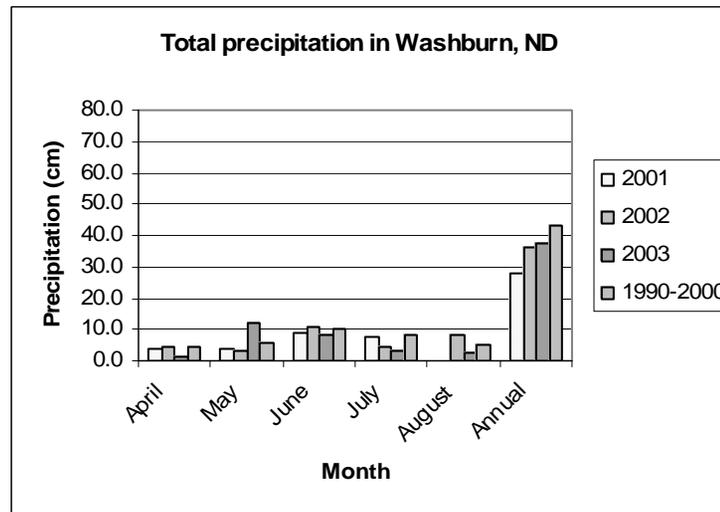
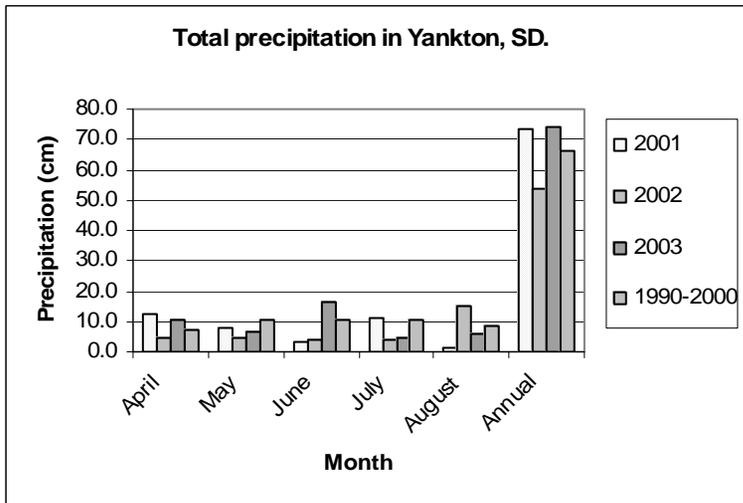
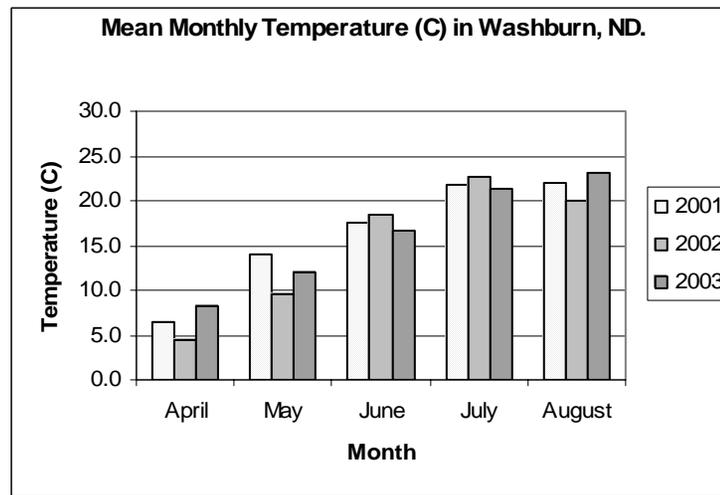
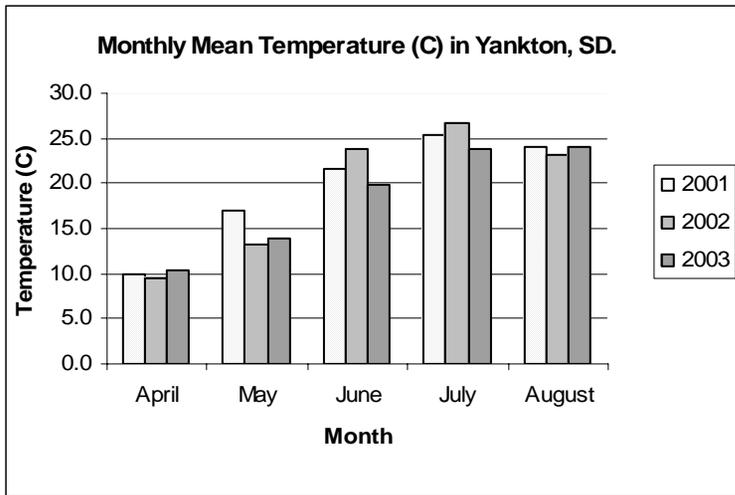


Figure 1.2. Mean monthly temperature (°C) and total precipitation during the breeding season and annually in North and South Dakota in 2001-2003, and from 1990-2000.

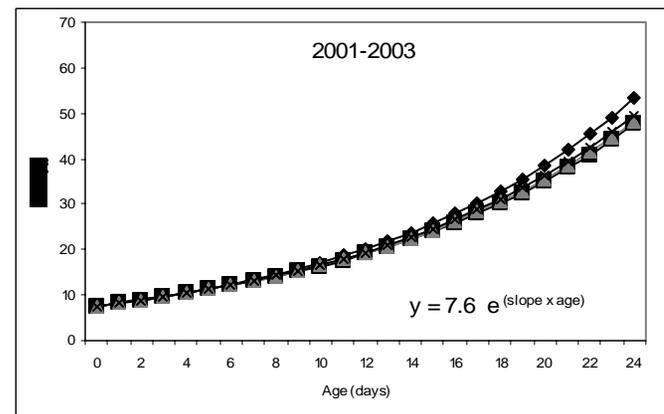
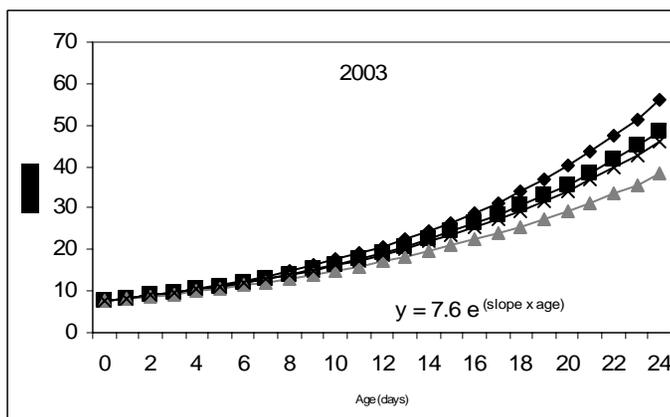
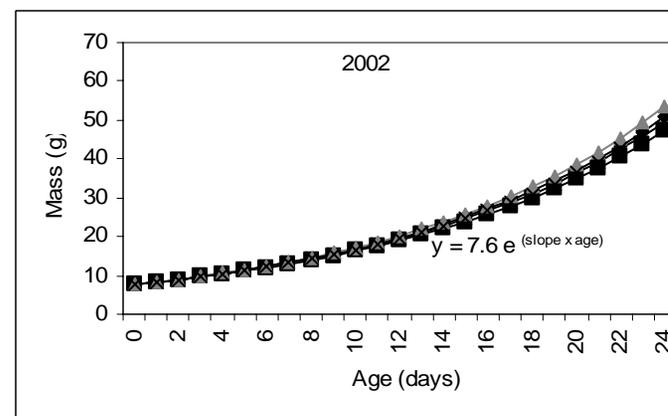
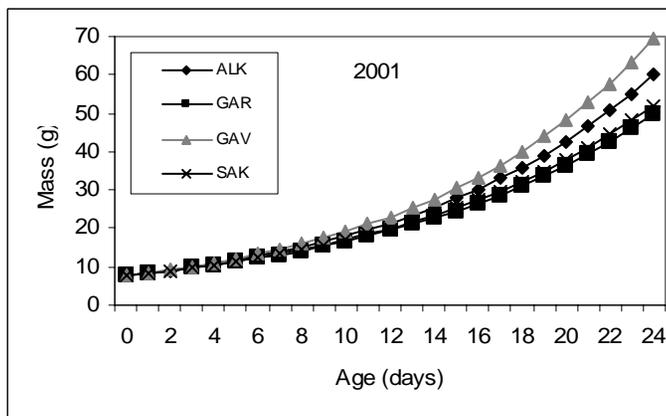


Figure 1.3. Predicted piping plover chick growth curves for body mass (g) at four sites in North and South Dakota, 2001-2003, and years pooled. Individual points in regression were means for each brood by age. See Table 1.9 for slopes for each year and site.

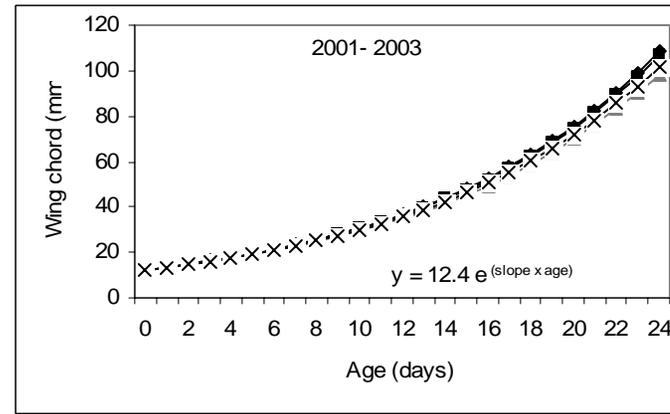
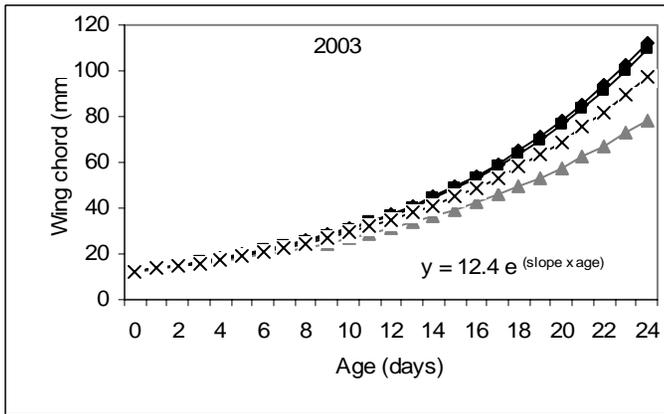
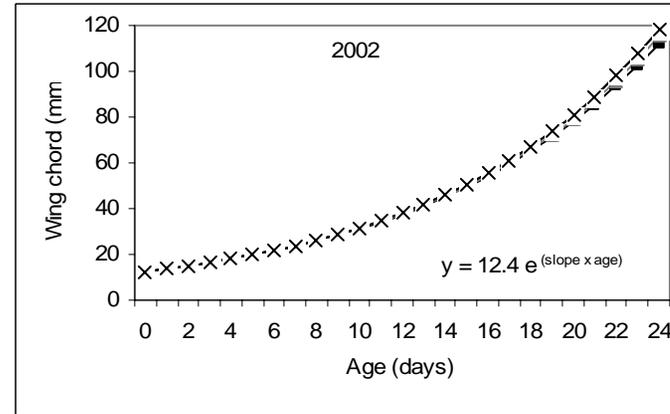
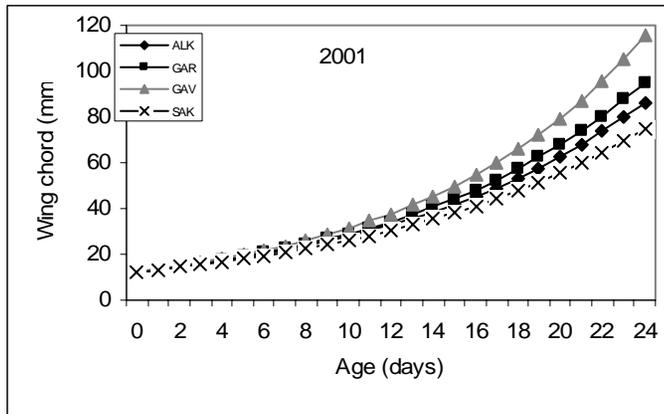


Figure 1.4. Predicted piping plover chick growth curves for wing chord (mm) at four sites in North and South Dakota, 2001-2003, and years pooled. Individual points in regression were means for each brood by age. See Table 1.9 for slopes for each year and site.

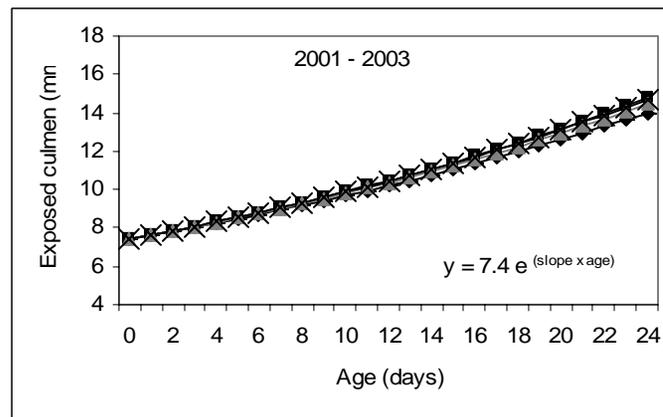
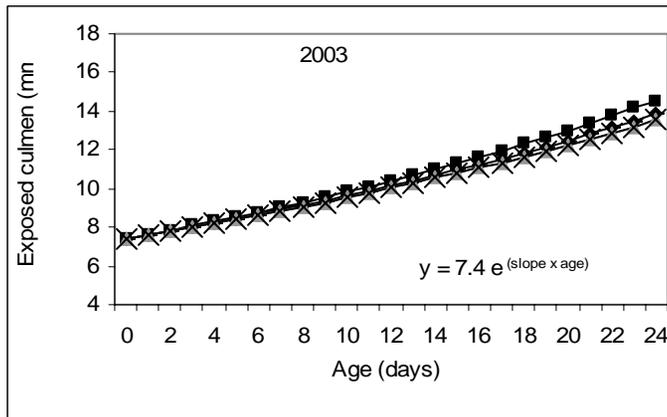
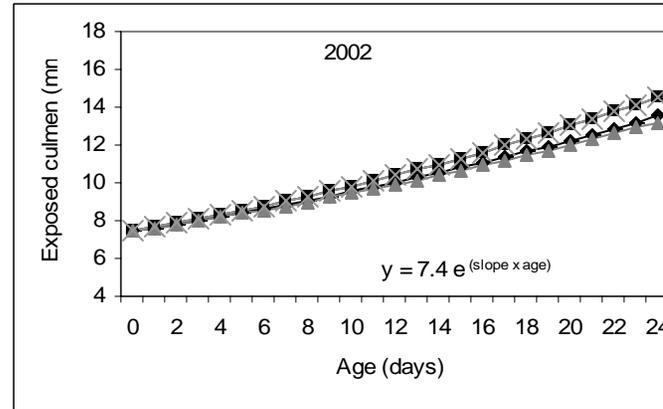
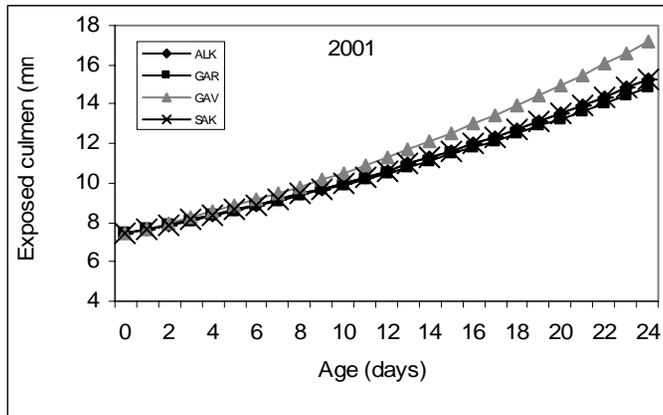


Figure 1.5. Predicted piping plover chick growth curves for exposed culmen (mm) at four sites in North and South Dakota, 2001-2003, and years pooled. Individual points in regression were means for each brood by age. See Table 1.9 for slopes for each year and site.

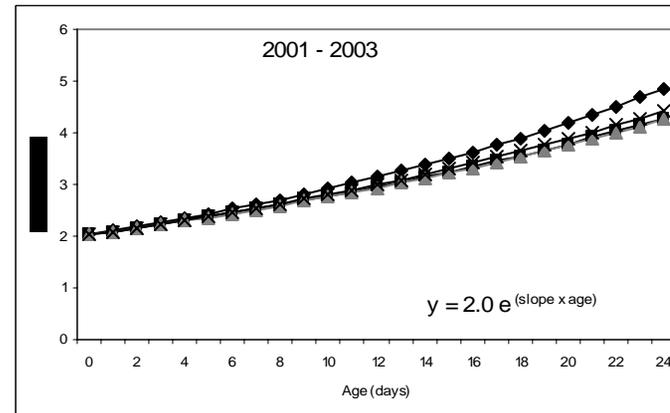
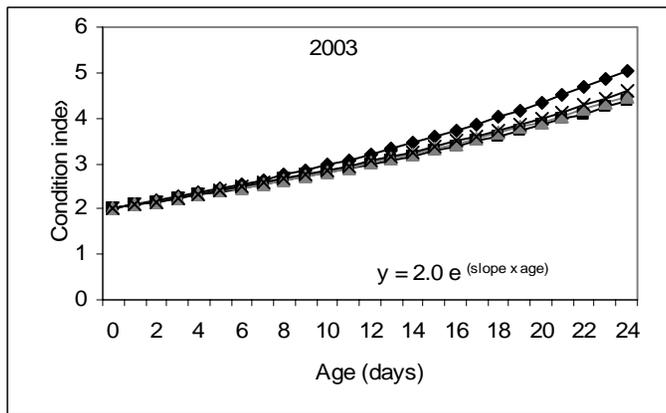
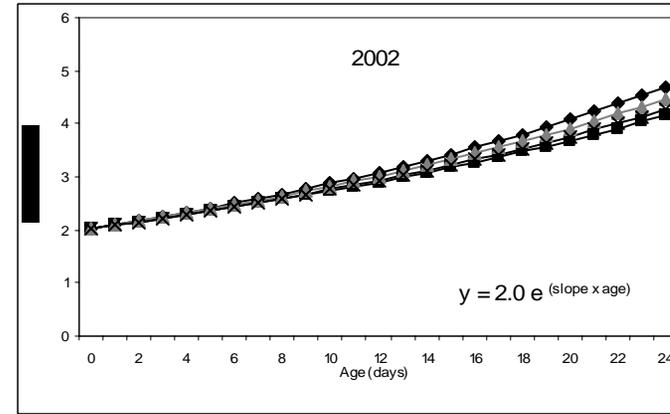
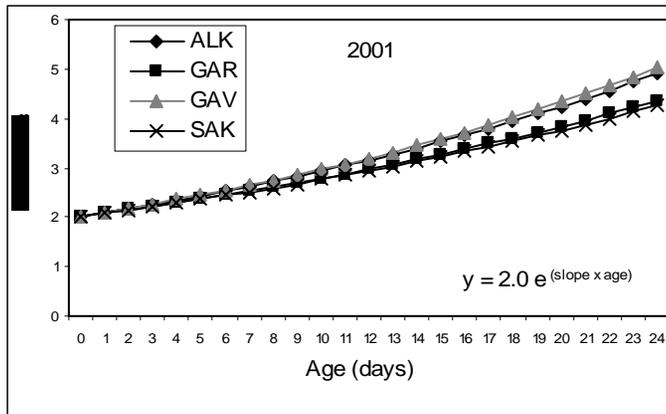


Figure 1.6. Predicted piping plover chick growth curves for condition index (weight / culmen) at four sites in North and South Dakota, 2001-2003, and years pooled. Individual points in regression were means for each brood by age. See Table 1.9 for slopes for each year and site.

