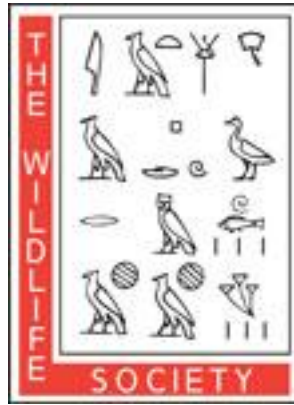


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# Piping Plover Chick Foraging, Growth, and Survival in the Great Plains

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**ABSTRACT** We tested the hypothesis that piping plover (*Charadrius melodus*) habitat quality and chick survival on the Missouri River, USA, were lower on a cold-water reservoir and downstream from a hypolimnetic (cold-water) release dam with diel water fluctuations (Garrison Dam) than downstream from an epilimnetic dam (Gavins Point Dam). Plovers in adjacent alkali wetlands provided an index to the maximum reproductive potential in the region. Chicks gained weight more rapidly in the alkali wetlands than on epilimnetic and hypolimnetic river reaches. Invertebrate numbers and biomass were higher in the wetlands and epilimnetic reach, but chick survival was lower on the epilimnetic reach. Thus, piping plovers adapted to a variety of prey densities, and other factors, likely predation, reduced survival rates in the epilimnetic reach. Temporal and spatial variability in site quality indices suggests the need for a regional management strategy with different strategies at each site. Managers can minimize effects of local fluctuations in resource abundance and predators by ensuring protection of or creating geographically dispersed habitat. (JOURNAL OF WILDLIFE MANAGEMENT 72(3):682–687; 2008)

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**KEY WORDS** *Charadrius melodus*, foraging, Great Plains, growth, habitat, hypolimnetic, invertebrates, Missouri River, piping plover, survival.

The Great Plains piping plover (*Charadrius melodus*) is threatened by low reproductive success and habitat loss (U.S. Fish and Wildlife Service [USFWS] 1985). From 1995 to 2000, the estimated fledging rate on the Missouri River, USA, was 0.62 fledglings per pair, with annual rates ranging from 0 chicks to 2.0 chicks per pair in different portions of the drainage (Niver 2000). Reproduction may be affected by predation, habitat loss, human disturbance, and water management (USFWS 1994). Additional data are needed to determine if piping plover (hereafter plover) reproduction is limited by prey abundance at breeding sites (USFWS 1994).

Positive relationships among prey abundance, chick foraging rates, and chick survival have been reported for plovers in other systems (Corn and Armbruster 1993, Loegering and Fraser 1995, Nordstrom and Ryan 1996, Goldin and Regosin 1998, Elias et al. 2000). Low food abundance may slow development, and chicks that fail to attain certain mass thresholds may not survive (Ricklefs 1983, Loegering and Fraser 1995, Reed et al. 1999).

We expected plover productivity to vary among sections of the Missouri River that were subject to different temperature and water flow regimes, thus affecting prey availability. Below the Garrison Dam, a hypolimnetic (cold-water release) dam, water height fluctuates daily. Increasing water output during peak energy demands (hydropeaking) may 1) lower invertebrate abundance by stranding macroinvertebrates or moving them downstream (invertebrate drift), 2) change habitat in the channel, and 3) reduce food needed by invertebrates (Gislason 1985, Troelstrup and Hergenrader 1990, Hesse and Mestl 1993, Moog 1993). Invertebrate densities also may be lower on hypolimnetic river reaches

due to changes in temperature and nutrients (Cushman 1985, Saltveit et al. 1994).

Our objectives were to determine whether invertebrate indices and plover reproductive success were lower on the reservoir and the hypolimnetic reach with diel water fluctuations than on the epilimnetic reach and the alkali wetlands and to examine the relationship between prey availability and chick growth and survival.

