Population Demography of the Great Lakes Piping Plover

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Dedication

To the Piping Plovers.

Abstract

The Piping Plover (*Charadrius melodus*) is a rare shorebird currently restricted to three isolated nesting populations in the Great Lakes, Great Plains, and Atlantic Coast of North America; the Great Lakes population is federally endangered, numbering only 17 breeding pairs when listed in 1986. Once a population is already small, as most endangered populations are, random events such as severe weather or loss of genetic diversity caused by mating between closely related individuals can have a pronounced effect on population persistence. To reverse small population size, researchers must focus on determining the original and ongoing causes of population decline as well as developing an understanding of how small size influences existing population dynamics. In my dissertation, I assess the degree to which external factors have contributed to the currently small size of the Great Lakes population by identifying sources of mortality for adult Piping Plovers throughout the annual cycle (Chapters 1 & 2). In addition, I examine the influence of traits resulting from the small size of the Great Lakes population and may reinforce its imperiled status, including the degree of inbreeding depression (Chapter 3) as well as age-dependent survival and reproduction (Chapter 4). Finally, I assess the effectiveness of a conservation technique used to augment Great Lakes population size: the salvage and captive-rearing of abandoned eggs (Chapter 5). The questions posed in my dissertation are ones commonly asked by professionals responsible for the conservation of Piping Plovers. The answers to these questions are intellectually

interesting, but far greater value comes from the fact that they are relevant to on-the-ground conservation efforts. Implementing informed conservation strategies will not only support population growth in the Great Lakes, but is also widely applicable to shorebird species throughout North America.

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Preface

Once a population is already small, random events such as severe weather or lack of genetic diversity (caused by mating between closely related individuals) can have pronounced effects on population persistence. Understanding how small size influences population dynamics is imperative to designing effective conservation strategies and may guide use of techniques (e.g. captive-rearing) to alleviate small size and inbreeding depression (Caughley 1994). To reverse small population size, investigators must focus on determining the original and ongoing causes of population decline (Caughley 1994). To reverse small population size, researchers must focus on determining the original and ongoing causes of population decline (Caughley 1994). Population change results from four factors: birth, death, emigration and immigration. Despite their documented importance to population dynamics(Sæther and Bakke 2000), the influence of immigration/emigration and survival are challenging to measure because both require a population of marked individuals. With > 80% of breeding adults uniquely banded and a population size of < 75 breeding pairs, the Great Lakes piping plover (*Charadrius melodus*) population has offered a unique opportunity to investigate the influence of both factors.

This dissertation is composed of five separate investigations into the causes of small population size in the Great Lakes Piping Plover. Chapters 1 and 2 investigate some of the forces that may be reinforcing the small size of the Great Lakes population; specifically, the relation of nest abandonment to adult mortality and the influence of seasonality on annual survival. Chapters 3 and 4 address the influence of inbreeding depression and age-dependent survival and reproduction onthe persistence of the Great Lakes population. Finally, chapter 5 assesses the effectiveness of the salvage captive-rearing program that has been used to recover the Great Lakes Piping Plover population since 1992. Existing knowledge of population range and individual dispersal within the Great Lakes provides a unique opportunity to explore questions of small population dynamics. The questions posed in this dissertation are ones commonly asked by professionals responsible for the conservation of endangered species, and while the answers to these questions are intellectually interesting, far greater value comes from the fact that they are relevant to on-the-ground conservation efforts for piping plovers and other similar species.

This dissertation is not written in the first person, as it is a compilation of five manuscripts already published, submitted, or intended for publication. As such, the formats of the five chapters differ slightly according to the requirements of the journals for which they were intended. Chapter 1, “Apparent nest abandonment as evidence for breeding season mortality in Great Lakes Piping Plovers”, was published in the journal *The Auk* in 2010. Chapter 5, “Relative fitness of wild and captive-reared Piping Plovers: does egg salvage contribute to recovery of the endangered Great Lakes population?” was published in the journal *Biological Conservation* in 2008. Chapter 3, “Minimal Evidence for Inbreeding Depression in an Endangered Population of Piping Plovers (*Charadrius melodus*)”, was recently submitted to the journal *The Proceedings of the Royal Society: Biological Sciences*. Chapter 2, “Partitioning the annual survival of Great Lakes Piping Plovers”, and Chapter 4, “Age dependent survival and reproduction in Piping Plovers” are intended for publication in the *Journal of Animal Ecology* and *Ecology* respectively.