CHAPTER 2. PIPING PLOVER FORAGING SITE SELECTION ON THE MISSOURI RIVER

ABSTRACT

Foraging site selection involves balancing the costs and benefits of using a given site, and these choices can have an impact on survival and reproductive success. We studied piping plover (*Charadrius melodus*) foraging site selection during the breeding season on the Missouri River. On the Missouri River, piping plovers nest on sandbars and on the shores of rivers and reservoirs. Understanding piping plover habitat requirements is key to protecting habitat for this threatened species. We hypothesized that inter-island channels, inlets, and backwater areas (protected shoreline) would provide more food than the main channel shoreline. We compared piping plover use of protected shoreline and exposed shoreline to availability along two reaches of the Missouri River (Gavins and Garrison). We also tested the prediction that invertebrate indices were higher on protected shoreline than on exposed shoreline. We then compared chick use to availability of foraging habitat within the foraging territory. Foraging adult plovers selected protected shoreline more often than expected based on availability (use: $92.1\% \pm 3.3$; availability: $57.7\% \pm 4.7$). At Gavins, invertebrate biomass and numbers were higher along the protected shoreline (biomass: 19.5 ± 3.7 ; numbers: 13.1 ± 2.1) than the exposed shoreline (biomass: 11.2 ± 3.7 ; numbers: 6.1 ± 1.7). At Garrison and Sakakawea, invertebrate indices along the protected and exposed shoreline did not differ. Invertebrate numbers were higher in the saturated (10.4 ± 1.5) and moist (6.8 ± 0.5) habitats, than in the vegetated (4.6 ± 0.5) and dry (2.9 ± 4.6) habitats. At Gavins and Garrison, foraging piping plover chicks used saturated (Gavins: 26.2%; Garrison: 41%) and moist (Gavins: 47.1%; Garrison: 50.6%) habitats more than vegetated (Gavins: 2.8%; Garrison: 0.6%) and dry (Gavins: 0.1%; Garrison: 3.6%), based on availability. On the Missouri River, protected shorelines were important foraging sites for piping plovers during the breeding season. We also found that sandbars with low-lying moist habitat are

important to foraging chicks. When managing or creating sandbars, ensuring the availability of these habitats will benefit piping plovers on the Missouri River.

INTRODUCTION

Habitat selection involves a series of individual choices that balance the costs and benefits of using a given site. Costs and benefits include predation risk to adults and young, competition and prey availability (Jones 2001). Habitat selection can have an impact on survival and reproductive success and thus affects the fitness of adults and young.

Research on piping plover habitat selection in the Northern Great Plains has focused on nest site selection. In the alkali wetlands in North Dakota, nest sites had more clumped vegetation than random sites, resulting in larger areas of unvegetated beach, and greater gravel abundance than at unoccupied sites (Prindiville Gaines and Ryan 1988). On the Niobrara River in Nebraska, piping plovers nested on sandbars with a large amount of sand and thick vegetative clumps (Adolf 1998). Piping plovers nested on islands that were at least 1.3% “high sand” and more than 9% “low sand” (Adolf 1998). On the Missouri and Cheyenne rivers in South Dakota, 92% of nests were located where vegetative cover within one meter of the nest was less than 5% (Dirks 1990). According to Schwalbach (1988), piping plovers selected nest sites that provided wide visibility, protection from terrestrial predators, isolation from human disturbance, and protection from rises in river levels.

In contrast to nesting habitat, foraging habitat of Great Plains piping plovers has received little attention. Overwintering piping plovers in coastal areas often forage on tidal flats: adult piping plovers on the Laguna Madre in Texas used bayshore tidal flats proportionately more than shoreline beach (Drake et al. 2001). Along the Texas Gulf Coast, overwintering plovers used bayshore tidal flats at lower tides and moved to beach habitat as bayshore flats were inundated by the rising tide (Zonick 2000). Along the Gulf Coast, overwintering piping plovers foraged on sandflats near inlets, on mudflats and on the foreshore (Nicholls and Baldassarre 1990). Along the Atlantic Coast, wintering piping plovers foraged on sandflats near inlets, tidal creeks, dune ponds and along the open shoreline (Nicholls and Baldassarre 1990).

During the breeding season, the Atlantic Coast piping plovers forage largely along protected shoreline. On Assateague Island (Virginia), more than 70% of piping plover

broods foraged along protected shoreline (sites other than the ocean intertidal zone), such as bay intertidal zones, impoundments and storm pools (Patterson 1988). Broods foraging on bay intertidal zones had higher survival than broods on the high energy ocean side (Loefering and Fraser 1995). In addition, plovers more often selected nest sites near these bay intertidal zones (Loefering and Fraser 1995). On New York barrier islands, all beach segments with ephemeral pools or bay tidal flats were used for brood rearing, compared to less than 50% use of beach segments without these habitats (Elias et al. 2000). In addition, chick survival was higher on beach segments with ephemeral pools than on segments without ephemeral pools (Elias et al. 2000). These studies indicate that foraging plovers select protected shoreline, and that protected shoreline might provide higher quality foraging sites.

On the Missouri River, piping plovers nest on sandbars and along the shoreline of rivers and reservoirs from Nebraska to Montana. Piping plovers breeding on the Missouri River must select locations with suitable nesting sites and foraging sites for both adults and chicks. The inter-island channels, inlets, and backwater areas (protected shoreline) on the Missouri River might be the functional equivalent of coastal bay intertidal flats, as they may offer greater invertebrate abundance than other habitats. Invertebrate drift is high downstream of dams with hydro-peaking (fluctuating water releases, such that highest release levels correspond temporally with peak power demand) (Troelstrup and Hergenrader 1990). Backwater areas may have higher invertebrate numbers due to lower drift (Troelstrup and Hergenrader 1990).

In the Mississippi River, total macroinvertebrate densities were greater in backwater areas than in the main channel (Anderson and Day 1986; Sheaffer and Nickum 1986). In addition, shallow water with high light penetration in backwater areas supported macrophyte beds. In these low-dissolved oxygen sites, detritus feeding crustaceans and a diverse community of littoral insects were present rather than the endobenthic collector-filterers common in the main channel (Anderson and Day 1986). Macroinvertebrate densities on the Mississippi river were highest in high silt areas, which had low water velocity; areas with sand substrates had lowest macroinvertebrate densities and diversity compared to silt (Anderson and Day 1986).

The Great Plains piping plover population was listed as threatened in 1986 due to declining numbers, low productivity and threats to its habitat. In a Biological Opinion issued under section 7 of the U.S. Endangered Species Act, the U.S. Fish and Wildlife Service found that U.S. Army Corps of Engineers management of the Missouri River were likely to jeopardize the continued existence of the piping plover (USFWS 2000). Dam construction on the Missouri River had changed flow dynamics, leading to decreased creation of sandbar nesting habitat, increased encroachment by vegetation, and lower nutrient addition to existing sandbars (Hesse and Mestl 1993; Niver 2000; USFWS 2000). Changes in the flow regime have been found to affect plover productivity: Following record flows in 1996 and 1997 that created an abundance of habitat complexes, adult numbers and productivity increased on the Missouri River (Niver 2000). In 2003, the Fish and Wildlife Service reversed itself and issued a no jeopardy opinion for the operation of the Missouri River (USFWS 2003). In that opinion, USFWS included the following reasonable and prudent measures: implementation of flow enhancement, habitat restoration, habitat creation and habitat enhancement (USFWS 2000; USFWS 2003). An understanding of piping plover habitat selection is required to protect and manage habitat for this species.

The goal of this study was to determine habitat selection by adult piping plovers at a landscape scale and by chicks at the foraging site. In addition, because habitat use alone is insufficient to gauge habitat quality (Van Horne 1983; Wolff 1995), we compared invertebrate indices along different shoreline types as an index of habitat quality to determine if habitat selection was associated with prey availability.

The first objective was to compare use to availability of foraging habitats at the landscape scale. Prior to beginning the study, we observed that piping plovers foraged primarily in backwater areas. We tested the prediction that adult and young plovers used protected sites (backwater, pools, channels) more than expected based on availability. We also tested the prediction that invertebrate indices were higher on protected shoreline than on exposed shoreline.

The second objective was to compare chick use to availability of foraging habitat within the foraging territory. We predicted that chicks spent proportionately more time foraging in the saturated and moist substrates than other substrates compared to

availability and that invertebrate indices would be higher in saturated and moist habitats than other habitats.

STUDY AREA

On the upper Missouri River, piping plovers nest from southeast South Dakota to Fort Peck Lake in northeast Montana (Niver 2000). We studied piping plovers on three reaches of the Missouri River (two riverine and one reservoir). Study sites included the Gavins Reach in South Dakota, downstream of the Gavins Point Dam, the Garrison Reach downstream of the Garrison Dam and Lake Sakakawea upstream of the Garrison Dam in North Dakota.

METHODS

Shoreline type selection at the landscape scale

We surveyed islands on Garrison Reach and Gavins Reach, and the shoreline on Lake Sakakawea during the pre-hatching period (late April to late May) and the chick-rearing period (early July to late July). We walked the shoreline with a GPS unit and measured the length of protected shoreline (inter-island channels, lagoons, pools) and exposed shoreline (facing the main river channel or open lake). We counted the number of adult piping plovers foraging within 10 m of the shoreline, and categorized their location as exposed (facing the main river channel or open lake) or protected (inter-island channels, lagoons, pools). Surveys were completed before noon, and the same person completed all of the surveys. To determine the advisability of pooling reaches, years and breeding periods, we compared the ratio of use to availability (ratio = % use / % available) among reaches, years, and breeding periods (pre-chick and chick-rearing period) with an analysis of variance. We tested whether there was a difference between the percent use of shoreline type and percent availability with a paired t test.

We did not measure the protected and exposed shoreline available to chicks. We compared the frequency of brood observations in protected and exposed shoreline with a Chi-Square test.

Chick habitat selection within a foraging territory

Habitat types

We identified four habitat categories: Saturated habitats were adjacent to the water's edge, retained a wet sheen, and water appeared at the surface when pressure was applied. Moist habitats had dark but not saturated sand. Dry sand was light in color. The vegetated habitat consisted of dry sand with 10% or more plant cover.

Habitat use

We located chicks every four days from hatching to age 22 days, at which time chicks could fly. We conducted 2-min instant behavioral observations on each chick within a brood, recording habitat use and chick behavior at the start of the observation period, and then at 10-sec intervals. We calculated the proportion of observations in which chicks were foraging in different habitats (saturated, moist, dry, vegetation). If the chick disappeared from view during an observation, the clock was stopped, and resumed when the chick was spotted, if the time elapsed was less than 5 min. After 5 min, if the chick was not spotted, the observation was deleted. This might have biased the data against observations in vegetation. All observations were 120 sec.

At the end of the time budget observations, we measured the amount of available habitat (saturated, moist, dry, vegetation) on a 50-m transect perpendicular to the shoreline through the location where the chick was first seen. We compared the proportion of time the chicks spent foraging in a habitat (proportion of 10-sec observations in the habitat) to the proportion of available habitat measured, using compositional analysis (Aebischer et al. 1993). Sandbar width ranged from less than 100 m to over 500 m, and some sandbars were highly vegetated in the center. Since transects were 50 m in length, they did not cover the whole width of the island, and in some cases underestimated the amount of vegetation and dry sand on the sandbar. Values of zero for use and availability were assigned a proportion of 0.01 (Aitchison 1986; Aebischer et al. 1993).

Invertebrate indices

We obtained invertebrate indices at chicks' foraging sites every eight days, and identified the location as exposed or protected shoreline. We placed paint stirrers coated with Tanglefoot Insect Trap Coating (The Tanglefoot Company, Grand Rapids, MI 49504) in each habitat along transects on each territory. We started transects at the water's edge nearest the chick location at the beginning of the first 10-sec observation. Transects were conducted immediately following behavioral observations. Stirrers were placed in pairs, one vertically in the sand (with tanglefoot on both sides) and one horizontally on the ground (tanglefoot on one side), 5 cm apart, for 30 min. The catch area for the traps was 64.5 cm² (21.5 cm x 3 cm) for the horizontal stick and 129 cm² for the vertical stick. We sampled invertebrates in saturated, moist, dry and vegetated habitats. We placed chicken wire cages (diameter = 0.5 m, height = 0.6 m, mesh size: 2.5 cm) around each set of traps to prevent bird injury. Cages may influence capture rate and complicate comparisons with previous studies. We counted, measured and identified invertebrates to order. We calculated invertebrate catch rates (number of invertebrates/half hour), and estimated biomass (mg dry weight/half hour). We used invertebrate length measurements to calculate biomass based on an equation developed with data from a range of invertebrate orders (Dry Weight (mg) = (0.0305) (Length(mm))^{2.62}); Rogers et al 1976). We compared invertebrate indices at exposed and protected shorelines and among habitat types with an ANOVA on ranks followed by a Fisher's LSD for significant effects ($P \leq 0.05$). We used the statistical analysis software (SAS) for analyses (SAS 2004).

RESULTS

Adult shoreline type selection

Chick habitat selection

Habitat type

At Gavins Reach and Garrison Reach, saturated and moist habitats were selected more than dry habitats and vegetation based on availability (Gavins: Wilks' lambda =

0.44, $F_{3,18} = 7.7$, $P = 0.002$; Garrison: Wilks' lambda = 0.19, $F_{3,11} = 15.8$, $P = 0.0003$, Table 2.2). Chick use of habitat at Sakakawea was proportional to availability (Wilks' lambda = 0.69, $F_{3,7} = 1.0$, $P = 0.43$; Table 2.2).

Shoreline type

Chicks did not use protected shoreline more than exposed shoreline, although at Gavins Reach use of protected shoreline was marginally significantly higher than exposed shoreline (Chi-Square test; Garrison: $\chi^2 = 0.62$, $P = 0.43$, $n = 33$; Gavins: $\chi^2 = 3.67$, $P = 0.055$, $n = 24$; Sakakawea, $\chi^2 = 0.059$, $P = 0.81$, $n = 29$; Figure 2.1).

Invertebrate indices

Habitat type

Invertebrate biomass and numbers varied among habitats and reaches, and there was a significant reach by habitat interaction (Table 2.3). When reaches were pooled, invertebrate biomass was greatest in the saturated and lowest in the dry habitat; numbers were highest in the saturated and moist habitats and lowest in the dry habitat (Table 2.3). Invertebrate biomass was higher in the saturated than in the other habitats, except at Garrison Reach (Table 2.3).

At Garrison Reach, biomass in the dry habitat was lower than in the other habitats, and numbers in the saturated were lower than in the moist and dry habitats. At Gavins Reach, invertebrate numbers were higher in the saturated than in the dry and vegetation. At Sakakawea, numbers were highest in the saturated, followed by moist, and lowest in the dry habitat and vegetation (Table 2.3).

Shoreline type

At Gavins Reach, mean invertebrate biomass and number in the saturated and moist habitats were higher along the protected shoreline than the exposed shoreline (Table 2.4). At Garrison Reach and Sakakawea, there was no difference in invertebrate biomass and abundance between the protected and exposed shoreline (Table 2.4).

DISCUSSION

The fact that adult piping plovers on the Missouri River preferred protected shoreline over exposed shoreline is consistent with results from breeding piping plovers on the East Coast (Loefering and Fraser 1995; Elias et al. 2000) and of wintering piping plovers, which used bayshore tidal flats more than ocean shoreline (Nicholls and Baldassarre 1990; Zonick 2000).

We hypothesized that protected shoreline played a key role in supporting piping plover prey. The higher invertebrate indices in some of our backwater areas may be due to lower drift (Troelstrup and Hergenrader 1990). At Gavins Reach, piping plover selection of protected shorelines was most likely driven by higher invertebrate numbers and biomass. At Garrison Reach and Sakakawea, invertebrate indices were not higher along the protected than the exposed shoreline. However, invertebrate indices on these reaches in both the protected and exposed shoreline were lower than at the protected shoreline at Gavins Reach, and biomass was lower than at the exposed sites at Gavins Reach. Perhaps the colder water at Garrison Reach and Sakakawea resulted in lower productivity even at protected shorelines, leading to a lack of difference in invertebrate indices between exposed and protected shoreline at these two cold water reaches. Daily fluctuations in water levels at Garrison Reach might also negatively affect invertebrates in shallow, protected areas, since they might become stranded as water levels drop. Although invertebrate indices were not higher in protected than exposed shoreline at Garrison Reach, the fact that adult plovers preferred these areas indicates protected shorelines might have importance on another level. The more gradually sloping protected shoreline might offer more foraging area as the water recedes, compared to exposed shoreline which drops off more abruptly. At Sakakawea, backwater areas were probably deeper than along the river reaches, and less productive for that reason.