## STUDY AREA

We studied plovers on 3 stretches of the Missouri River (2 riverine and one reservoir) and in the alkali wetlands of North Dakota, USA, from 2001 to 2003. Missouri River sites were the Gavins Reach (9 islands) in South Dakota, USA, downstream of the Gavins Point Dam (Gavins; 42°78'N, 97°15'W), the Garrison Reach (4 islands) downstream of the Garrison Dam (Garrison; 47°28'N, 101°09'W), and Lake Sakakawea (4 sections of shoreline) upstream of the Garrison Dam in North Dakota (47°59'N, 101°34'W). Water is released from the bottom of the Garrison Dam (hypolimnetic), resulting in cold water in the Garrison Reach (Jun temp approx. 11° C; U.S. Geological Survey [USGS] 2006), whereas water is released near the top of the Gavins Dam (epilimnetic), resulting in warmer water (Jun temp approx. 22° C; USGS 2006) in the Gavins Reach. Garrison is a hydropeaking dam with diel flow patterns. In the alkali wetlands, we observed broods on the Williams Nature Conservancy Preserve (3 lakes; 47°52'N, 100°77'W), and on private land monitored by the Audubon National Wildlife Refuge (3 lakes; 48°13'N, 101°41'W).

## METHODS

### Invertebrate Numbers and Biomass

We collected indices of invertebrate abundance every 8 days after chicks hatched. We placed paint stirrers coated with

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Tanglefoot Insect Trap Coating (The Tanglefoot Company, Grand Rapids, MI) in each habitat along transects on each territory. Transects were 50 m long, perpendicular to the water's edge, and bisected the area used for foraging during a 5-minute observation preceding invertebrate sampling. We placed stirrers in pairs 5 cm apart, one stirrer vertical in the sand with tanglefoot on both sides and one horizontal on the ground with tanglefoot on the upward side. The catch area for the traps was 64.5 cm<sup>2</sup> (21.5 cm × 3 cm) for the horizontal stick and 129 cm<sup>2</sup> for the vertical stick. We sampled invertebrates in saturated, moist, dry, and vegetated habitats for 30 minutes. We placed chicken-wire cages (diam = 0.5 m, ht = 0.6 m, mesh size = 2.5 cm) around each pair of stirrers to prevent bird injury. We counted, measured, and identified invertebrates to order. We estimated biomass (mg dry wt) using an equation developed for a variety of invertebrates (dry wt [mg] = 0.0305 × length [mm]<sup>2.62</sup>; Rogers et al. 1976). We estimated the invertebrate biomass consumed by chicks (mg/min) at each site (biomass consumption index = mean individual invertebrate biomass [mg] × foraging rate [no. pecks/min]). We assumed that the proportion of pecks resulting in a capture was 100% and was the same in all habitats.

### Chick Foraging Rates, Growth Rates, and Survival

We attempted to observe chicks every 4 days until they were 22 days old or we observed them flying. We considered chicks fledged if they were alive at ≥18 days, based on the youngest chicks we observed flying and on other Great Plains studies (Haig 1992, Murphy et al. 2001). We searched islands for adults and chicks by walking the shoreline and the interior. We considered chicks <18 days old dead if we failed to find them on 2 consecutive visits.

Beginning on hatch day, we caught chicks every 4 days using butterfly nets, and weighed them (±0.1 g) on an electric scale (Ohaus Corporation, Florham, NJ). We color-banded chicks with one color band on the tarsus to identify individuals within a brood. We estimated daily survival rates for chicks accounting for dependence within broods (Flint et al. 1995). Every 4 days, we recorded individual chick foraging rates (pecks/min) and proportion of time chicks spent foraging during a 2-minute interval (Loefering and Fraser 1995).

### Statistical Analyses

We compared invertebrate indices among sites and years with a 2-way analysis of variance (ANOVA) on ranks, followed by a pair-wise comparison with Fisher's Least Significant Difference test if we found significant differences (Akritas et al. 1997). When we found significant differences or interactions among years and sites, we analyzed effects of year and site separately.