Chapter 1

Apparent nest abandonment as evidence for breeding season mortality in Great Lakes Piping Plovers

NESTING STUDIES TYPICALLY recognize three principle nest fates: successful, depredated, or abandoned (Arnold et al. 1995, Ackerman et al. 2003, Bonnot et al. 2008). Abandonment is usually defined as lack of parental attendance of an otherwise intact clutch or healthy brood and is interpreted as a behavioral decision to cease parental investment (Székely et al. 1996, Ackerman et al. 2003). This decision may be motivated by declining parental condition (Arnold et al. 1995), poor coordination of incubation relief between pair members (Cézilly 1993), perceived predation risk (Holt 1994), partial clutch or brood loss (Székely and Cuthill 2000, Ackerman et al. 2003), opportunities for additional matings (van Dijk et al. 2007), competition for nest sites (Hötker 2000), conspecific brood parasitism (Nielsen et al. 2006), interspecific brood parasitism (Hosoi and Rothstein 2000), ectoparasitism (Norcross and Bolen 2002), inclement weather (Simeone et al. 2002), or investigator disturbance (Thorn et al. 2005). Another potential explanation for nest abandonment is parental mortality, wherein lack of nest attendance or brood care is not a behavioral decision but an inevitable consequence of mortality to an attendant adult. However, this source of abandonment has only been acknowledged anecdotally (e.g., Yorio and Boersma 1994, Wiktander et al. 2001, Cohen et al. 2006). A notable exception was Neuman et al. (2004), who used nest-monitoring histories from a color-banded population of Snowy Plovers (*Charadrius alexandrinus*) to infer that approximately 40% of nest abandonments involved the death of an attendant adult. Here we combine long-term nest-monitoring data with formal mark-resighting analyses to show that parental mortality is indisputably the most common cause of clutch abandonment in Great Lakes Piping Plovers (*Charadrius melodus*).

Conservation efforts for the Piping Plover have historically concentrated on fecundity rather than adult survival (Larson et al. 2002, Elliott-Smith and Haig 2004). In the Great Lakes, Piping Plover nesting beaches have been regularly monitored to record the identity of color-marked plovers, identify nesting distributions, facilitate nest site protection, and collect data on annual reproduction (U.S. Fish and Wildlife Service 2003). Regular site visits have allowed monitors to rapidly identify cases of clutch abandonment and collect unattended clutches for captive-rearing(Powell et al. 1997, Roche et al. 2008). However, if clutches were unattended due to mortality of adult plovers, then the true costs associated with abandonment were much higher than the loss of a single clutch. Because most adult plovers were uniquely banded and conspicuously visible in open beach habitats, monitors were able to distinguish between nest abandonments where both adult plovers were still known to be alive (i.e., nest desertion) versus cases where one or both of the attendant adults were no longer present at the breeding site (i.e., potential disappearance). However, disappearance of a nesting plover does not necessarily imply mortality; these events could represent detection failure or temporary emigration rather than mortality (Dinsmore 2008). Distinguishing among these different possibilities is important for understanding the demographic consequences of nest abandonment.

To determine if disappearances were caused by detection failure, we conducted a detailed analysis of within-season detection probabilities for uniquely banded plovers during the 2008 breeding season to determine if plovers remained at local nesting sites but managed to avoid detection. We conducted an among-year (1993-2008) mark-resighting study to determine if disappearing plovers were dying or temporarily emigrating from the breeding grounds. To further explore whether nest failures caused by the disappearance of a nesting adult could be attributed to breeding season mortality, we assessed the influence of all types of Piping Plover nest failure on subsequent apparent survival of the affected adults. Finally, we characterized the sex and age distributions of nesting versus disappearing plovers and identified the timing and potential causes of adult disappearances associated with nest abandonment.

METHODS

*Study area***—**In recent years, Great Lakes Piping Plovers have nested along the lower and upper peninsulas of Michigan; Long Island, Wisconsin; and the Bruce Peninsula of Ontario, Canada (U.S. Fish and Wildlife Service 2003). For our among year mark-recapture analysis we used plovers banded throughout this entire region from 1993 – 2008. In 2008, daily or near-daily monitoring at 13 separate nesting sites facilitated estimation of breeding season detection probabilities (Fig. 1).