Chicks at Gavins Reach were more often found near the protected than the exposed shoreline, but this was not the case at Garrison Reach. Since we did not measure available protected shoreline for chicks, we could not compare use of protected shoreline to availability. Garrison Reach might have less protected shoreline available to chicks, particularly as water levels rise at certain times of the day.

At the territory scale, at Gavins Reach and Garrison Reach, chicks spent proportionately more time feeding in the saturated and moist zones than in the vegetation and dry habitats. Invertebrate indices varied among these habitats for the different sites. At Gavins Reach, the saturated habitat had higher invertebrate indices than dry or vegetated habitats. At Garrison Reach, indices were higher in the moist than in the dry. Although invertebrate indices tended to be higher in the preferred habitats, the lack of a clear pattern indicates that chicks might also prefer to forage along the shoreline, where visibility of predators is better. Moreover, the invertebrate indices may not perfectly reflect prey available to piping plovers.

At both the territory and landscape scales, piping plovers selection varied among reaches, and although one component of selection is invertebrate abundance, other components must come into play as well. Habitat selection in terms of resource availability could be adaptive and lead to increased fitness if no differential costs related to other factors such as predation exist at these sites.

MANAGEMENT IMPLICATIONS

We found differences in habitat selection at both the landscape (exposed vs. protected shoreline) and territory scale (saturated and moist vs vegetation and dry habitats), underscoring the importance of understanding selection at different scales when considering habitat protection, management or creation.

On the Missouri River, protected shorelines, which include backwater areas, inlets, inter-island channels and ephemeral pools, are important foraging sites for piping plovers during the breeding season. Flow management on the Missouri River should incorporate techniques that allow processes that drive the creation of these shorelines. In addition, when creating artificial sandbars, inlets and pools should be included in the design.

Plovers foraged primarily along the shoreline, in saturated and moist habitats. These low-lying parts of sandbars with no steep escarpments need to be maintained in order to retain high quality plover foraging habitat. To maximize the amount of saturated

and moist habitats when engineering habitats for piping plovers, sandbars should be designed to slope gently into the water.

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Table 2.1. Availability (mean % of perimeter of island) and use (mean % of adults in protected shoreline) of protected shoreline by piping plover adults on the Missouri River in North and South Dakota, 2001-2003; *n* equals the number of surveys.

Year	Reach	Time of year	Island	% Availability	% Use
2001	GAR	POST	HH	65.52	100.00
2001	GAR	POST	PAR	55.67	60.00
2001	GAR	POST	STNWL	70.84	100.00
2001	GAV	POST	7815	90.49	77.78
2001	GAV	POST	788	88.06	50.00
2001	GAV	POST	799	42.45	100.00
2002	GAR	POST	PAR	66.47	100.00
2002	GAR	POST	STNWL	68.04	100.00
2002	GAR	PRE	HH	40.54	100.00
2002	GAR	PRE	STNWL	71.78	100.00
2002	GAR	PRE	PAR	48.58	100.00
2002	GAV	PRE	788	63.77	71.43
2002	GAV	PRE	799A	36.13	66.67
2002	GAV	PRE	7953	40.12	100.00
2003	GAR	POST	PAR	79.67	100.00
2003	GAR	PRE	PAR	74.79	100.00
2003	GAV	POST	788	32.68	100.00
2003	GAV	POST	793.5	88.72	100.00
2003	GAV	POST	795.5	46.94	100.00
2003	GAV	PRE	788	35.41	100.00
2003	GAV	PRE	795.5	61.90	100.00
2003	GAV	PRE	793.5	0.99	100.00

Table 2.2. Piping plover chick habitat availability (% transect in each habitat type), use (% time chicks spent in each habitat) and preference based on compositional analysis, on three Missouri River reaches in North and South Dakota, 2001-2003. Habitat variables followed by the same letter are not different ($\alpha = 0.05$).

Habitat type	% Use	% Availability	Habitat preference
Garrison (<i>n</i> = 14)			
Saturated	41	22.4	A
Moist	50.6	29.9	A
Dry	3.6	28.7	B
Vegetation	0.6	4.9	B
Gavins (<i>n</i> = 21)			
Saturated	26.2	7.4	A
Moist	47.1	60.7	A
Dry	0.1	5.5	B
Vegetation	2.8	18.5	B
Sakakawea (<i>n</i> = 10)			
Saturated	22.2	3.5	
Moist	27.4	34.8	
Dry	25.1	14.6	
Vegetation	18.9	47	

Table 2.3. Invertebrate abundance and biomass (mean mg dry weight per set) \pm SE in habitats during chick-rearing period in North Dakota and South Dakota, 2001-2003. Results of ANOVA on ranks followed by Fisher's LSD for significant effects ($P \leq 0.05$). Habitats with the same letters are not significantly different.

Habitat	<i>n</i>	Biomass ^a					Numbers ^b						
		Mean	\pm	SE	<i>F</i> ₃	<i>P</i>	Mean	\pm	SE	<i>F</i> ₃	<i>P</i>		
Garrison													
Saturated	24	4.2	\pm	1.2	A	4.6	0.005	4.1	\pm	0.6	BC	5.3	0.003
Moist	24	4.5	\pm	1.0	A			7.6	\pm	1.1	A		
Dry	20	2.1	\pm	0.7	B			3.1	\pm	0.6	C		
Vegetation	17	4.5	\pm	1.0	A			6.5	\pm	1.0	AB		
Gavins													
Saturated	28	24.8	\pm	3.8	A	11.4	< 0.0001	14.9	\pm	3.5	A	11.4	< 0.0001
Moist	28	7.9	\pm	1.6	B			7.4	\pm	0.9	AB		
Dry	16	10.6	\pm	5.1	B			3.0	\pm	1.0	C		
Vegetation	24	6.5	\pm	1.4	B			5.2	\pm	0.7	B		
Sakakawea													
Saturated	21	10.9	\pm	2.3	A	14.8	< 0.0001	11.5	\pm	1.7	A	21.1	< 0.0001
Moist	20	2.9	\pm	0.7	B			5.1	\pm	0.7	B		
Dry	16	1.7	\pm	0.5	B			2.6	\pm	0.6	C		
Vegetation	21	2.2	\pm	0.8	B			2.3	\pm	0.3	C		

Habitat	<i>n</i>	Biomass ^a					Numbers ^b						
		Mean	±	SE	<i>F</i> ₃	<i>P</i>	Mean	±	SE	<i>F</i> ₃	<i>P</i>		
All reaches pooled													
Saturated	73	14	±	1.9	A	20.1	< 0.0001	10.4	±	1.5	A	20.2	< 0.0001
Moist	72	5.4	±	0.8	B			6.8	±	0.5	A		
Dry	52	4.6	±	1.7	C			2.9	±	0.4	C		
Vegetation	62	4.5	±	0.7	B			4.6	±	0.5	B		

^aTwo Way ANOVA on ranks: habitat: $F_{3,247} = 22.8$, $P < 0.0001$; reach: $F_{2,247} = 3.1$, $P = 0.05$; habitat x reach: $F_{6,247} = 7.5$, $P < 0.0001$

^bTwo Way ANOVA on ranks: habitat: $F_{3,247} = 23.1$, $P < 0.0001$; reach: $F_{2,247} = 12.1$, $P < 0.0001$; habitat x reach: $F_{6,247} = 5.1$, $P < 0.0001$

Table 2.4. Invertebrate biomass (Mean mg dry weight per set), and number in saturated and moist habitats, along protected and exposed shoreline at the three Missouri River reaches in North and South Dakota, during the chick-rearing period, 2001-2003. Results of ANOVA on ranks comparing exposed and protected shoreline, followed by Fisher's LSD for significant effects ($P \leq 0.05$).

Site	<i>n</i>	Biomass					Number				
		Mean	±	SE	F_1	P	Mean	±	SE	F_1	P
Gavins											
Protected	24	19.5	±	3.7	4.2	0.05	13.1	±	2.1	11.9	0.002
Exposed	12	11.2	±	3.7			6.1	±	1.7		
Garrison											
Protected	16	4.3	±	1.0	0.03	0.87	6.0	±	0.8	0.0	1.0
Exposed	17	3.7	±	0.7			6.1	±	0.9		
Sakakawea											
Protected	12	4.9	±	1.0	0.3	0.6	7.5	±	1.3	0.0	1.0
Exposed	14	8.8	±	3.2			9.2	±	2.3		

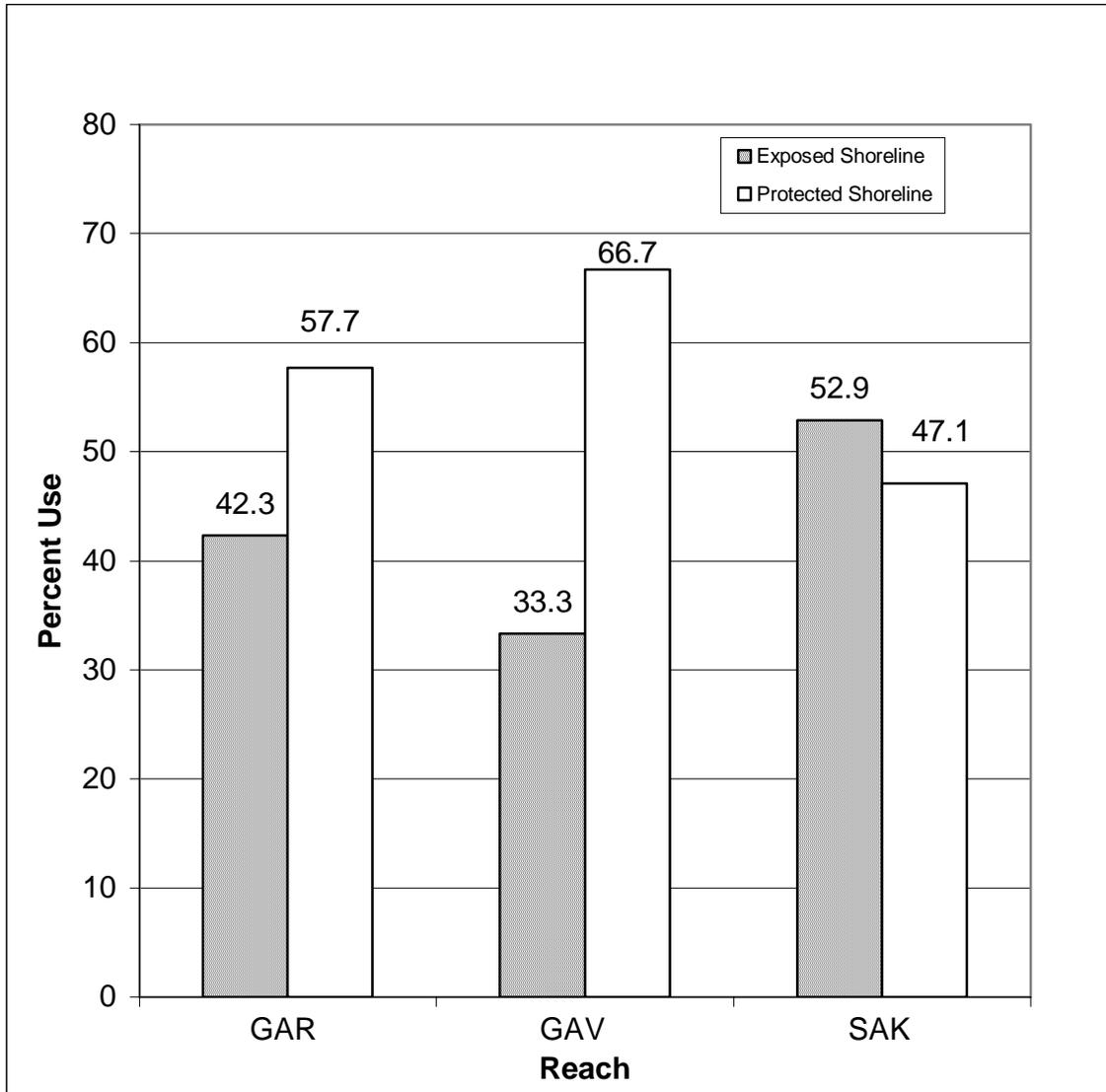


Figure 2.1. Piping plover chick use of exposed and protected shoreline habitat at Garrison (GAR), Gavins (GAV), and Lake Sakakawea (SAK), in North and South Dakota, 2000-2003.

CHAPTER 3. PIPING PLOVER CHICK DIET IN THE GREAT PLAINS

ABSTRACT

Prey selection and foraging strategies can impact avian fitness, yet very little is known about the diet of the piping plover, a threatened species. Understanding piping plover diet in the Great Plains can aid managers in deciding how to manage and create high quality habitat. We used two techniques to determine piping plover chick diet. We collected fecal samples, and identified to order and counted the invertebrate parts in the samples. We then calculated the percent occurrence (samples containing taxa / total samples) of each taxa in the samples. We determined the stable nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) isotope ratios of piping plover chick feathers grown at the site, and for the most common invertebrates at each site. We used the range of enrichment levels found in the literature for feathers to determine the expected range of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in piping plover chick diets. Because of the lack of differentiation in invertebrate signatures, stable isotope analysis was not useful in differentiating among potential insect prey. However, Coleoptera were within the range of piping plover diet signatures at the three river sites. Although Diptera occurred more frequently (23% - 64%) at all sites (sticky traps), Coleoptera occurred most frequently in the fecal samples (fecal analysis; 69% to 89%). Preferential selection of Coleoptera could be due to higher nutritive value, ease of capture or handling, or palatability.

INTRODUCTION

Prey availability, selection, and foraging strategies can impact avian fitness by affecting the net energy intake over time, and the amount of time available for other activities (Krebs and Cowie 1976). Understanding piping plover prey selection in the Great Plains can aid in deciding how to manage and create high quality habitat, yet there is little published on the diet of the piping plover, a federally listed species.

Previous studies have examined piping plover diet on the Magdalen islands, Quebec (Shaffer and Laporte 1994) and in the Great Lakes (Cuthbert et al. 1999). These studies based piping plover diet composition on fecal samples (Shaffer and Laporte 1994) and gizzard contents (Cuthbert et al. 1999).

It is difficult to determine piping plover diet by observing foraging birds, because their prey is too small to identify at a distance. Fecal analysis has been used as an alternative to emetics (stomach content analysis), because it is less invasive, and larger sample sizes may be obtained by this technique (Pearson Ralph et al. 1985). However, interpretation of diets through fecal analysis may be inaccurate because of differential digestion of soft-bodied invertebrates (Rosenberg and Cooper 1990). Nevertheless, parts of some soft-bodied invertebrates, such as flies (Diptera), have been found in droppings (Rundle 1982; Pearson Ralph et al. 1985; Drost et al. 2001).

Stable isotope analysis is a method that allows researchers to examine avian diets in a relatively non-invasive way. Feather stable isotope values reflect the diet during the period of feather growth (Hobson and Clark 1992a). Thus stable isotope analysis of avian feathers may be used to obtain information on the relative contributions of prey items in chicks' diet (Hobson and Clark 1992; Alexander et al. 1996; Sydeman et al. 1997; Hobson 1999).

The ratio of the heavy to light nitrogen isotopes ($^{15}\text{N}/^{14}\text{N}$, denoted as $\delta^{15}\text{N}$) and the carbon isotopes ($^{13}\text{C}/^{12}\text{C}$, denoted as $\delta^{13}\text{C}$) in consumer tissues exhibits a stepwise increase (enrichment) at each trophic level (DeNiro and Epstein 1981). The whole body of an animal is enriched in heavier isotopes relative to its diet by an average of 3‰ for

nitrogen and 1‰ for carbon (DeNiro and Epstein 1978; DeNiro and Epstein 1981; Peterson and Fry 1987). However, each tissue of an organism may show a different level of enrichment (Hobson and Clark 1992).

Some difficulties associated with stable isotope analysis involve determining the enrichment rate for a particular species or tissue (Mizutani et al. 1991; Hobson and Clark 1992a; Mizutani et al. 1992; Hobson and Clark 1992b; Mizutani et al. 1992; Bearhop et al. 1999; Bearhop et al. 2002; Pearson et al. 2003). In addition, the isotopic signature among prey taxa might not be sufficiently distinct to differentiate potential prey items. There is also a lack of information about enrichment factors for different types of diets. Crows raised on fish had lower enrichment rates than those raised on a plant-based diet; enrichment also may vary due to nutritional stress and individual species (Hobson and Clark 1992b). There currently are few data on stable isotope feather enrichment factors for birds feeding on invertebrates.

A recent study on swallows, obligate insectivores, obtained diet-blood enrichment rates of 2.9‰ for ^{15}N (Morrissey et al. 2004; Table 3.1). Garden warblers (*Sylvia borin*) on a controlled diet (14.2% protein, 10% fat, 5% sugars) had feather isotope enrichment factors of 2.7‰ for ^{13}C and 4.0‰ for ^{15}N (Hobson and Bairlein 2003; Table 3.1). Yellow-rumped warblers (*Dendroica coronata*) fed a diet composed of 97% insects showed feather enrichment relative to diet of 4.3‰ (± 0.1) for ^{13}C and 3.5‰ (± 0.1) for ^{15}N (Pearson et al. 2003; Table 3.1).

In this study we assessed plover chick diet based on droppings analysis and stable isotope analysis. We compared piping plover chick diet and prey availability at four Missouri River sites. We compared the proportion of the most frequent taxa in the diet (based on fecal analysis) to their availability in the chicks' foraging habitat. We then compared the results obtained by the two methods.

STUDY AREA

On the upper Missouri River, piping plovers nest from southeast South Dakota to Fort Peck Lake in northeast Montana (Niver 2000). We studied piping plovers on three reaches of the Missouri River (two riverine and one reservoir). Study sites included the

Gavins Reach in South Dakota, downstream of the Gavins Point Dam, the Garrison Reach downstream of the Garrison Dam and Lake Sakakawea upstream of the Garrison Dam in North Dakota. In the alkali wetlands, we observed broods on the Williams Nature Conservancy Preserve, and on private land monitored by the Audubon National Wildlife Refuge.