We calculated chick growth rates for each site with a regression of the natural log of mean brood mass on age (days). We compared the slopes of the growth rates (mass) among sites using linear regression with indicator variables for the sites. We compared daily survival rates among sites and years with a 2-way ANOVA. We calculated brood

mean weight for chicks (age 4–5 days and 8–9 days) and compared mass of chicks that survived with mass of chicks that died with a 2-tailed *t*-test. We examined the relationship between chick daily survival rates and invertebrate indices (invertebrate no., invertebrate biomass, biomass consumption index [mg/min], Coleoptera biomass) with a Spearman rank correlation. We used SAS for statistical analyses (SAS Institute Inc., Cary, NC). We report means ± standard error.

## RESULTS

### Invertebrate Numbers and Biomass

In all years, invertebrate biomass was higher ( $P < 0.001$ ) at the alkali wetlands (22.2 mg) and Gavins (15.4 mg, epilimnetic river reach) than at Garrison (4.1 mg, hypolimnetic river reach; Table 1). Invertebrate biomass at the epilimnetic site was higher ( $P < 0.05$ ) in 2001 (24.9 mg) and 2002 (17.2 mg) than in 2003 (1.2 mg); invertebrate biomass at Sakakawea (reservoir) was higher ( $P < 0.05$ ) in 2001 (15.7 mg) than in 2002 (4.8 mg) and 2003 (1.3 mg; Table 1). The greater biomass at the alkali wetlands and the epilimnetic site was driven primarily by greater numbers of invertebrates at those sites, but in 2002 and 2003, mean size of captured invertebrates was larger at the epilimnetic site (Table 1). Coleoptera (beetles) contributed disproportionately to the biomass at the epilimnetic site in 2001 (12.8 mg) and 2002 (10.5 mg), but coleopteran biomass decreased ( $P < 0.05$ ) there in 2003 (1.5 mg; Table 1).

### Chick Foraging Rates, Growth Rates, and Survival

Foraging rates and proportion of time spent foraging were similar across years and within sites (Le Fer 2006). Chick foraging rates were higher for chicks 3–10 days old ( $P = 0.02$ ) and 11 days to fledging ( $P = 0.004$ ) at the hypolimnetic site than at other sites (Table 2). Chicks 3–10 days old at the alkali wetlands spent less time foraging (0.43,  $P = 0.002$ ) than did chicks at the hypolimnetic site (0.69), epilimnetic site (0.78), and reservoir (0.64); chicks 11 days to fledging at the alkali sites (0.51) and the reservoir (0.53) spent less time foraging ( $P = 0.007$ ) than did chicks at the hypolimnetic (0.82) and epilimnetic (0.83) river sites (Table 2). In 2001–2003, the biomass consumption index was lower ( $P = 0.001$ ) for chicks age 3–10 days at the alkali wetlands (5.0 mg/min) than on the Missouri River (hypolimnetic: 9.7 mg/min; epilimnetic: 10.6 mg/min; reservoir: 6.2 mg/min); for chicks 11 days old to fledging, the biomass consumption index was lowest ( $P = 0.001$ ) at the alkali wetlands (5.6 mg/min) and the reservoir (9.6 mg/min; hypolimnetic: 2.6 mg/min; epilimnetic: 1.7 mg/min; Table 2).

Combining all years, chicks gained mass more rapidly ( $P < 0.001$ ) at the alkali wetlands (slope = 0.081) than at the epilimnetic (0.077) or hypolimnetic (0.076) sites (Table 3; Fig. 1). In 2001 ( $P < 0.001$ ) and 2002 ( $P < 0.001$ ), chick growth rates were higher at the epilimnetic (2001: slope = 0.092; 2002: slope = 0.081) than at the hypolimnetic site (2001: slope = 0.078; 2002: slope = 0.076; Table 3; Fig. 1). In 2003 ( $P < 0.001$ ), mass growth rates were highest at the

**Table 1.** Mean invertebrate biomass (mg dry wt), invertebrate numbers, Coleoptera biomass (mg), Coleoptera numbers  $\pm$  standard error per set of sticky traps, and individual invertebrate biomass (mg) in saturated and moist habitats during the chick-rearing period. We collected invertebrates in North and South Dakota, USA, 2001–2003, on paint stirrers covered with Tanglefoot insect coating and placed for 30 minutes. If global model was significant, we show main effects.