METHODS

Surface invertebrate sampling

We sampled relative invertebrate abundance at pre-hatching and post-hatching breeding stages. Invertebrate sampling began when pairs were identified at sites. We collected data on invertebrate abundance every 15 days prior to chick hatching, and every eight days post-hatching. We measured windspeed and temperature at the start of collection time. We placed paint stirrers coated with Tanglefoot Insect Trap Coating (The Tanglefoot Company, Grand Rapids, MI 49504) in each habitat along transects on each territory. Sticks were placed along transects based on the center of foraging activity from the foraging observation period immediately preceding sampling. Stirrers were placed in pairs, one vertically in the sand (with Tanglefoot on both sides) and one horizontally on the ground (Tanglefoot on upward side), 5 cm apart, for 30 min. The catch area for the traps was 64.5 cm² (21.5 cm x 3 cm) for the horizontal stick and 129 cm² for the vertical stick. We sampled invertebrates in saturated, moist, dry and vegetated habitats. We placed chicken wire cages (diameter = 0.5 m, height = 0.6 m, mesh size = 2.5 cm) around each set of traps to prevent bird injury. We counted invertebrates and identified them to order. We calculated the percent occurrence of each taxa (samples containing taxa / total samples) at each site. To determine the relative importance of each taxa at each site, we compared percent occurrence of each taxa among sites with an ANOVA on ranks followed by a Fisher's LSD when *P*-values were significant ($P \leq 0.05$; SAS 2004).

Stable Isotope Analysis

We pulled three feathers from the upper tail coverts of pre-fledging chicks (ages 14 to 22 days) in 2002 for stable isotope analysis. We collected invertebrate samples for stable isotope analysis in pitfall traps filled with alcohol, placed for 8 hrs in the brood foraging territory. Invertebrates were immediately placed in labeled containers filled with alcohol. We identified the most common species to family.

We rinsed the feathers in alcohol and oven-dried them at 60°C for 3 hours. Invertebrates were rinsed in alcohol and oven-dried at 60°C for 48 hrs. We crushed samples with a shaker with a ball bearing (WIG-L-BUG, Cresenl Corp.), weighed the powder to the nearest hundredth of a milligram (Mettler Toledo MT5 scale), and placed in tin capsules (5 x 9 mm, Costech Analytical Technologies, 26074 Avenue Hall, Suite 14, Valencia, CA 91355). Invertebrate and feather samples weighed 1.0 ± 0.4 mg. Feather samples from individual broods were analyzed separately. We combined invertebrates from several brood locations within the same reach.

We sent the samples to the University of Waterloo Environmental Isotope Lab for analysis (University of Waterloo, 200 University Avenue West, Waterloo, Ontario, Canada N2L 3G1). Samples were analyzed for Nitrogen and Carbon on an Isochrom Continuous Flow Stable Isotope Mass Spectrometer (Micromass) coupled to a Carlo Erba Elemental Analyzer (CHNS-O EA1108). The Nitrogen standards were IAEA-N1 and IAEA-N2 (both Ammonium Sulphate) and the Carbon standards were IAEA-CH6 (sugar), EIL-72 (cellulose) and EIL-32 (graphite). The relative difference between ratios of the sample and standard gases (δ) were calculated using the following equation:

$\delta_X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where X is ^{15}N or ^{13}C and R is the ratio $^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$. R_{standard} for ^{13}C was Pee Dee belemnite and for ^{15}N was atmospheric nitrogen. The measurement accuracy was $\pm 0.2\%$ for Carbon and $\pm 0.3\%$ for Nitrogen.

Because stable isotope signatures can vary among geographic locations (Hobson 1999), we analyzed invertebrates and feathers from each site separately. We calculated the mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for each taxa at each site. We applied enrichment numbers to the ^{15}N and ^{13}C for growing chick feathers to obtain the predicted range of dietary signatures

of piping plover chick prey. We used the range of enrichment levels found in the literature for feathers (0.2 – 4.3‰ for ^{13}C and 1.0 – 5.3‰ for ^{15}N).

Fecal analysis

We opportunistically collected fecal samples as we caught and measured chicks. We stored the fecal samples in ethanol (95%) then used dissecting microscopes to sort through contents, teasing them apart with dissecting needles. We identified to order and counted all the recognizable invertebrate parts in the samples. We calculated the percent occurrence in the fecal samples of each taxa (samples containing taxa / total samples) for each brood. To determine the relative importance of each taxa in chicks' diets, we compared percent occurrence of each taxa among sites with an ANOVA on ranks followed by a Fisher's LSD when P -values were significant ($P \leq 0.05$). We included samples with no invertebrates in the analysis, because these samples could have contained invertebrate larvae, which would have been completely digested. We used the statistical analysis software (SAS) for analyses (SAS 2004).

RESULTS

Diet analysis based on stable isotopes

Isotopic signatures for both piping plover chicks and invertebrates varied among sites (piping plover chick feathers: $\delta^{13}\text{C}$: - 22.4 to - 16.6‰; $\delta^{15}\text{N}$: 8.3 to 13.4‰; Coleoptera (Cicindelidae (tiger beetles)): $\delta^{13}\text{C}$: - 25.3 to - 19.5‰; $\delta^{15}\text{N}$: 7.0 to 11.2‰; Table 3.2). Because we did not analyze multiple samples per site, we can not tell if there was more variation among sites than within sites. Stable isotope signatures overlapped among invertebrate orders (Table 3.2). The average $\delta^{13}\text{C}$ for chick feathers from Gavins and Alkali was higher than for Sakakawea and Garrison (ANOVA, $F_{3,162} = 12.5$, $P < 0.0001$; Figure 3.1). The average $\delta^{15}\text{N}$ for chick feathers was higher at Sakakawea than the other three sites (ANOVA, $F_{3,162} = 21.4$, $P < 0.0001$; Figure 3.1). Because of site differences in stable isotope signatures, we examined dietary composition for each site separately.

Using the mean of $\delta^{13}\text{C}$ for chick feathers, and the enrichment levels from the literature ($\delta^{13}\text{C}$: 0.2 to 4.3‰; $\delta^{15}\text{N}$: 1 to 5.2‰), we calculated the predicted range for piping plover prey at each site. The predicted range at Alkali was -24.4 to -20.3‰ for $\delta^{13}\text{C}$ and 4.7 to 8.9‰ for $\delta^{15}\text{N}$. At Alkali, the taxa occurring within the predicted range of dietary signatures included bees (Halictidae) and flies (Chloropidae) (Table 3.2, Figure 3.2). At Garrison, the predicted range was -26.7 to -22.6‰ for $\delta^{13}\text{C}$ and 3.8 to 8.0‰ for $\delta^{15}\text{N}$. At Garrison, bees (Halictidae) and beetles (Silphidae) were within the range of dietary signatures (Table 3.2, Figure 3.3). At Gavins, the predicted range was -20.9 to -16.8‰ for $\delta^{13}\text{C}$ and 3.1 to 7.3‰ for $\delta^{15}\text{N}$. At Gavins, tiger beetle larvae and adults (Cicindelidae) and Araneae were within the range of dietary signatures (Table 3.2, Figure 3.4). At Sakakawea, the predicted range was -26.3 to -22.2‰ for $\delta^{13}\text{C}$ and 8.2 to 12.4‰ for $\delta^{15}\text{N}$. At Sakakawea, the range included two beetle taxa (Cicindelidae, Carabidae), and two fly taxa (Chloropidae, Dolichopodidae; Table 3.2; Figure 3.5).

Fecal analysis

We collected 224 fecal samples from 64 broods from 2001 to 2003 (67 in 2001, 95 in 2002, 62 in 2003). Invertebrate percent occurrence (# of samples containing taxa / # of samples) in fecal samples did not differ among sites for any taxa (Table 3.3). Coleoptera (beetles) occurred most frequently at all of the sites (ANOVA on ranks, Alkali: $F_3 = 20.0$, $P < 0.0002$; Garrison: $F_3 = 35.2$, $P < 0.0001$; Gavins: $F_3 = 44.3$, $P < 0.0001$; Sakakawea: $F_3 = 22.6$, $P < 0.0001$, Figure 3.6). There were no differences in the occurrence of Diptera (flies) or that of other taxa (Lepidoptera, Homoptera, Hemiptera, Hymenoptera, Araneae) in the fecal samples at any of the sites (Figure 3.6).

Invertebrate availability

Diptera (flies) were captured on sticky traps at all of the sites (Table 3.4). Coleoptera (beetles) occurred more frequently on sticky traps at Gavins than at the other sites (Table 3.4). Other taxa (Hemiptera, Homoptera, Hymenoptera, Odonata, Orthoptera, Araneae) occurred at higher frequencies at Alkali and Gavins than at

Garrison and Sakakawea (Table 3.4). In particular, Orthoptera occurred more frequently at Alkali and Gavins than at Garrison and Sakakawea (Table 3.4). Homoptera frequencies were higher at Gavins than at Alkali and Garrison, and higher at Sakakawea than Garrison (Table 3.4).

Diptera (flies) occurred at a higher frequency than Coleoptera (beetles) and other taxa (Hemiptera, Homoptera, Hymenoptera, Odonata, Orthoptera, Araneae) at all of the sites (ANOVA on ranks, Alkali: $F_{2,21} = 47.8$, $P < 0.0001$; Garrison: $F_{2,25} = 51.9$, $P < 0.0001$; Gavins: $F_{2,27} = 22.6$, $P < 0.0001$; Sakakawea: $F_{2,16} = 26.2$, $P < 0.0001$, Figure 3.7). Coleoptera (beetle) occurrence was lower than other taxa at Alkali, Garrison and Sakakawea, but similar to other taxa at Gavins (Figure 3.7).

Resource consumption and availability

Diptera (flies) were found in fecal samples in lower proportion than their availability at all of the sites (ANOVA on ranks, Alkali: $F_{1,37} = 475.8$, $P < 0.0001$; Garrison: $F_{1,41} = 256.3$, $P < 0.0001$; Gavins: $F_{1,49} = 334.8$, $P < 0.0001$; Sakakawea: $F_{1,25} = 552.3$, $P < 0.0001$, Figure 3.8). Chicks fed on Coleoptera (beetles) in higher amounts than proportionately available at Alkali, Garrison and Sakakawea (ANOVA on ranks, Alkali: $F_{1,37} = 12.9$, $P = 0.001$; Garrison: $F_{1,41} = 39.9$, $P < 0.0001$; Sakakawea: $F_{1,25} = 17$, $P = 0.0004$, Figure 3.8). At Gavins the proportion of Coleoptera (beetles) in the diet was similar to occurrence (ANOVA on ranks, $F_{1,49} = 1.4$, $P = 0.24$, Figure 3.8). The frequency of other taxa in chick diets was lower than occurrence at all sites (ANOVA on ranks, Alkali: $F_{1,37} = 135.7$, $P < 0.0001$; Garrison: $F_{1,41} = 27.6$, $P < 0.0001$; Gavins: $F_{1,49} = 40.3$, $P < 0.0001$; Sakakawea: $F_{1,25} = 20.9$, $P = 0.0001$, Figure 3.8).

DISCUSSION

Although Diptera (flies) were captured on sticky sticks more frequently at all sites, Coleoptera (beetles) were more frequent in droppings, suggesting that piping plover chicks preferentially preyed on Coleoptera (beetles). It is possible that dropping analysis underestimated the frequency of flies, which are softer bodied than beetles, in the diet. However, other studies have found fly parts in fecal samples. In a study in Canada,

31.5% of piping plover droppings contained fly parts (Shaffer and Laporte 1994). Dropping analyses of insectivorous passerines have also found fly parts (74.6% occurrence in Southwestern Willow Flycatcher (*Empidonax traillii*) droppings), 3 to 10% in insectivorous birds along the Colorado river in Arizona (Drost et al. 2001; Yard et al. 2004).

Given the lack of differentiation in the invertebrate isotopic signatures and the number of potential prey items, we could not use mixing models to assess piping plover chick diets. Taxa with signatures outside of the predicted ranges could have still been prey items for plovers, since any number of prey combinations can result in the predicted signatures. Therefore, the technique was not useful for assessing piping plover prey items. However, Coleoptera (beetles) were within the range of piping plover diet signatures at the 3 river sites, and they were present in a high proportion of fecal samples from all of the sites. They represented 23 to 64% of surface invertebrate occurrences on sticky traps. Although Ephrydidae, shore flies very common at Alkali along the water's edge where the plovers often foraged, had high $\delta^{15}\text{N}$ values compared to potential piping plover prey, it is possible that they were included in their diet in small amounts, but that the lower $\delta^{15}\text{N}$ values of other prey items obscured their signature. However, this would still suggest high consumption of taxa other than Ephrydidae, since substantial numbers of prey with lower $\delta^{15}\text{N}$ would have to have been consumed to produce the signatures found in chick feathers. In addition, fecal sample analysis indicates that Coleoptera (beetles) may have been consumed in greater amounts than Diptera (flies). We were unable to conduct stable isotope analyses on all potential prey items, since we did not have enough material for analysis from taxa trapped in smaller amounts. Although fecal sampling is time consuming, stable isotope analysis did not offer the resolution necessary to differentiate prey items at the level of order, or at the fine-scale trophic level (plovers feeding on herbivores vs. predators).

Several studies on piping plovers and killdeer indicated that beetles were a part of plover diets. On the Magdalen islands, Quebec, beetles (35%) and flies (31%) were most often found in adult piping plover fecal samples (Shaffer and Laporte 1994). In the Great Lakes, the most common insects in piping plover gizzards were Hymenoptera (32%), Coleoptera (beetles, 29%) and Diptera (flies, 28%; Cuthbert et al. 1999). Esophageal

contents of killdeer feeding in impoundments in Missouri had high occurrences of adult (40%) and larval (20%) beetles, as well as fly larvae (40%), but no adult flies (Rundle 1982). In the Great Lakes, Hymenoptera and Coleoptera (beetles) predominated in chick gizzards (Cuthbert et al. 1999), although Diptera (diptera) predominated in the habitat sampled (Nordstrom and Ryan 1996). At Big Quill Lake, Saskatchewan, diet consisted mainly of Coleoptera (42%), Hemiptera (21%), and Diptera (12%; Whyte 1985).

Piping plover chicks in North and South Dakota are generalists, feeding on Coleoptera and Diptera, both of which were common in terrestrial samples. Other species found in terrestrial samples in smaller amounts were not clearly represented in fecal samples. Prey selection may be determined by factors other than availability, such as handling time, and energetic and nutritional content (Krebs and Cowie 1976). Pienkowski (1984) found that as weather conditions improved (temperature, wind, rain), leading to increased prey availability, ringed plovers became more selective for larger prey. Chicks may decrease handling time by feeding on larger and slower prey (beetles). Chicks may also differentially select for prey with higher nutritional value.

The natural history and habitat of the piping plover prey base appears to be varied. Tiger beetles (Cicindelidae) inhabiting sandy beaches are predators on other invertebrates, which may include herbivores or prey with aquatic life cycles (Borror, Tripplehorn and Johnson 1992). The varied natural history of the prey available to piping plover chicks, ranging from insects with a mud or water-inhabiting larval stage (Dolichopodidae), to terrestrial predators (Cicindelidae, Araneae) underscores the need to manage at both the aquatic and terrestrial levels. Aquatic invertebrates and invertebrates inhabiting vegetation may be important to potential plover prey, such as predatory beetles and spiders.

Understanding piping plover diet is important to help drive management decisions regarding maintaining, creating, and protecting foraging habitat. Vegetation on sandbars may support prey eaten by plovers, but the fact that plovers prefer to nest in more open areas must also be taken into consideration. We recommend maintaining some vegetation on the sandbars for the lower part of the terrestrial food chain, and maintaining aquatic conditions that support aquatic invertebrates (slow, shallow water).

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Table 3.1. Diet-tissue ^{13}C and ^{15}N isotope enrichment factors (‰) for feathers and blood from studies of insectivorous and fish-eating birds.

Species	Scientific name	tissue type	prey source	^{13}C	^{15}N	Source
Yellow-rumped warbler	<i>Dendroica coronata</i>	feather	97% insects	4.3	3.5	Pearson et al. 2003
Swallows	<i>Tachycineta thalassina</i> , <i>Tachycineta bicolor</i> , <i>Stelgidopteryx serripennis</i>	blood	insects	.	2.9	Morrissey et al. 2004
Common merganser	<i>Mergus merganser</i>	blood	fish	.	1.0	Morrissey et al. 2004
Ring-billed Gull	<i>Larus delawarensis</i>	feather	perch	0.2	3.0	Hobson and Clark 1992b
American Crow	<i>Corvus brachyrhynchos</i>	feather	perch	1.0	2.0	Hobson and Clark 1992b
Cormorant, Shag, Goosander	<i>Phalacrocorax carbo</i> , <i>Phalacrocorax aristotelis</i> , <i>Mergus merganser</i>	feather	fish	2.3	4.2	Bearhop 1999
Cormorant	<i>Phalacrocorax</i>	feather	mackerel	3.6	3.6	Mizutani et al. 1991
Black-tailed Gull	<i>Larus crassirostris</i>	feather	saurel	3.6	5.3	Mizutani et al. 1992
Nankeen Night Heron	<i>Nycticorax caledonicus</i>	feather	saurel	3.2	4.2	Mizutani et al. 1992
Great White Egret	<i>Egretta alba</i>	feather	saurel	3.1	3.9	Mizutani et al. 1992
Grey Heron	<i>Ardea cinerea</i>	feather	saurel	3.4	4.3	Mizutani et al. 1992
Humboldt's Penguin	<i>Spheniscus humboldti</i>	feather	anchovy	2.9	4.8	Mizutani et al. 1992
Common Cormorant	<i>Phalacrocorax carbo</i>	feather	mackerel	3.8	3.7	Mizutani et al. 1992
Garden Warbler	<i>Sylvia borin</i>	feather	control diet	2.7	4.0	Hobson and Bairlein 2003

Table 3.2. Mean (\pm SE) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for terrestrial invertebrates and piping plover chick feathers collected from four sites in North and South Dakota in 2002. All samples contained several individuals.