Site	2001			2002			2003			2001–2003		
	<i>n</i>	$\bar{x}$	SE	<i>n</i>	$\bar{x}$	SE	<i>n</i>	$\bar{x}$	SE	<i>n</i>	$\bar{x}$	SE
Invertebrate biomass <sup>a</sup>												
Alkali	7	35.9 A <sup>b</sup>	17.4	8	40 A	12.9	8	9.5 A	2.4	23	22.2 A	6.1
Hypolimnetic	6	5.3 B	1.4	10	4.5 B	1.4	8	2.9 B	0.3	24	4.1 C	0.7
Epilimnetic	8	24.9 Aa <sup>c</sup>	4.9	11	17.2 Aa	3.7	9	6 Ab	1.2	28	15.4 A	2.3
Reservoir	7	15.7 Ba	5.4	10	4.8 Bb	1.3	4	4 ABb	1.3	21	8.3 B	2.2
Invertebrate no. <sup>d</sup>												
Alkali	7	29.3 Aab	7.3	8	49.8 Aa	15.5	8	12.9 b	3.7	23	30.7 A	6.6
Hypolimnetic	6	4.5 C	0.8	10	5.9 C	1	8	7	1.2	24	5.9 C	0.6
Epilimnetic	8	11.9 ABa	1.4	11	13.8 Ba	3.6	9	5.1 b	0.7	28	10.5 B	1.6
Reservoir	7	10.7 Ba	2.7	10	8.2 BCb	1.4	4	7.6 b	3	21	8.9 BC	1.2
Coleoptera biomass <sup>e</sup>												
Alkali	7	0.4 B	0.2	8	0.1 B	0	8	0	0	23	0.2 B	0.1
Hypolimnetic	6	0.7 B	0.6	10	1.2 B	1.1	8	0.2	0.1	24	0.8 B	0.5
Epilimnetic	8	12.8 Aa	4.4	11	10.5 Aa	3.5	9	1.5 b	0.5	28	8.3 A	2.1
Reservoir	7	2 B	1.6	10	0.5 B	0.5	4	0.1	0	21	0.9 B	0.6
Coleoptera no. <sup>f</sup>												
Alkali	7	0.2 BC	0.1	8	0.1 B	0.1	8	0.1	0.1	23	0.2 B	0
Hypolimnetic	6	0.1 C	0	10	0.1 B	0.1	8	0.1	0	24	0.1 B	0
Epilimnetic	8	2.3 Aa	0.6	11	1.1 Aab	0.3	9	0.7 b	0.3	28	1.3 A	0.3
Reservoir	7	1.6 B	1.1	10	0.2 B	0.1	4	0.3	0.2	21	0.7 B	0.4
Individual invertebrate biomass <sup>g</sup>												
Alkali	7	1.1 a	0.3	8	0.5 Bb	0.1	8	1 ABab	0.3	23	0.9 B	0.2
Hypolimnetic	6	1.3	0.3	10	1 B	0.4	8	0.5 C	0.1	24	0.9 B	0.2
Epilimnetic	8	2 a	0.2	11	1.6 Aab	0.4	9	1.2 Ab	0.2	28	1.6 A	0.2
Reservoir	7	1.5 a	0.2	10	0.6 Bb	0.1	4	0.7 BCb	0.3	21	0.9 B	0.1