Site		$\delta^{13}\text{C}$	\pm	SE	$\delta^{15}\text{N}$	\pm	SE	<i>n</i>
Alkali								
Araneae								
	Araneae 4	-20.1	\pm	.	7.1	\pm	.	1
	Araneae 5	-22.0	\pm	.	9.0	\pm	.	1
Coleoptera								
	Histeridae	-26.2	\pm	0.2	8.2	\pm	0.0	2
Diptera								
	Ephydriidae	-22.7	\pm	0.1	9.8	\pm	0.4	3
	Chloropidae	-21.0	\pm	0.2	7.4	\pm	0.4	8
	Dolichopodidae	-20.1	\pm	0.3	7.4	\pm	0.7	11
Hymenoptera								
	Formicidae (ants)	-19.4	\pm	0.1	9.1	\pm	0.1	2
	Halictidae	-24.6	\pm	0.2	6.1	\pm	0.9	4
	Piping plover	-20.1	\pm	0.4	9.9	\pm	0.5	9
Garrison								
	Araneae	-21.9	\pm	0.3	7.3	\pm	0.3	4
Coleoptera								
	Silphidae	-25.6	\pm	0.2	7.4	\pm	0.1	4
	Cicindelidae (tiger beetles)	-22.0	\pm	1.6	8.1	\pm	1.0	3
Diptera								
	Dolichopodidae	-21.9	\pm	.	8.6	\pm	.	1
Hymenoptera								
	Halictidae	-24.0	\pm	0.3	3.1	\pm	1.4	3
	Piping plover	-22.4	\pm	0.2	9.0	\pm	0.2	14
Gavins								
Araneae								
	Araneae 2	-20.2	\pm	.	7.2	\pm	.	1
	Araneae 3	-19.5	\pm	0.2	7.4	\pm	0.0	2
Coleoptera								
	Silphidae	-24.1	\pm	0.0	8.0	\pm	0.6	2
	Cicindelidae (tiger beetles)	-19.5	\pm	0.6	7.0	\pm	0.4	5
	Cicindelidae larvae (tiger beetles)	-17.8	\pm	.	4.7	\pm	.	1
	Chrysomelidae	-26.1	\pm	0.1	5.5	\pm	0.4	5

Diptera								
	Dolichopodidae	-18.8	±	.	8.3	±	.	1
	Ephydriidae	-20.8	±	.	8.6	±	.	1
	Piping plover	-16.6	±	0.4	8.3	±	0.2	14
Sakakawe								
	Araneae							
	Araneae 4	-24.2	±	.	14.2	±	.	1
	Araneae 5	-21.7	±	.	12.3	±	.	1
	Araneae 6	-25.1	±	0.0	16.4	±	0.0	2
	Coleoptera							
	Carabidae	-22.8	±	0.1	10.6	±	0.1	2
	Cicindelidae (tiger beetles)	-25.3	±	0.2	11.2	±	0.2	7
	Diptera							
	Dolichopodidae	-23.1	±	.	9.1	±	.	1
	Chloropidae	-22.9	±	.	11.8	±	.	1
	Hemiptera							
	Miridae	-22.1	±	.	7.7	±	.	1
	Hymenoptera							
	Halictidae	-24.7	±	0.2	5.7	±	0.0	4
	Piping plover	-22.0	±	0.1	13.4	±	0.3	17

Table 3.3. Percent occurrence of invertebrate taxa ((# of samples containing taxa / # of samples) (100)) (\pm SE) in piping plover chick fecal samples collected in North and South Dakota 2001-2003. Results of ANOVA on ranks comparing taxa occurrence among sites. The sampling unit was the brood.

Taxa	Percent Occurrence										<i>F</i>	<i>P</i>
	All sites (<i>n</i> = 4)		Alkali (<i>n</i> = 16)		Garrison (<i>n</i> = 16)		Gavins (<i>n</i> = 23)		Sakakawea (<i>n</i> = 9)			
None	15	\pm 3.1	21	\pm 8.6	8	\pm 4.2	17	\pm 5.3	9	\pm 4.8	1.8	0.62
Diptera	15	\pm 3	14	\pm 4.6	18	\pm 7.1	13	\pm 5.7	15	\pm 6.3	1.2	0.76
Coleoptera	77	\pm 3.9	69	\pm 11	82	\pm 6.7	76	\pm 5.6	89	\pm 7.9	3	0.39
Other	7	\pm 1.6	4	\pm 2.5	10	\pm 4.1	9	\pm 2.6	4	\pm 2.9	3.2	0.37
Lepidoptera	0.4	\pm 0.4	0	\pm 0	2	\pm 1.6	0	\pm 0	0	\pm 0	3	0.39
Homoptera	0.4	\pm 0.3	0	\pm 0	2	\pm 1.2	0	\pm 0	0	\pm 0	6.1	0.11
Hemiptera	2	\pm 0.9	2	\pm 1.6	0	\pm 0	3	\pm 1.8	3	\pm 2.8	2.4	0.5
Hymenoptera	4	\pm 1.3	2	\pm 2.1	7	\pm 3.7	4	\pm 1.9	0	\pm 0	3.9	0.28
Araneae	1	\pm 0.7	0	\pm 0	0	\pm 0	3	\pm 1.7	1	\pm 1.4	4.3	0.23
Unknown	43	\pm 4.1	38	\pm 9.1	48	\pm 7.8	40	\pm 6.2	48	\pm 13	1	0.79

Table 3.4. Invertebrate composition (\pm SE) (% occurrence = # of samples containing taxa / # of samples) of surface invertebrates on sticky traps in piping plover chick foraging territories. Data collected in North and South Dakota, 2001-2003. Results of ANOVA on ranks followed by Fisher's LSD for comparisons with significant differences ($P \leq 0.05$). For a given taxon, sites with the same letter are not significantly different. n is the number of foraging territories.

Taxa	Percent Occurrence				<i>F</i>	<i>P</i>
	Alkali ($n = 23$)	Garrison ($n = 27$)	Gavins ($n = 28$)	Sakakawea ($n = 18$)		
Diptera	100 \pm 0	100 \pm 0	100:0	100 \pm 0	0.0	1.00
Coleoptera	25 \pm 6 B	23 \pm 5 B	64:7 A	31 \pm 9 B	21.1	0.0001
Other	80 \pm 5 A	48 \pm 6 B	70:7 A	62 \pm 9 B	12.9	0.01
Hemiptera	8 \pm 4	9 \pm 4	2:2	13 \pm 7	3.1	0.38
Homoptera	23 \pm 8 BC	14 \pm 4 C	44:8 A	34 \pm 8 AB	10.2	0.02
Hymenoptera	16 \pm 6	15 \pm 5	14:5	13 \pm 5	0.5	0.93
Odonata	3 \pm 2	0 \pm 0	0:0	0 \pm 0	6.4	0.09
Orthoptera	32 \pm 8 A	5 \pm 4 B	40:7 A	6 \pm 4 B	24.1	< 0.0001
Araneae	8 \pm 4	7 \pm 3	12:5	7 \pm 6	0.9	0.80

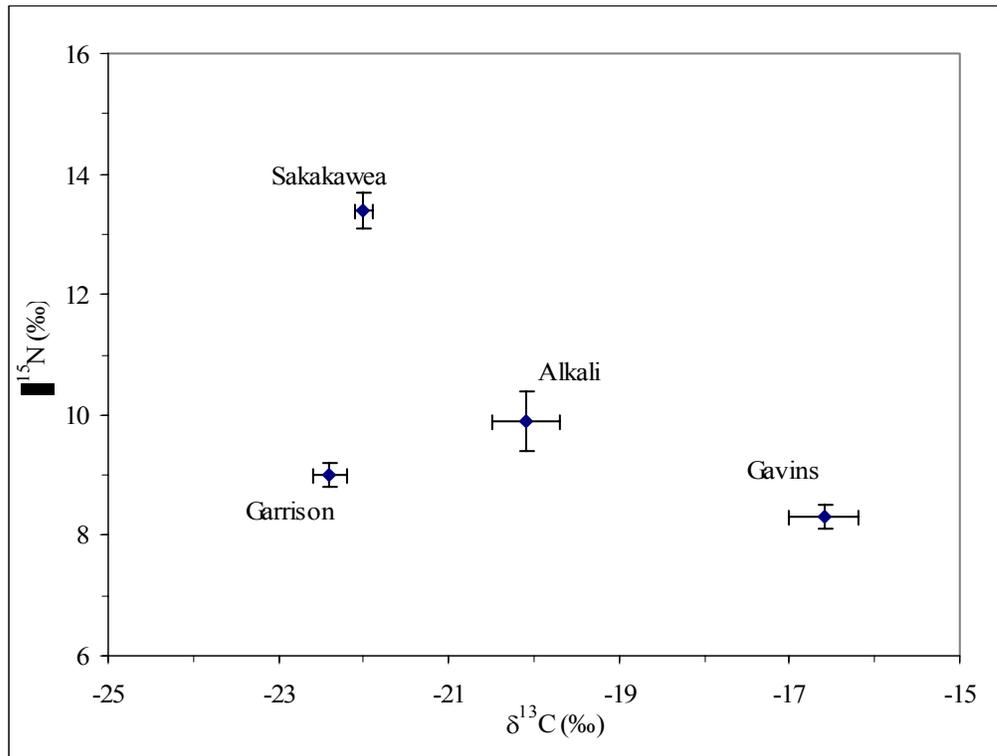


Figure 3.1. Mean carbon and nitrogen isotope signatures (bars represent \pm SE) in piping plover chick feathers at Alkali, Garrison, Gavins and Sakakawea, North and South Dakota, in 2002.

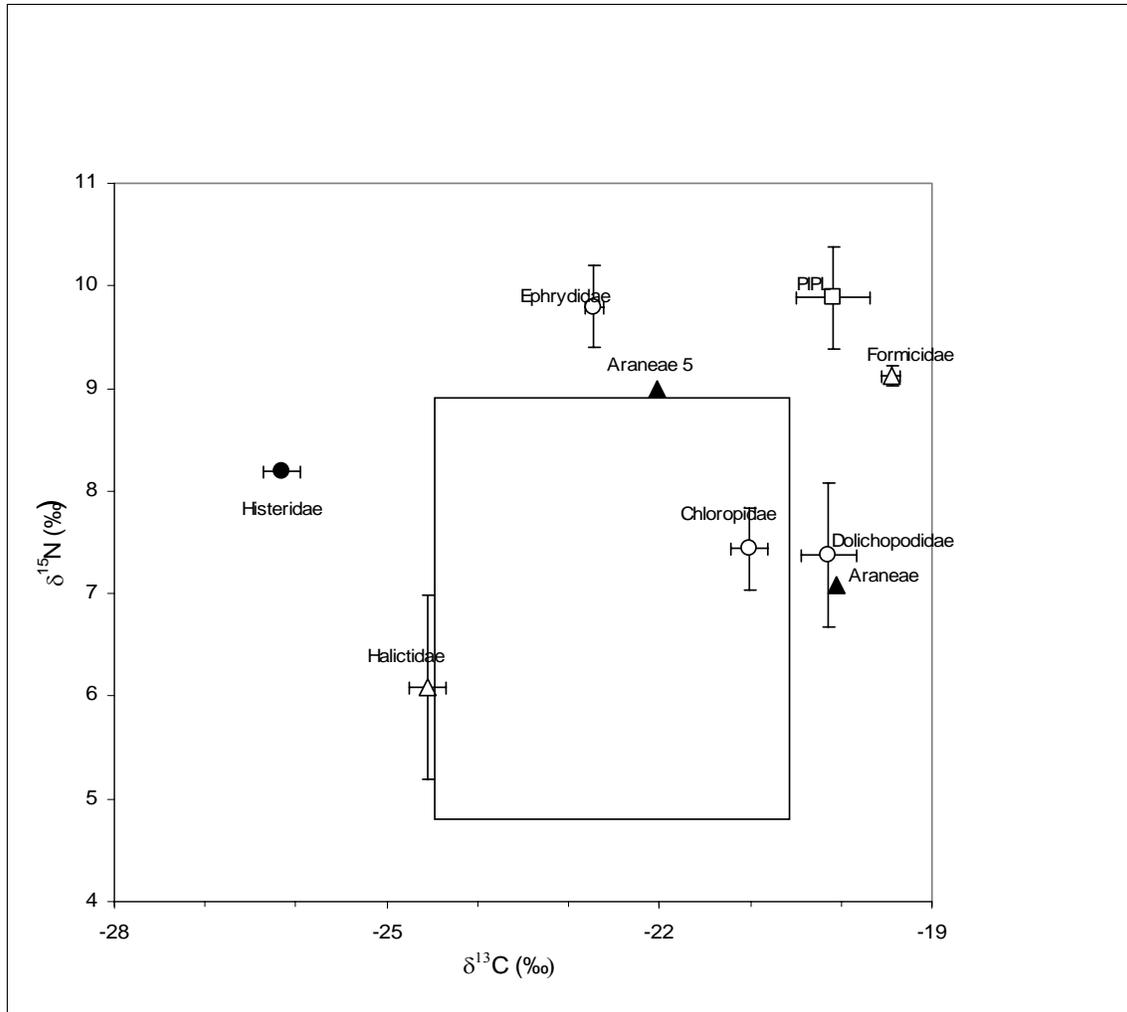


Figure 3.2. Mean carbon and nitrogen isotope signatures (bars represent \pm SE) in piping plover chick feathers and invertebrates at Alkali sites, North Dakota, in 2002. The box represents the predicted range for prey based on stable isotope enrichment from the literature (^{13}C : 0.2 - 4.3‰; ^{15}N : 1.0 - 5.2‰). Open square: Piping plover; open circle: Diptera (flies); closed circle: Coleoptera (beetles); open triangle: Hymenoptera (bees); closed triangle: Araneae (spiders).

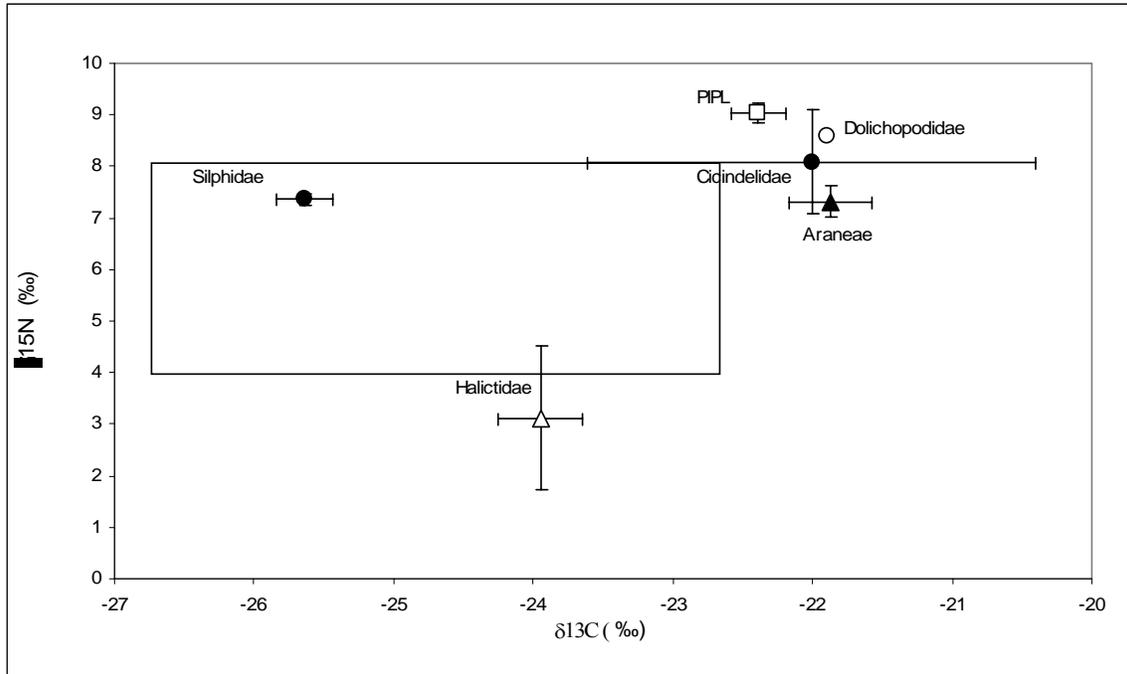


Figure 3.3. Mean carbon and nitrogen isotope signatures (bars represent \pm SE) in piping plover chick feathers and invertebrates at Garrison, North Dakota, in 2002. The box represents the predicted range for prey based on stable isotope enrichment from the literature (^{13}C : 0.2 - 4.3‰; ^{15}N : 1.0 - 5.2‰). Open square: Piping plover; open circle: Diptera (flies); closed circle: Coleoptera (beetles); open triangle: Hymenoptera (bees); closed triangle: Araneae (spiders).

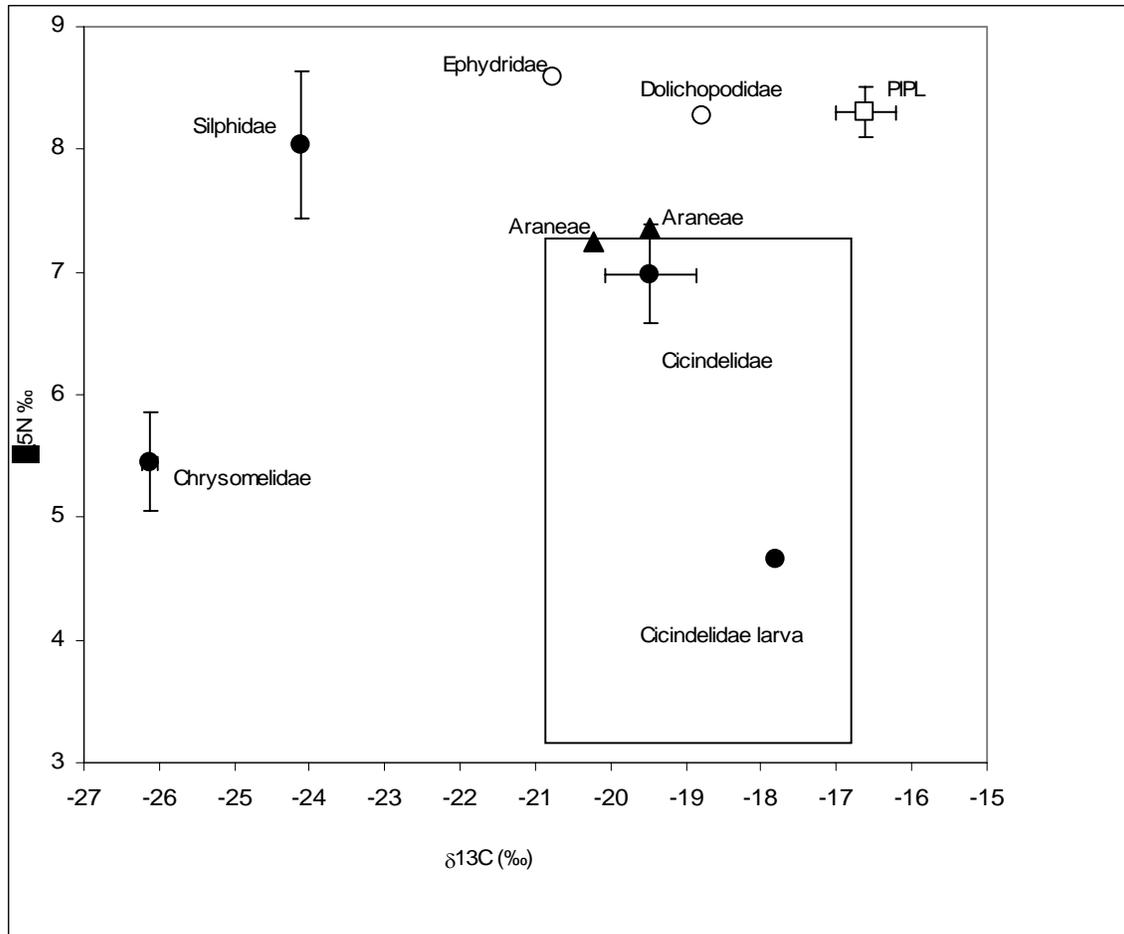


Figure 3.4. Mean carbon and nitrogen isotope signatures (bars represent \pm SE) in piping plover chick feathers and invertebrates at Gavins, South Dakota, in 2002. The box represents the predicted range for prey based on stable isotope enrichment from the literature (^{13}C : 0.2 - 4.3‰; ^{15}N : 1.0 - 5.2‰). Open square: Piping plover; open circle: Diptera (flies); closed circle: Coleoptera (beetles); open triangle: Hymenoptera (bees); closed triangle: Araneae (spiders).