<sup>a</sup> Invertebrate biomass = sum of individual invertebrate biomass trapped/30 min. Analysis of variance (ANOVA) on ranks: site:  $F_{3,95} = 19.9$ ,  $P < 0.001$ ; yr:  $F_{2,95} = 15.2$ ,  $P < 0.001$ ; site  $\times$  yr:  $F_{6,95} = 1.4$ ,  $P = 0.21$ .  
<sup>b</sup> Site means with the same letter within columns are not significantly different ( $\alpha = 0.05$ ).  
<sup>c</sup> Site means with the same letter within rows are not significantly different ( $\alpha = 0.05$ ).  
<sup>d</sup> ANOVA on ranks: site:  $F_{3,95} = 13.1$ ,  $P < 0.001$ ; yr:  $F_{2,95} = 2.9$ ,  $P = 0.06$ ; site  $\times$  yr:  $F_{6,95} = 2.7$ ,  $P = 0.02$ .  
<sup>e</sup> ANOVA on ranks: site:  $F_{3,95} = 17.5$ ,  $P < 0.001$ ; yr:  $F_{2,95} = 3.3$ ,  $P = 0.04$ ; site  $\times$  yr:  $F_{6,95} = 0.66$ ,  $P = 0.7$ .  
<sup>f</sup> ANOVA on ranks: site:  $F_{3,95} = 20.3$ ,  $P < 0.001$ ; yr:  $F_{2,95} = 2.1$ ,  $P = 1.3$ ; site  $\times$  yr:  $F_{6,95} = 1.1$ ,  $P = 0.36$ .  
<sup>g</sup> Individual invertebrate biomass = sum of individual invertebrate biomass/no. individuals. ANOVA on ranks: site:  $F_{3,95} = 13.9$ ,  $P < 0.001$ ; yr:  $F_{2,95} = 14.5$ ,  $P < 0.001$ ; site  $\times$  yr:  $F_{6,95} = 1.6$ ,  $P = 0.15$ .

**Table 2.** Mean foraging rates (pecks/min), proportion of time foraging, and estimated biomass consumed (mg/min)  $\pm$  standard error for piping plover chicks aged day 3–10 and day 11 to fledging, in North and South Dakota, USA, 2001–2003. Results of analysis of variance (ANOVA) on ranks comparing sites.

Site	Day 3–10			Day 11–fledge		
	<i>n</i>	$\bar{x}$	SE	<i>n</i>	$\bar{x}$	SE
Foraging rate <sup>a</sup>						
Alkali	21	5.8 B <sup>b</sup>	0.9	15	6.5 B	1.5
Hypolimnetic	16	10.8 A	1.9	11	14.2 A	1.3
Epilimnetic	21	6.7 B	0.7	14	9.2 B	0.7
Reservoir	13	7.2 B	1.3	4	8.4 B	3.4
Proportion of time foraging <sup>c</sup>						
Alkali	21	0.43 B	0.06	19	0.51 B	0.09
Hypolimnetic	16	0.69 A	0.07	12	0.82 A	0.05
Epilimnetic	21	0.78 A	0.06	14	0.83 A	0.04
Reservoir	13	0.64 A	0.08	5	0.53 B	0.18
Biomass consumption index <sup>d</sup>						
Alkali	21	5 C	1	15	5.6 B	1.2
Hypolimnetic	16	9.7 AB	2.1	11	12.7 A	2.6
Epilimnetic	21	10.6 A	1.2	14	15.1 A	1.7
Reservoir	13	6.2 BC	0.9	4	9.6 B	1.8

<sup>a</sup> ANOVA on ranks: day 3–10:  $F_{3,70} = 3.3$ ,  $P = 0.02$ ; day 11 to fledge:  $F_{3,43} = 5.1$ ,  $P = 0.004$ .  
<sup>b</sup> Site means with the same letter within columns are not significantly different ( $\alpha = 0.05$ ).  
<sup>c</sup> ANOVA on ranks: day 3–10:  $F_{3,70} = 5.4$ ,  $P = 0.002$ ; day 11 to fledge:  $F_{3,49} = 4.7$ ,  $P = 0.007$ .  
<sup>d</sup> Biomass consumption index = average invertebrate individual biomass  $\times$  foraging rate; ANOVA on ranks: day 3–10:  $F_{3,70} = 3.9$ ,  $P = 0.001$ ; day 11 to fledge:  $F_{3,43} = 5.9$ ,  $P = 0.001$ .



**Table 3.** Slopes of regressions of natural log of mass of piping plover chicks on age in days at 4 sites in North and South Dakota, USA, in 2001–2003. Mass was the mean mass of surviving chicks in each brood for each chick age.

Site	2001–2003 <sup>a</sup>		2001 <sup>b</sup>		2002 <sup>c</sup>		2003 <sup>d</sup>	
	Slope	SE	Slope	SE	Slope	SE	Slope	SE
Alkali	0.081 A <sup>e</sup>	0.002	0.086 AB	0.004	0.079 AB	0.002	0.083 A	0.002
Hypolimnetic	0.076 B	0.001	0.078 B	0.003	0.076 B	0.002	0.077 B	0.002
Epilimnetic	0.077 B	0.001	0.092 A	0.003	0.081 A	0.002	0.067 C	0.002
Reservoir	0.078 AB	0.002	0.08 B	0.005	0.078 AB	0.002	0.075 B	0.003

<sup>a</sup>  $F_{3,581} = 1641, P < 0.001$ .  
<sup>b</sup>  $F_{3,148} = 481, P < 0.001$ .  
<sup>c</sup>  $F_{3,237} = 738, P < 0.001$ .  
<sup>d</sup>  $F_{3,196} = 747, P < 0.001$ .  
<sup>e</sup> Sites with the same letter within yr (columns) are not significantly different ( $\alpha = 0.05$ ).

alkali wetlands (0.083) and lowest at the epilimnetic site (0.067; Table 3).

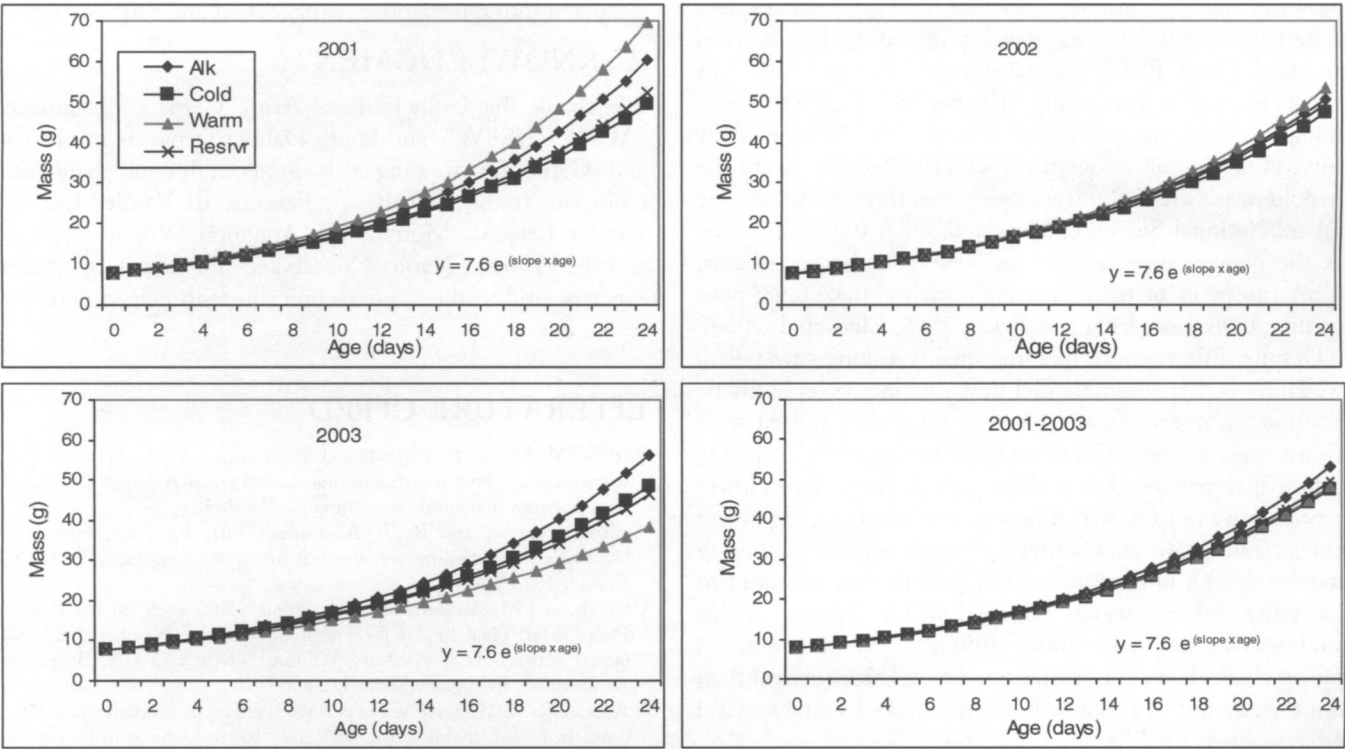
Chick daily survival rates for the 3 years pooled were higher ( $P = 0.03$ ) at the hypolimnetic (0.985) than at the epilimnetic (0.853) site (Table 4). There was no site  $\times$  year interaction. Chicks that survived to fledging were heavier at age 4–5 days and 8–9 days than were chicks that did not fledge (4–5 days:  $9.5 \pm 0.2$  g, vs.  $8.3 \pm 0.2$  g,  $t_{125} = -3.9, P < 0.001$ ; 8–9 days:  $16.0 \pm 0.3$  g, vs.  $14.2 \pm 0.6$  g,  $t_{105} = 2.1, P = 0.04$ ).