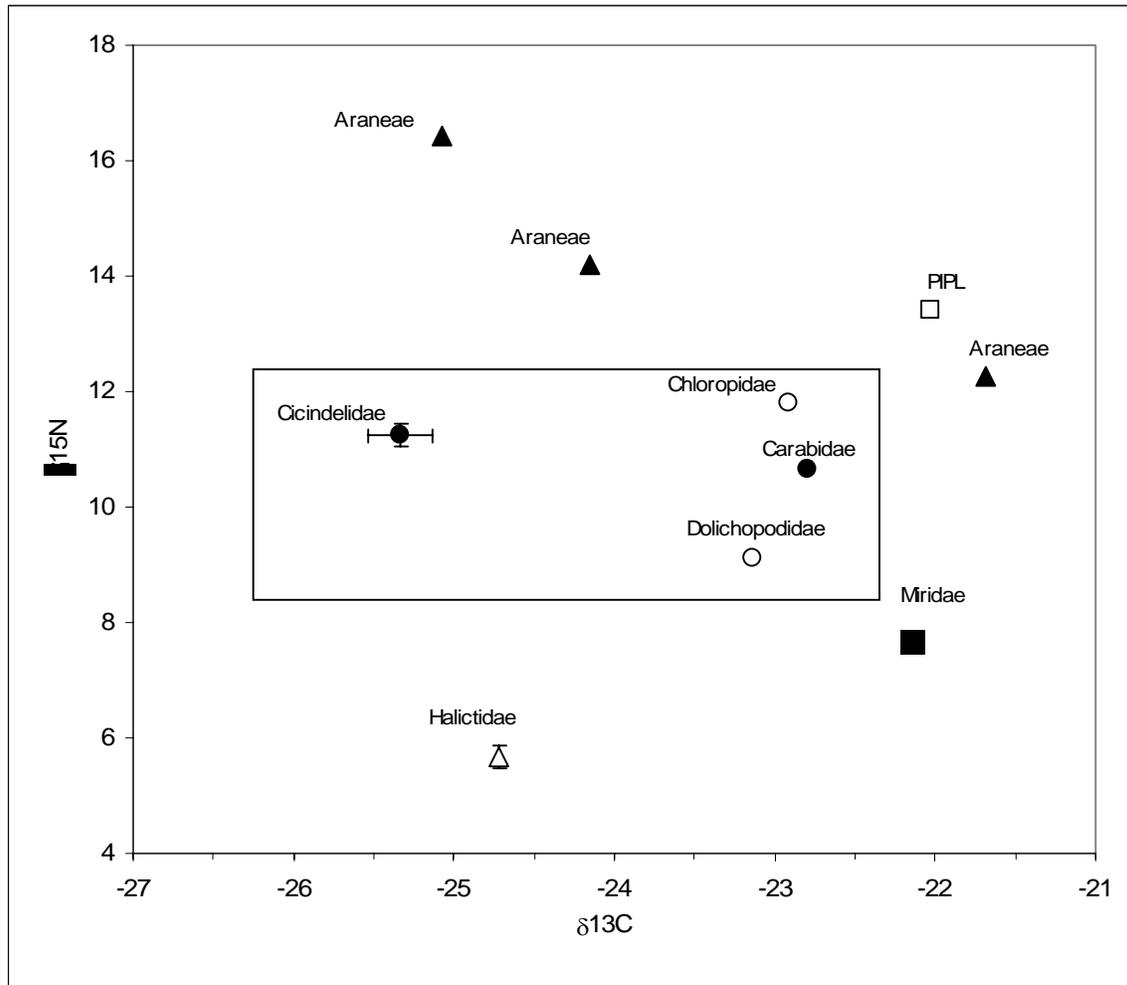


Figure 3.5. Mean carbon and nitrogen isotope signatures (bars represent \pm SE) in piping plover chick feathers and invertebrates at Sakakawea, North Dakota, in 2002. The box represents the predicted range for prey based on stable isotope enrichment from the literature (^{13}C : 0.2 - 4.3‰; ^{15}N : 1.0 - 5.2‰). Open square: Piping plover; open circle: Diptera (flies); closed circle: Coleoptera (beetles); open triangle: Hymenoptera (bees); closed triangle: Araneae (spiders).

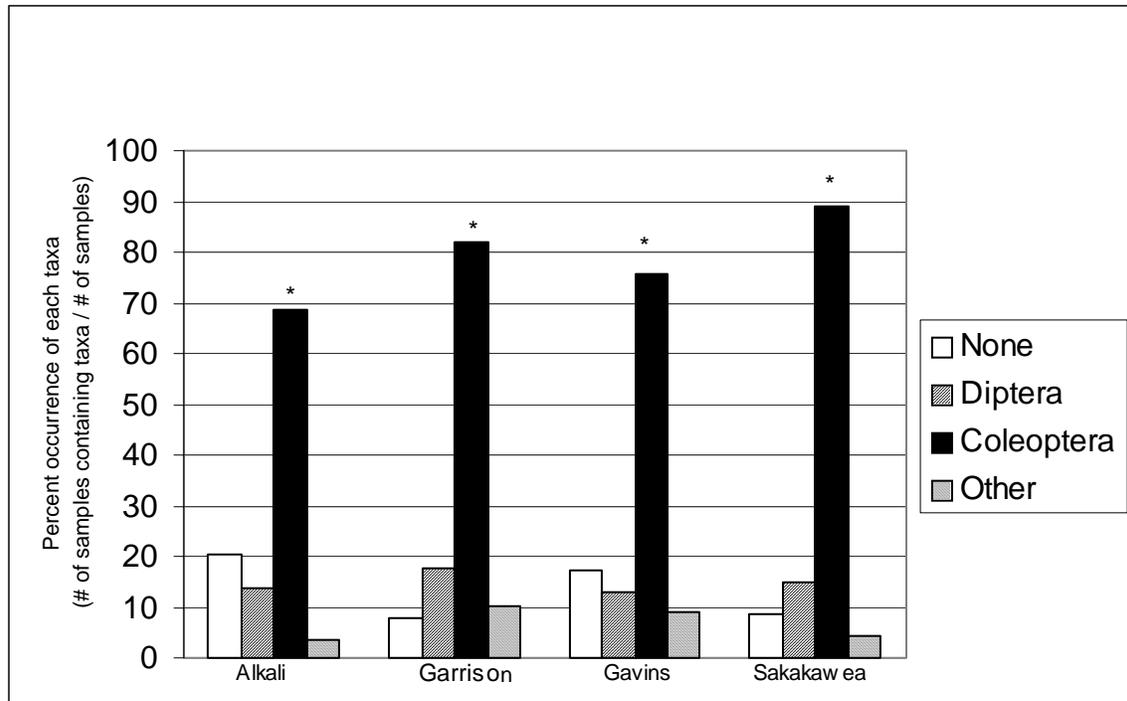


Figure 3.6. Relative contribution of major prey taxa to piping plover chick diet, based on fecal samples collected 2001-2003 at four sites in North and South Dakota. Asterisk indicates taxon with a higher frequency of occurrence than other taxa in fecal samples for a given site, based on an ANOVA on ranks followed by a Fisher's LSD for effects with significant P values ($P \leq 0.05$). The sampling unit is the brood territory.

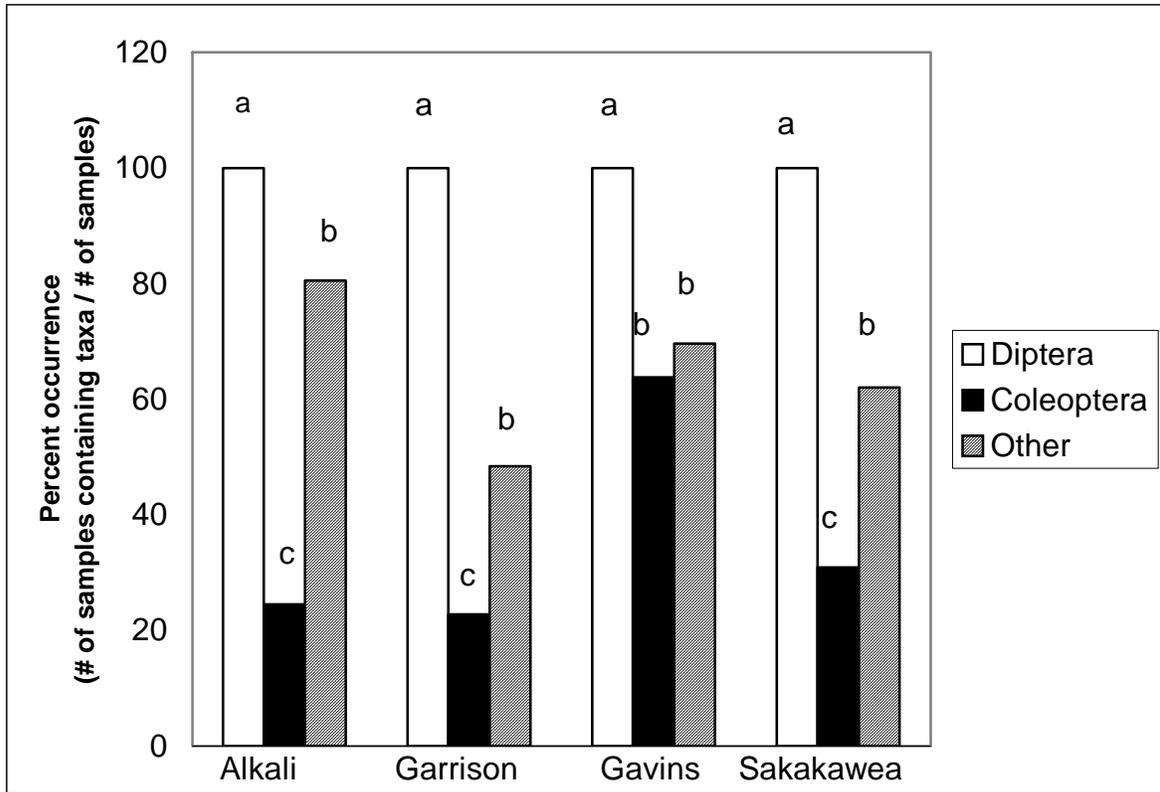


Figure 3.7. Invertebrate composition (% occurrence = # of samples containing taxa / # of samples) of surface invertebrates on sticky traps in piping plover foraging sites. Data collected at four sites in North and South Dakota. Results of an ANOVA on ranks followed by a Fisher's LSD for effects with significant P values ($P \leq 0.05$), comparing occurrence of different taxa within each site. Taxa with the same letters are not significantly different. The sampling unit is the brood territory.

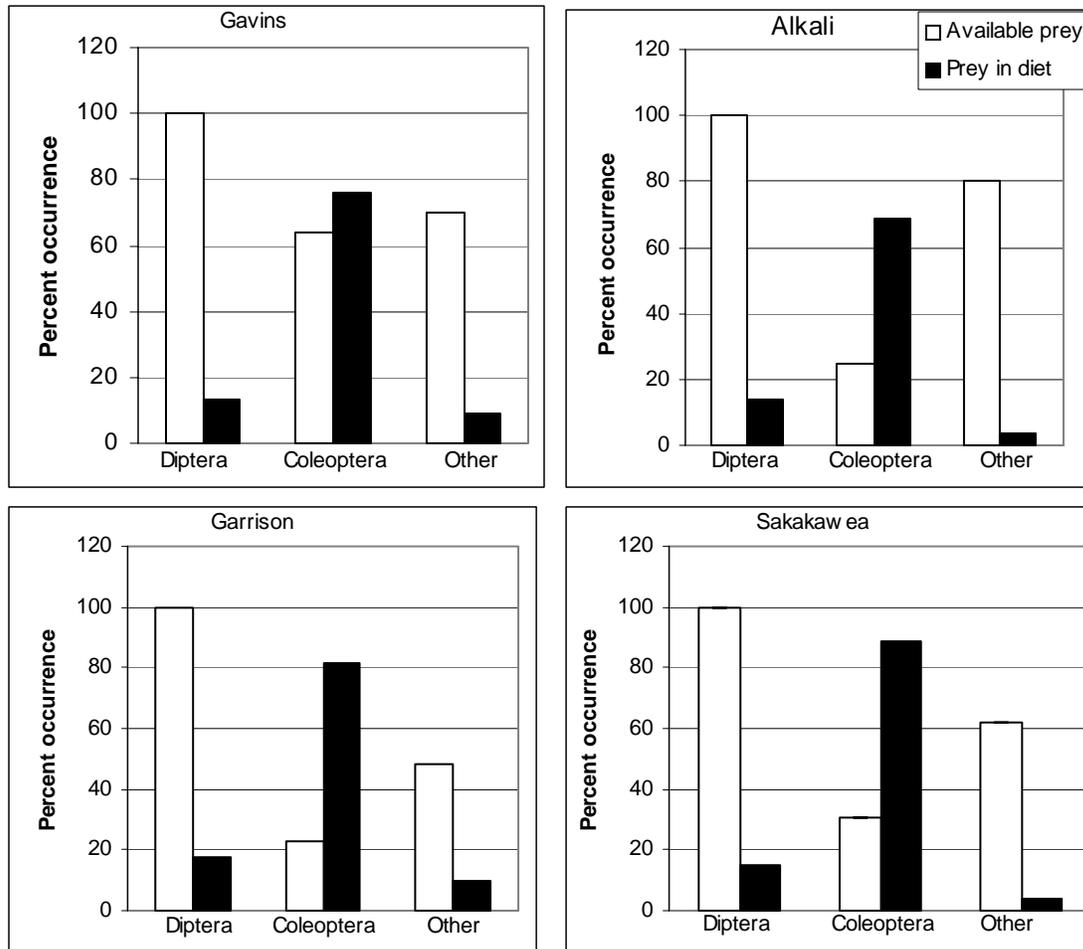


Figure 3.8. Occurrence of prey taxa in the field (based on sticky traps) and in chick diet (based on fecal samples) at four sites in North and South Dakota, 2001-2003.

CHAPTER 4. SYNTHESIS

Overview

Habitat selection

Results supported our prediction that piping plovers preferred protected shoreline over exposed shoreline. Preference for protected shoreline could not be directly explained by differences in prey availability. At Gavins Reach, piping plover selection of protected shorelines was most likely driven by higher invertebrate numbers and biomass. The higher invertebrate indices in some of our backwater areas may be due to lower drift (Troelstrup and Hergenrader 1990). At Garrison Reach and Sakakawea, invertebrate indices were not higher along the protected compared to the exposed shoreline. Perhaps the colder water at Garrison Reach and Sakakawea resulted in lower productivity even at protected shorelines, leading to a lack of difference in invertebrate indices between exposed and protected shoreline at these two cold water reaches. Lower invertebrate indices in Sakakawea backwater areas may be due to the deeper, colder water at this site. These deeper backwater areas may not be the functional equivalent of protected shoreline on the rivers. Daily fluctuations in water levels at Garrison Reach could negatively affect invertebrates in shallow, protected areas, since they may become stranded as water levels drop. Although invertebrate indices were not higher in protected than exposed shoreline at Garrison Reach, the fact that adult plovers preferred these areas indicates protected shorelines might be important for other reasons. The more gradual slopes at protected shorelines might offer more foraging area as the water recedes, compared to exposed shoreline which drops off more abruptly.

At the territory scale, at Gavins Reach and Garrison Reach, chicks spent proportionately more time feeding in the saturated and moist zones than in the vegetation and dry habitats. At Sakakawea, chicks did not use one habitat type more than another, even though invertebrate numbers were higher in the saturated and moist than the other two habitats, and biomass was highest in the moist habitat. At Gavins Reach, the saturated habitat had higher invertebrate indices than dry or vegetated habitats. At Garrison Reach, indices were higher in the moist than in the dry habitat. Although invertebrate indices tended to be higher in the preferred habitats, the lack of a clear

pattern indicates that chicks might also prefer to forage in the saturated and moist habitats because they are located along the less vegetated shoreline, which offers greater visibility to predators. It is also possible that our sampling techniques underestimated some available prey species, and that available prey would have been higher in backwater areas if we had been able to capture these.