There was no relationship between chick daily survival rates and invertebrate numbers or biomass, Coleoptera biomass, or biomass consumption index (Spearman rank correlation, invertebrate no.:  $r_s = -0.09, P = 0.4, n = 90$ ; invertebrate biomass:  $r_s = -0.15, P = 0.16, n = 90$ ;

Coleoptera biomass:  $r_s = -0.05, P = 0.61, n = 90$ ; biomass consumption index:  $r_s = 0.1, P = 0.4, n = 67$ ).

DISCUSSION

Warm water temperatures, variation in water temperature, less scouring flows, lack of diel water fluctuations, habitat, or food differences may explain the greater number of invertebrates in the epilimnetic river reach (Cushman 1985, Troelstrup and Hergenrader 1990, Hesse and Mestl 1993, Moog 1993, Saltveit et al. 1994). 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). In addition, cold water releases downstream of dams may affect



**Figure 1.** Predicted piping plover chick growth curves for body mass (g) at 4 sites in North and South Dakota, USA, 2001–2003, and years pooled. Mass was the mean mass within broods (Alk = Alkali,  $n = 69$  chicks; Cold = hypolimnetic,  $n = 78$  chicks; Warm = epilimnetic,  $n = 104$  chicks; Resrvr = Reservoir,  $n = 64$  chicks).

**Table 4.** Piping plover mean chick daily survival rates  $\pm$  standard error in North and South Dakota, USA, 2001–2003. Results of 2-way analyses of variance comparing daily survival rates among sites.<sup>a</sup> Sample size is the number of broods.

Site	<i>n</i>	$\bar{x}$	SE
Alkali	23	0.932 AB <sup>b</sup>	0.024
Hypolimnetic	22	0.985 A	0.005
Epilimnetic	29	0.853 B	0.042
Reservoir	20	0.923 AB	0.025

<sup>a</sup> Site:  $F_{3,94} = 3.25$ ,  $P = 0.03$ ; yr:  $F_{2,94} = 0.01$ ,  $P = 0.99$ ; site  $\times$  yr:  $F_{6,94} = 0.97$ ,  $P = 0.45$ .