Prey selection

Although Diptera (flies) were captured on sticky sticks more frequently at all sites, Coleoptera (beetles) were more frequent in fecal samples, suggesting that piping plover chicks preferentially preyed on Coleoptera (beetles). Stable isotope analysis did not offer the resolution necessary to differentiate prey items at the level of order, or at the fine-scale trophic level (plovers feeding on invertebrate herbivores vs. predators). Although the stable isotope analysis was not useful for assessing piping plover prey items, Coleoptera (beetles) were within the range of piping plover diet signatures at the three river sites, and they were present in a high proportion of fecal samples from all of the sites. Although it is possible that dropping analysis underestimated the frequency of flies, which are softer bodied than beetles, other studies have found fly parts in fecal samples. Our trapping technique also may differentially trap flying and active invertebrates, overestimating flies and underestimating beetles. However, our results are consistent with results from other studies on piping plovers where beetles were a substantial part of plover diets (29 to 42% of their diets) and flies represented 12 to 31% of their diets (Shaffer and Laporte 1994; Cuthbert et al. 1999; Nordstrom and Ryan 1996; Whyte 1985).

Our data indicate that piping plover chicks in North and South Dakota are generalists, feeding on Coleoptera and Diptera, the most common taxa in terrestrial samples. Other species found in terrestrial samples in smaller amounts were not consistently represented in fecal samples. Prey selection may be determined by factors other than availability, such as handling time, and energetic and nutritional content (Krebs and Cowie 1976). Pienkowski (1984) found that as weather conditions improved (temperature, wind, rain), leading to increased prey availability, ringed plovers became more selective for larger prey. Chicks may decrease handling time by feeding on larger

and slower prey (beetles), or chicks may also differentially select for prey with higher nutritional value.

Chick foraging and growth rates may be influenced by prey size and mobility (fast moving, smaller, Diptera vs slower, larger, Coleoptera), as well as digestibility, nutritive value, and handling time. Larger invertebrates (Coleoptera) may have a higher energy return for the amount of energy exerted in capture, and a longer handling time due to their larger size (compared to Diptera). Coleoptera numbers, Coleoptera biomass and individual invertebrate size were higher at Gavins than at the other sites, but the estimated biomass consumed at Garrison and Gavins did not differ. Chicks at Garrison may spend more time foraging to compensate for lower prey availability.

The natural history and ecology of the piping plover prey base appears to be varied. Tiger beetles (Cicindelidae) inhabiting sandy beaches are predators on other invertebrates, which may include herbivores or prey with aquatic life cycles (Borror, Tripplehorn and Johnson 1992). Aquatic invertebrates and invertebrates inhabiting vegetation may be important to potential plover prey, such as predatory beetles and spiders. The varied natural history of the prey available to piping plover chicks, ranging from insects with a mud or water-inhabiting larval stage (Dolichopodidae), to terrestrial predators (Cicindelidae, Araneae) underscores the need to manage at both the aquatic and terrestrial levels.

Factors limiting productivity

Prey availability and foraging strategies

When years were pooled (2001-2003), the sites hypothesized *a priori* to have higher invertebrate indices (Alkali and Gavins) had higher biomass during the chick-rearing period than the two cold water river sites (Garrison is downstream of a cold water release dam and Sakakawea is a deep reservoir). The higher invertebrate biomass indices at Alkali and Gavins were due to higher invertebrate numbers and higher individual invertebrate size, respectively. The lower invertebrate biomass at Garrison (2001 to 2003), than Sakakawea, also a cold water system, could be due to the fluctuating water levels at Garrison. Overall, invertebrate indices (biomass and numbers) were higher at Alkali and Gavins than at Garrison, the cold water, hydro-peaking site.

In this dynamic system, we found annual differences as well as site differences in invertebrate indices. Annual variation may be due to changes in rainfall, summer temperatures, water levels, or time since the last spring flooding event. For example, lower invertebrate indices at Gavins in 2003 could be due to lower summer temperatures (June and July) in South Dakota in 2003, or to lower nutrient availability over time, as time since the high winter flows (1996 and 1997) increases. At Sakakawea, higher invertebrate indices in 2001 than in the following years coincided with lower reservoir levels and lower precipitation in July. Since these environmental factors vary spatially and temporally, retaining a diverse, geographically dispersed system can minimize adverse local annual impacts on the population.

In the Great Plains, chicks appear to use different foraging strategies relative to prey availability and characteristics. Chicks “adjusted” to lower invertebrate numbers by foraging at higher rates or increasing the amount of time spent foraging. In North and South Dakota, chicks age 3 to 10 days, an important age for growth and survival, spent less time foraging at Alkali, where invertebrate abundance was high. At Gavins, foraging rates were low, but the proportion of time foraging was high, and estimated biomass consumed was high, due also to the high density of larger taxa (Coleoptera) at this site. At Garrison, with low invertebrate indices, foraging rates and the proportion of time foraging were high, and so estimated biomass consumed was similar to Gavins, and higher than Alkali, a site with high invertebrate indices. At Sakakawea, where foraging rates were average, the proportion of time foraging was high. Previous studies on piping plovers have found that chicks spent more time foraging at sites with higher prey availability (Loefering and Fraser 1995; Goldin and Regosin 1998; Elias et al. 2000). However, adult spotted sandpipers in Minnesota spent less time (30% of time) foraging when prey numbers were high compared to times with low prey availability (65% of time foraging) (Maxson and Oring 1980). Foraging time decreased as food increased to a certain level, then leveled off even if prey abundance continued to increase (Maxson and Oring 1980).

We found no direct relationship between chick size or chick daily survival rates and invertebrate indices. Brood survival was lower at the site with high invertebrate indices (Gavins), and highest at the site with the lowest invertebrate indices (Garrison).

The lack of a relationship between invertebrate indices and chick survival could be due to the sampling technique (overestimating flies), differential chick success rates depending on prey species; and the assumption that each peck is successful. Since success rates may change from site to site based on prey species, estimated biomass consumed may not accurately reflect chick intake at each site. However, it is also possible that other factors, particularly predation, have a greater impact than prey availability on chick survival.

Chick survival and growth rates

Growth rate differences among sites reflected trends in invertebrate numbers: Chick growth rates were higher at Alkali, where invertebrate biomass was greatest. In 2001 and 2002, chicks at Alkali and Gavins, sites with high invertebrate biomass, had high growth rates for weight and condition indices (mass / exposed culmen). In 2003, this pattern was present at Alkali, but not at Gavins, which had high invertebrate indices, and the lowest chick growth rates for mass of all of the sites. However, in 2003, rates of condition indices (mass / exposed culmen) were still higher at Gavins than at Garrison.

In our study, chicks that were larger at early stages (age 4 to 5 days, and 8 to 9 days) were more likely to survive to fledging. Larger chicks are less likely to die of exposure or predation than smaller chicks. In addition, chicks that fledge at a heavier weight may be more likely to survive during migration and into the following year (Sagar and Horning 1990; Keedwell 2003).

In our study, chick size at 4 to 5 days and 8 to 9 days did not vary among sites, and thus did not explain differential survival among sites. Even though chicks at our sites were heavier, daily survival rates were lower than at Assateague Island National Seashore, Maryland (0.96) at all of our study sites (0.92-0.93) except Garrison (0.99) (Loegering and Fraser 1995). The Great Plains chick daily survival rates were lower than those on New York barrier islands, even at the poor quality habitats (no pools or tidal flats) in New York (high quality: 0.97 – 0.98; poor quality: 0.96; Elias et al. 2000). Growth rates do not appear to be driving the differences in chick survival.

Predators

Predation is a possible factor differentially affecting chick survival. However, sites with higher frequencies of predator tracks did not have lower chick survival. Other studies have found that the main predators on Great Plains piping plovers are avian, and except for gulls, we did not quantify avian predator presence (Kruse et al. 2001; Knetter et al. 2002). American kestrels (*Falco sparverius*) and great horned owls (*Bubo virginianus*) caused the majority of chick mortalities in the Alkali wetlands and on the Missouri River (Kruse et al. 2001; Knetter et al. 2002). Kruse et al. (2001) attributed high predation rates at Gavins to habitat changes, particularly the fact that islands were small and isolated. In addition, due to the limited amount of available habitat, the same habitat was used year after year, increasing predators' ability to key into them from year to year (Kruse et al. 2001). Thus, creating dynamic sandbar complexes that change in size and location and that increase the area of unused habitat, could decrease predator efficiency (Kruse et al. 2001).

The lack of a direct relationship between chick survival rates and chick growth rates or prey availability, and the lack of a relationship between mammalian predator indices and chick survival rates indicate that another factor is affecting chick mortality. Knetter et al. (2002) suggested that in the alkali wetlands, avian predators may have a greater impact on piping plover chick survival than mammalian predators. Differences in survival rates among sites are most likely caused by differences in avian predator numbers, which we did not measure. At Gavins in 2002 and 2003, adult plovers were found dead in a manner consistent with avian (great horned owl) predation (decapitated, wings clipped). In addition, predation rates may have been exacerbated in years when chick growth rates were lower, or when chicks spent more time foraging due to lower prey availability. At sites with higher chick mortality (Gavins), managing vegetation along the shoreline to decrease piping plover vulnerability to mammalian predators and managing the surrounding landscape to minimize elevated perches for avian predators may increase chick survival rates.

MANAGEMENT IMPLICATIONS

Habitat improvements

We found differences in habitat selection at both the landscape (exposed vs protected shoreline) and territory scale (saturated and moist vs vegetation and dry habitats), underscoring the importance of understanding selection at different scales when considering habitat protection, management or creation.

On the Missouri River, protected shorelines, which include backwater areas, inlets, inter-island channels and ephemeral pools, are important foraging sites for piping plovers during the breeding season. Flow management on the Missouri River should incorporate techniques that allow processes that drive the creation of these shorelines. In addition, when creating artificial sandbars, inlets and pools should be included in the design.

Plovers foraged primarily along the shoreline, in saturated and moist habitats. These low-lying parts of sandbars with no steep escarpments need to be maintained in order to retain high quality plover foraging habitat. To maximize the amount of saturated and moist habitats when engineering habitats for piping plovers, sandbars should be designed to slope gently into the water.

Understanding piping plover diet is important to help drive management decisions regarding maintaining, creating, and protecting foraging habitat. Vegetation on sandbars may support prey eaten by plovers, but the fact that plovers prefer to nest in more open areas and that vegetation may decrease predator visibility must also be taken into consideration.

Manage for a diverse, complex system

This study underscores the variability in different indices among the four sites we studied in the Great Plains. The fact that invertebrate indices, predation pressures, chick growth rates and chick survival varied among the sites, suggests the need for different management strategies at each site. In addition, these factors may vary from year to year.

The Great Plains, and particularly the Missouri River, are a dynamic system, in which piping plovers move among different habitat types from year to year depending on conditions (weather, hydrological conditions and cycles, management impacts) (Haig and Oring 1988a; Haig and Oring 1988b; Knetter et al. 2002; USFWS 2003; Haig et al. 2005). Prey availability does not appear to be limiting piping plover productivity at any of the sites. Decreasing predation pressure at Alkali and Gavins may increase productivity at these sites. At Garrison and Sakakawea, lower predation pressure appears to compensate for lower prey availability.

A system of rotating releases, with changes in water levels along different sections of the Missouri every few years, would increase nutrient value of sandbars, decrease the ability of predators to key into certain areas, and more closely duplicate the historic disturbance regime. High spring flows every few years would allow scouring of sandbars to decrease vegetation and increase habitat available to plovers, and increase nutrient levels to enhance prey numbers on the sandbars. The management plan in the Great Plains should include maintenance, creation and regular evaluation of foraging sites on sandbars and along reservoirs. The importance of maintaining a variety of suitable habitats along the Missouri River has been reinforced by the results of the 2001 census, documenting decreased numbers in Prairie Canada (due to habitat loss, including drought and flooding) along with an increase on the Missouri River (Montana, North Dakota, South Dakota; Haig et al. 2005). A combination of lower summer flows that expose more shoreline, spring flows that help create new nutrient-rich sandbar habitat, and creation of new habitat are all positive options for maintaining or creating critical piping plover habitat. Adaptive management and further studies are needed to evaluate the long-term relative value of each of these processes.

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Appendix A. Geographical latitudes, longitudes and river mile locations of surveyed islands in North and South Dakota, 2001-2003.

Reach	Latitude	Longitude	River mile
Gavins	42.89N	97.39W	780-799
Garrison	47.31N	101.1W	1355-1376
Lake Sakakawea	47.61N	101.34W	

Appendix B. Mean invertebrate numbers (per set) and biomass (mg dry weight) \pm SE in each habitat by reach and year during the pre-hatching period.

Habitat	Year	Site	<i>n</i>	Biomass		Number	
				Mean \pm SE	Mean \pm SE		
Saturated							
	2001	All	25	16.4 \pm 3.7		8.2 \pm 1.8	
	2002	All	37	14.4 \pm 4.4		8.9 \pm 2.2	
	2003	All	24	4.0 \pm 1.1		5.2 \pm 2.2	
	All	Alkali	24	9 \pm 1.6		10.9 \pm 3.1	
	All	Gavins	33	21.4 \pm 5.2		12.7 \pm 3.6	
	All	Garrison	28	22.9 \pm 16.9		2.6 \pm 0.8	
	All	Sakakawea	17	3.6 \pm 2.2		3.2 \pm 1.5	
	2001	Alkali	5	8.6 \pm 4.4		4.5 \pm 1.7	
	2001	Garrison	4	3.2 \pm 1.9		3.4 \pm 1.4	
	2001	Gavins	13	24.0 \pm 5.8		10.7 \pm 2.8	
	2001	Sakakawea	3	13.5 \pm 11.4		9.7 \pm 7.7	
	2002	Alkali	10	10.5 \pm 2.5		15.6 \pm 5.0	
	2002	Garrison	9	13.7 \pm 8.7		1.8 \pm 0.5	
	2002	Gavins	10	30.0 \pm 13.3		15.1 \pm 4.9	
	2002	Sakakawea	8	0.4 \pm 0.2		1.0 \pm 0.3	
	2003	Alkali	6	7.4 \pm 3.3		11.8 \pm 8.0	
	2003	Garrison	4	2.3 \pm 1.9		5.0 \pm 4.4	
	2003	Gavins	9	3.0 \pm 1.4		1.9 \pm 0.7	
	2003	Sakakawea	5	3.3 \pm 2.2		3.4 \pm 1.8	
Moist							
	2001	All	42	6.0 \pm 2.5		2.8	0.6
	2002	All	39	16.6 \pm 10.3		10.4	2.8
	2003	All	23	8.1 \pm 1.8		6	1.4

All	Alkali	25	8.4 ± 3.0	9.6 ± 3.6
All	Garrison	28	22.1 ± 14.2	1.9 ± 0.7
All	Gavins	33	11.2 ± 2.3	9.3 ± 2.0
All	Sakakawea	18	3 ± 1.0	3.2 ± 0.8
2001	Alkali	10	2.5 ± 1.8	2.1 ± 0.6
2001	Garrison	12	3.8 ± 3.6	1.4 ± 0.7
2001	Gavins	15	12.5 ± 2.9	4.1 ± 1.2
2001	Sakakawea	5	4.8 ± 3.1	3.4 ± 1.9
2002	Alkali	9	6.4 ± 1.9	18.2 ± 9.1
2002	Garrison	12	47.0 ± 42.3	1.7 ± 1.0
2002	Gavins	10	12.0 ± 2.5	20.4 ± 4.9
2002	Sakakawea	8	1.0 ± 0.3	1.9 ± 0.4
2003	Alkali	6	14.8 ± 9.6	9.2 ± 4.7
2003	Garrison	4	1.3 ± 0.5	4.3 ± 3.0
2003	Gavins	8	4.0 ± 0.7	5.1 ± 1.2
2003	Sakakawea	5	2.6 ± 1.1	5 ± 2.3
Dry				
2003	All	17	8.0 ± 3.1	9.5 ± 4.7
2002	All	29	8.1 ± 2.3	4.5 ± 1.6
2001	All	25	4.1 ± 1.3	1.3 ± 0.5
All	Alkali	13	3.5 ± 1.4	9.1 ± 5.5
All	Garrison	19	6.5 ± 2.9	7.5 ± 6.2
All	Gavins	22	10.8 ± 2.9	5.5 ± 1.9
All	Sakakawea	17	2.6 ± 1.9	1.9 ± 0.8
2001	Alkali	3	2.4 ± 2.4	0.8 ± 0.8
2001	Garrison	10	0.4 ± 0.3	1.3 ± 1.0
2001	Gavins	8	12.4 ± 5.3	1.7 ± 0.8
2001	Sakakawea	4	10.7 ± 10.6	1 ± 0.7
2002	Alkali	6	3.8 ± 2.7	3.9 ± 2.4
2002	Garrison	6	19.8 ± 8.3	0.9 ± 0.3
2002	Gavins	9	11.5 ± 4.3	10.4 ± 4.4
2002	Sakakawea	8	0.6 ± 0.4	1.2 ± 0.6
2003	Alkali	4	5.8 ± 3.9	10.6 ± 8.5

2003	Garrison	3	6.1 ± 4.5	27.7 ± 24.2
2003	Gavins	5	4.1 ± 1.8	3.9 ± 1.7
2003	Sakakawea	5	1.6 ± 1.0	3.4 ± 2.6

Vegetation

2001	All	30	3.3 ± 1.1	7.1 ± 2.9
2002	All	32	6.2 ± 1.6	1.2 ± 0.3
2003	All	22	3.7 ± 1.2	4.7 ± 1.3
All	Gavins	30	7.2 ± 1.5	6.3 ± 1.5
All	Alkali	25	3.5 ± 1.0	3.1 ± 1.2
All	Sakakawea	15	3.5 ± 2.4	5.6 ± 4.5
All	Garrison	14	1.8 ± 1.0	1.7 ± 0.6
2001	Alkali	10	4.1 ± 2.2	1.5 ± 0.5
2001	Garrison	5	0.1 ± 0.0	0.3 ± 0.3
2001	Gavins	13	4.2 ± 1.9	1.4 ± 0.4
2001	Sakakawea	2	1.7 ± 1.7	0.5 ± 0.5
2002	Alkali	9	3.5 ± 1.5	4.0 ± 2.3
2002	Garrison	6	2 ± 1.1	2.0 ± 0.7
2002	Gavins	9	12.3 ± 2.9	10.9 ± 3.7
2002	Sakakawea	8	5.7 ± 4.5	1.1 ± 0.4
2003	Alkali	6	2.4 ± 1.4	3.1 ± 1.5
2003	Garrison	3	4.4 ± 4.0	22.7 ± 20.7
2003	Gavins	8	6.2 ± 2.5	6.9 ± 2.4
2003	Sakakawea	5	0.8 ± 0.3	3.0 ± 1.6

Appendix C. Mean invertebrate numbers (per set) and biomass (mg dry weight) \pm SE per set of sticky traps in each habitat by site and year during the chick rearing period.

Habitat	Year	Site	<i>n</i>	Biomass		Number	
				Mean \pm SE		Mean \pm SE	
Saturated							
	2001	All	27	30.7	\pm 9.0	16.7	\pm 3.7
	2002	All	39	18.3	\pm 3.9	27.0	\pm 8.1
	2003	All	29	6.7	\pm 1.4	9.1	\pm 1.8
	All	Alkali	22	32.4	\pm 11.7	45.9	\pm 13.2
	All	Garrison	24	4.2	\pm 1.2	4.1	\pm 0.6
	All	Gavins	28	24.8	\pm 3.8	14.9	\pm 3.5
	All	Sakakawea	21	10.9	\pm 2.3	11.5	\pm 1.7
	2001	Alkali	6	58.5	\pm 38.5	37.3	\pm 13.4
	2001	Garrison	6	10.5	\pm 4.1	3.6	\pm 0.9
	2001	Gavins	8	35.7	\pm 6.6	14.7	\pm 2.4
	2001	Sakakawea	7	18.5	\pm 5.2	12.4	\pm 2.6
	2002	Alkali	8	35.7	\pm 13.1	83.20	\pm 31.2
	2002	Garrison	10	1.9	\pm 0.5	3.70	\pm 0.80
	2002	Gavins	11	30.1	\pm 6.3	21.90	\pm 8.20
	2002	Sakakawea	10	7.6	\pm 2.1	10.90	\pm 2.50
	2003	Alkali	8	9.5	\pm 3.8	15.1	\pm 5.2
	2003	Garrison	8	2.5	\pm 0.5	5.0	\pm 1.2
	2003	Gavins	9	8.6	\pm 2.8	6.2	\pm 1.7
	2003	Sakakawea	4	5.7	\pm 1.8	11.2	\pm 5.0
Moist							
	2001	All	27	11.4	\pm 2.1	11.4	\pm 2.8
	2002	All	39	5.5	\pm 0.9	8.8	\pm 1.3
	2003	All	29	4.9	\pm 0.9	7.2	\pm 1.4

All	Alkali	23	12.0 ± 2.0	16.2 ± 3.8
All	Gavins	28	7.9 ± 1.6	7.4 ± 1.2
All	Garrison	24	4.5 ± 1.0	7.5 ± 1.1
All	Sakakawea	20	2.9 ± 0.7	5.1 ± 0.7
2001	Alkali	7	18.2 ± 4.8	24.6 ± 9.4
2001	Garrison	6	2.7 ± 0.8	5.0 ± 1.4
2001	Gavins	8	16.5 ± 3.6	11.5 ± 2.4
2001	Sakakawea	6	4.8 ± 1.9	5.3 ± 1.9
2002	Alkali	8	8.9 ± 2.5	14.3 ± 5.5
2002	Garrison	10	6.6 ± 2.3	8.0 ± 1.7
2002	Gavins	11	5.0 ± 1.2	8.6 ± 1.7
2002	Sakakawea	10	2.3 ± 0.8	5.7 ± 0.6
2003	Alkali	8	9.6 ± 2.4	10.8 ± 4.2
2003	Garrison	8	3.3 ± 0.6	9.0 ± 2.4
2003	Gavins	9	3.6 ± 0.9	4.1 ± 1.0
2003	Sakakawea	4	1.5 ± 0.9	3.3 ± 1.1

Dry

2001	All	18	4.6 ± 2.5	2.8 ± 0.5
2002	All	33	5.2 ± 2.3	3.5 ± 0.6
2003	All	20	1.2 ± 0.3	2.2 ± 0.5
All	Alkali	19	2.2 ± 0.5	2.7 ± 0.6
All	Garrison	20	2.1 ± 0.7	3.1 ± 0.6
All	Gavins	16	10.6 ± 5.1	3.0 ± 1.0
All	Sakakawea	16	1.7 ± 0.5	2.6 ± 0.6
2001	Alkali	3	4.3 ± 2.3	3.0 ± 2.1
2001	Garrison	6	0.9 ± 0.4	2.9 ± 0.9
2001	Gavins	5	12.5 ± 8.2	3.2 ± 0.9
2001	Sakakawea	4	0.4 ± 0.2	1.9 ± 1.1
2002	Alkali	8	1.4 ± 0.5	2.1 ± 0.8
2002	Garrison	9	3.5 ± 1.4	3.1 ± 1.2
2002	Gavins	7	15.1 ± 0.7	4.0 ± 2.0
2002	Sakakawea	9	2.7 ± 0.7	3.4 ± 0.9

2003	Alkali	8	2.0 ± 0.7	3.1 ± 1.0
2003	Garrison	5	1.0 ± 0.3	3.5 ± 0.6
2003	Gavins	4	0.2 ± 0.1	1.0 ± 0.6
2003	Sakakawea	3	0.3 ± 0.2	1.2 ± 0.7

Vegetation

2001	All	28	6.3 ± 6.5	3.9 ± 0.6
2002	All	29	3.8 ± 5.0	3.9 ± 0.6
2003	All	28	3.2 ± 2.6	5.6 ± 0.6

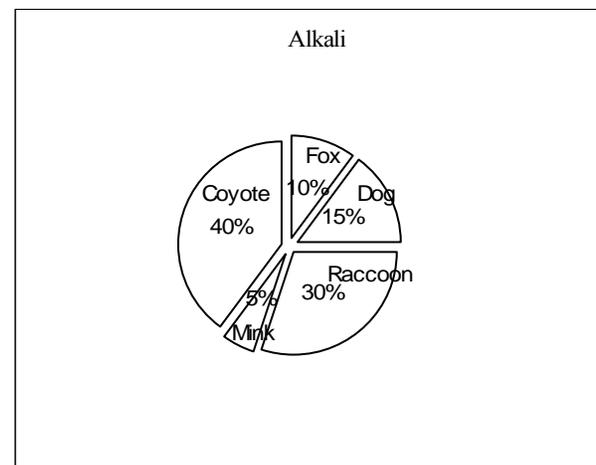
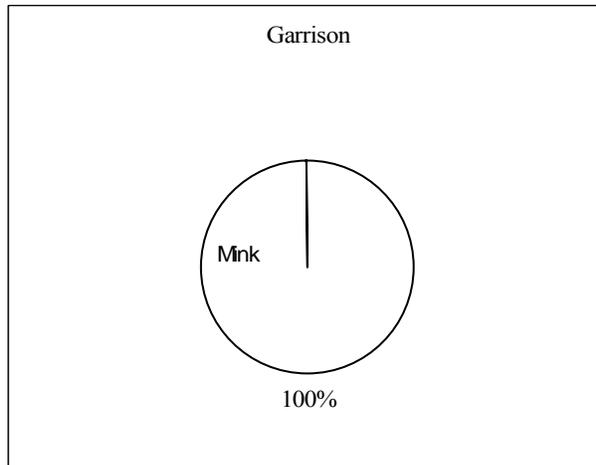
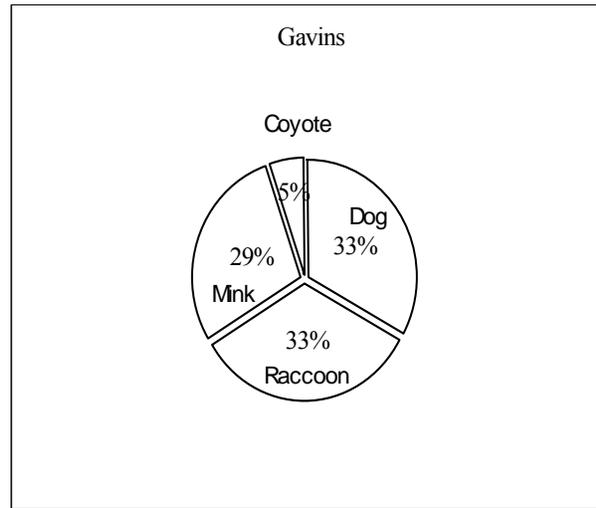
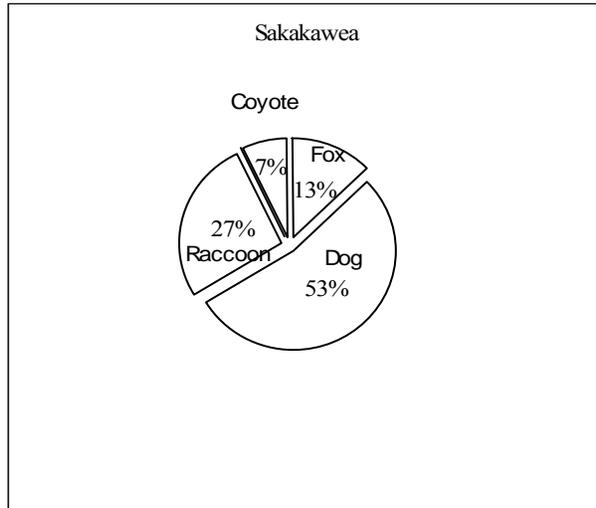
All	Alkali	23	4.3 ± 0.9	4.1 ± 0.5
All	Garrison	17	4.6 ± 1.0	6.5 ± 1.0
All	Gavins	24	6.5 ± 1.4	5.2 ± 0.7
All	Sakakawea	21	2.2 ± 0.8	2.3 ± 0.3

2001	Alkali	7	5.5 ± 1.0	4.1 ± 1.0
2001	Garrison	6	4.1 ± 1.6	3.3 ± 1.3
2001	Gavins	8	11.1 ± 3.3	6.7 ± 2.7
2001	Sakakawea	7	3.7 ± 2.3	2.9 ± 0.7

2002	Alkali	8	4.5 ± 2.2	3.9 ± 0.9
2002	Garrison	3	7.5 ± 4.3	9.0 ± 3.6
2002	Gavins	8	4.4 ± 1.8	4.5 ± 1.0
2002	Sakakawea	10	1.7 ± 0.6	1.8 ± 0.4

2003	Alkali	8	3.1 ± 0.8	4.4 ± 0.8
2003	Garrison	8	3.8 ± 0.7	7.9 ± 1.0
2003	Gavins	8	4.0 ± 1.3	5.9 ± 1.3
2003	Sakakawea	4	0.7 ± 0.2	2.5 ± 0.4

Appendix D. Percentage of mammalian predator track occurrences for each species (Coyote, Fox, Dog, Raccoon, Mink) at each site in North and South Dakota, 2001-2003, by species. Percent of tracks represented by each species.



Appendix E. River mile locations of islands surveyed for adult piping plover habitat use and availability study in North and South Dakota, 2001-2003.

Reach	Pre-hatching		Chick-rearing		
	2002	2003	2001	2002	2003
Gavins	781.5	788	781.5		788
	788	793.5	788		793.5
	795.3	795.5	799		795.5
	799				
Garrison	1361		1361	1361	
	1367	1367	1367	1367	1367
	1374		1374		

Vita

Danielle Le Fer

EDUCATION

Virginia Polytechnic Institute and State University, Blacksburg, VA 24061

Advisor: James Fraser (540-231-6064)

Ph.D. in Fisheries and Wildlife Science.

Dissertation: "Piping Plover Foraging Ecology in the Great Plains."

San Francisco State University, 1600 Holloway, S.F. CA 94132

Advisor: Tom Parker (415-338-2375)

M.S. in Ecology and Systematic Biology, Jan. 1999.

Thesis: "The Effect of Seasonality of Burn, Soil Moisture and Temperature on Chaparral Regeneration."

Barnard College, New York City, NY 10027

B.A. in Environmental Science, May 1984.

WORK EXPERIENCE

Wildlife Biologist, December 2004-present.

USFWS-Common Murre Restoration Project, POB 524, Fremont, CA 94560

- Assisted in the administration and implementation of the Common Murre Restoration Project. Deployed social attraction equipment onto offshore rock.
- Monitored seabird Common Murre and Brandt's Cormorant breeding biology.
- Conducted local and statewide seabird census surveys with ground and aerial techniques.
- Conducted Clapper Rail surveys.
- Produced reports, manuscripts; presented papers at conferences. Analyzed and interpreted data.

Research Assistant, Aug. 2000-present.

Virginia Polytechnic Institute, Dept. of Fisheries and Wildlife, Cheatham Hall, Blacksburg, VA 24061

- Designed and implemented Ph.D. research project on Piping Plover foraging ecology. Conducted adult surveys, behavioral observations, located nests, placed exclosures on nests, trapped adults on nests, measured eggs and chicks, and sampled for invertebrates.
- Trained and supervised 7 technicians per year (for 3 years) at 2 field stations in all aspects of data collection and data entry, including operation and care of an 18-foot outboard motorboat on the Missouri River. Coordinated activities with the U.S. Army Corps of Engineers, U.S.F.W.S., The Nature Conservancy.
- Data management and data entry, including hardware and software installation, troubleshooting, website set-up.
- Currently writing dissertation and manuscripts.

Biologist, July 1998-July 2000.

San Francisco Bay Bird Observatory, 1290 Hope St., Alviso, CA 95002

- Managed Coyote Creek Banding Station. Coordinated and trained volunteers, developed protocols, and developed new volunteer bander manual and workshops; collected measurement data on migratory and nonmigratory birds; inter-acted with Bird Banding Laboratory.
- Developed and conducted a study of avian abundance and richness in revegetated riparian sites, in order to evaluate riparian restoration projects. Conducted migratory and nonmigratory songbird censuses and vegetation surveys. Collected, entered, analyzed and interpreted data and wrote report.
- Researched seasonal variation in Virginia Rail and Sora density in tidal marshes. Job included trapping, censuses using call counts, transmitter attachment, telemetry, purchase and care of gear, data analysis, report writing, and supervising a field assistant. Maintained communications with the Santa Clara Valley Water District.
- Assessed seabird (California Gull and Forster's Tern) productivity in South San Francisco Bay; conducted colony nest counts and egg measurements; used kayaks.
- Conducted seabird and landbird surveys on bay islands. Operated outboard motorboat in S.F. Bay estuaries and sloughs.
- Assisted with winter Clapper Rail surveys for the U.S.F.W.S.
- Snowy Plover surveys; Botulism monitoring surveys with outboard motorboat.
- Liaison with Partners In Flight; participated in working group meetings; wrote the Brown Creeper species account for the Coniferous Forest Bird Conservation Plan and presented data.

Field Biologist, Rufous-Crowned Sparrow Study, Mar.-July 1997.

Dartmouth College, Environmental Science Program, 6182 Steele hall, Hanover, NH 03755

- Located nests, territory mapped, and conducted vegetation surveys for a study on the effect of fragmentation on breeding success.

Intern, Sept.-Nov. 1996.

Point Reyes Bird Observatory, 4990 Shoreline Hwy, Stinson Beach, CA 94970

- Operated mist nets, banded, aged and sexed birds; songbird surveys.
- Seabird surveys post oil spill.

Field Assistant, June-July 1996.

U. C. Sagehen Field Station, c/o U.C. Santa Barbara, POB 359, Los Olivos CA

- Conducted nest searches, nest box monitoring, vegetation surveys, and mist-netting.

Field Assistant, Nov. 1995-Mar. 1996.

Center for Tropical Research, UCLA, 1609 Hershey Hall, Los Angeles, CA 90095

- Collected data on tree phenology, frugivore feeding surveys, and hornbill movement and home range (radio-telemetry).

Interpretive Sign Design, June-Aug. 1995.

San Francisco Recreation and Parks, McLaren Lodge, Golden Gate Park, S.F. CA 94117

- Designed 4 interpretive signs for Glen Canyon Park.

Research Assistant, Sept. '92-Sept. '95.

San Francisco State University, 1600 Holloway, S.F. CA 94132

- Designed and implemented study; conducted plant surveys pre and post burn; laboratory experiments on seed viability under moist and dry conditions; collected and analyzed data; wrote thesis.

TEACHING EXPERIENCE

Teaching Assistant, Jan. 1994-June 1995.

San Francisco State University, 1600 Holloway, S.F. CA 94132

- Introductory Biology, Fall and Spring 1995.
- World of Plants, Spring 1994.

Environmental Education Instructor, Sept. 1987-May 1990.

Headlands Institute, GGNRA, Sausalito, CA 94965

- Developed and presented environmental education programs to students from Kindergarten to High School and adult programs.

MANUSCRIPTS

Le Fer, D. and V. T. Parker. 2005. The effect of seasonality of burn on seed germination in chaparral: the role of soil moisture. *Madrono* 52: 166-174.

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Le Fer, D. and J. D. Fraser. Piping Plover Foraging Ecology in the Great Plains. Annual Reports, 2001-2003. Prepared for the U.S. Army Corps of Engineers, Yankton, SD.

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Le Fer, D. Seasonal Variation in Virginia Rail and Sora Relative Densities in Tidal Marshes of Santa Clara County. March 2000. SFBBO. Report to the Santa Clara Valley Water District, CA.

PROFESSIONAL PRESENTATIONS

Danielle Le Fer, G. J. McChesney; M. W. Parker, H. R. Carter, and R. T. Golightly 2006. Factors influencing breeding phenology and productivity of Common Murres at Point Reyes, California.

Le Fer, D., J. D. Fraser and C. D. Kruse. 2003. "Variation in Piping Plover Foraging Site Quality in the Great Plains." Poster. American Ornithological Society, New Orleans, LA.

Le Fer, D., J. D. Fraser and C. D. Kruse. 2002. "Variation in Piping Plover Foraging Site Quality In the Great Plains." Annual meeting, Virginia Chapter of the Wildlife Society, Blacksburg, VA.

Le Fer, D., J. D. Fraser and C. D. Kruse. 2002. "Piping Plover Foraging Site Quality in Four Great Plains Habitats." North American Plover Species At Risk Conference, Ann Arbor, MI.

Le Fer, D., J. D. Fraser and C. D. Kruse. 2001. "Factors Affecting Piping Plover Foraging

Success and Reproductive Output in the Great Plains.” Missouri River Basin Piping Plover Working Group, Bismarck, ND.