<sup>b</sup> Sites with the same letter are not significantly different ( $\alpha = 0.05$ ).

invertebrate abundance and composition (Hesse and Mestl 1993). Invertebrate indices varied spatially and temporally. Thus, geographic dispersion of habitats may minimize plover population effects of local fluctuations in resource abundance.

Chick growth rate differences among sites reflected trends in invertebrate numbers. Higher chick growth rates at the alkali wetlands, compared with other habitats with higher biomass consumption indices and proportion of time spent foraging, may be due to differential success rates for prey capture across habitats or that more time spent foraging increases energetic requirements.

Chicks that were larger at early stages (4–5 days and 8–9 days old) were more likely to survive to fledging. Larger chicks may have higher endurance and less likelihood of predation than smaller chicks if their development is similar to king eider (*Anas spectabilis*) ducklings (Anderson and Alisauskas 2001). However, chick size at 4–5 days and 8–9 days did not vary among sites and, thus, did not explain differential survival among sites. Piping plover chick survival at other Great Plains sites also varied locally (0.60–1.16 chicks/pair) and temporally (Knetter et al. 2002). Even though chicks in the Great Plains were heavier, daily survival rates at all of our study sites (0.92–0.93) except the hypolimnetic site (0.99) were lower than those at Assateague Island National Seashore, Maryland, USA (0.96) and even at the poor-quality habitats on New York barrier islands, USA (no pools or tidal flats; high quality: 0.97–0.98; poor quality: 0.96; Loegering and Fraser 1995, Elias et al. 2000).

Despite differences in foraging quality among sites (alkali wetlands vs. hypolimnetic diel flow riverine, vs. epilimnetic riverine, vs. reservoir), and between these sites and Atlantic Coast sites, we did not find evidence that poorer site quality (fewer invertebrates, lower chick growth rates) led to lower reproductive output, which may be because 1) piping plover chicks can grow at a variety of rates without suffering mortality; 2) a lower threshold of growth that may lead to mortality was not widely achieved within habitats in our study (Loegering and Fraser 1995); or 3) predation on plover chicks had a far greater impact on chick survival than did the amount of available food and masked subtle survival effects caused by differential nutrition.

Decreasing predation pressure at the alkali wetlands and the epilimnetic site may increase productivity at these sites (Smith et al. 1993, Murphy et al. 2003). In our study, sites

with higher frequencies of predator tracks (mammal and gull) did not have lower chick survival (Le Fer 2006). However, other studies have indicated that avian predators, notably American kestrels (*Falco sparverius*) and great horned owls (*Bubo virginianus*) have important impacts on plover chick survival in the Great Plains (Kruse et al. 2001, Knetter et al. 2002). Although we did not quantify the presence of raptors, in 2002 and 2003 we found dead adult plovers at the epilimnetic site, decapitated, and with wings removed, suggesting predation by raptors.

## MANAGEMENT IMPLICATIONS

Spatial and temporal variability in site quality indices and predation pressure among the 4 sites and the fact that Great Plains piping plover numbers vary across habitat types from year to year depending on conditions (e.g., weather, hydrological conditions and cycles, and management impacts; Haig and Oring 1988a, b; Murphy et al. 2001; Knetter et al. 2002; Haig et al. 2005), suggests the need for a regional management strategy. Maintaining and creating nutrient-rich foraging habitat on sandbars and reservoir shoreline should be an important part of piping plover management in the Great Plains (USFWS 2003). A combination of lower summer flows that expose more shoreline, early spring flows that help create new nutrient-rich sandbar habitat, and engineering of new habitat are all positive options for maintaining or creating critical piping plover habitat. In addition, adjusting diel flow patterns to minimize impacts on invertebrates may increase site quality at the hypolimnetic site (Gislason 1985). The long-term relative value of each of these processes needs to be evaluated through adaptive management and further studies.

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