Monitoring Efforts—Surveys for Great Lakes plovers were conducted by local volunteers beginning in late April at contemporary nesting locations throughout Michigan. By mid-May Piping Plover monitors working for participating governmental, non-profit, and educational institutions began daily surveys of contemporary and historical nesting habitat throughout the region. When pairs with nests were discovered, nesting habitat was protected via partial beach closures (Melvin et al. 1991) and nests were protected with covered wire exclosures (Rimmer and Deblinger 1990, Melvin et al. 1992). Nests were monitored regularly throughout incubation and nest fates were recorded as hatched (≥ one egg hatched), depredated (eggs missing or destroyed), abandoned (intact eggs no longer tended by adults), or flooded. Since 1993, nesting plovers have been captured during incubation using single-chambered Potter traps (Lincoln 1947) and banded with unique combinations of US Geological Survey (USGS) aluminum bands and Darvic (Avinet Inc., Dryden, NY, USA) color bands, which facilitated future identification of banded individuals without recapture. At most sites with nesting pairs, plover monitors made regular visits through mid-July to check on the status of nests and chicks and to confirm the identity of plovers observed at each location. Chicks were banded before fledging with USGS aluminum bands and up to three Darvic bands. If they survived and recruited into the breeding population, they were marked with a full combination of up to 5 color bands upon first recapture. Adults that were not recaptured retained chick bands, which allowed for limited ability to identify individuals based on resighting information (Roche et al. 2008).

Data Summary and Analyses—We reviewed nesting records from 1993-2007 and further categorized abandoned nests into two separate categories (Neuman et al. 2004): 1) nests that stopped being tended concurrent with the apparent disappearance or known death of one or both members of the nesting pair (disappeared), versus 2) nests that stopped being tended but both members of the breeding pair were subsequently observed alive (desertion). We used the following criteria to categorize nesting plovers as disappeared: 1) the discovery of dead plovers or body parts in the vicinity of the nest (n = 6), or 2) the continuous incubation of a nest by only one member of a known pair for several days without any relief or re-engagement in pair-formation behavior by the remaining member of the pair (n = 17). If both members of a pair were not observed on the beach during a site visit, Great Lakes monitors were tasked with remaining at a nest site to observe the nest until an incubation switch occurred. Monitors also recorded three suspicious disappearances that occurred during the pre-nesting period (after the pair had been observed copulating, scraping, and involved in other courtship activities) and five apparent brood abandonments that occurred during the first week after hatching (well before plovers typically abandon their broods), and we also coded these eight plovers as 'disappeared' for purposes of survival analysis. When monitors supplied potential explanations for the disappearance of adults we coded these as disease, predation, weather, or unknown.

To determine if plovers that had disappeared remained alive on the breeding grounds but were simply going undetected, we used a Cormack-Jolly-Seber recaptures-only model in Program MARK (White and Burnham 1999) to estimate the probability of detecting plovers during sub-intervals of the breeding season. Because plover monitors have not historically recorded band combinations throughout the entire breeding season, our analysis of within-season detection rates was limited to data provided by monitors working at 13 participating locations during 2008 where band combinations were recorded on a near daily basis (Fig. 1). We divided the 2008 breeding season into 10 detection periods spanning 12 April through 25 July; all detection periods comprised 10 days except the first period which comprised 15 days (12 – 26 April). If a plover was observed at least once within a detection period it was considered present for the entire period.

To account for heterogeneity in these data we treated each of the 13 monitoring locations as a separate attribute group and we added occasion-specific covariates representing varying levels of monitoring effort by location and period, differences in breeding status among individual plovers, and individual differences in band type. We measured monitoring effort as the number of days (*n*) that monitoring occurred at each site during each 10-day detection period, which we standardized to a value between -1 and 1. Breeding status of each plover during each detection period was coded as 1 if the plover was tending eggs or chicks at any time during this period and 0 if not. Plovers that initiated more than one nesting attempt were also considered to be breeding during their renesting intervals. Plovers carrying non-individualized combinations of chick bands were coded with band type= 0 whereas plovers with individual-specific adult combinations were coded as band type = 1. This distinction allowed us to test for decreased detection probability (p') of plovers marked with ambiguous band combinations and for differences in apparent survival (ϕ') caused by limited fidelity of non-nesting plovers to specific nesting habitats (we use p' and ϕ' to discriminate detection and apparent survival probabilities during 10-day periods in 2008 from p and φ, which represent annual detection and apparent survival probabilities). The complement to apparent survival ($1 - \phi'$) could represent either mortality or emigration from intensively monitored breeding sites, such as early migration to the wintering grounds.

We conducted 1,000 bootstrap simulations on the fully-temporal model [$\phi'(t)$, $p'(t)$] and obtained an estimate of overdispersion of $\hat{c} = 1.96$, which we used to rank models based on Akaike's Information Criterion as adjusted for sample size and overdispersion ($QAIC_c$; Burnham and Anderson 2002, Cooch and White 2008). Because monitoring effort remained constant throughout the breeding season and we had no a priori knowledge regarding timing of breeding season mortality or emigration, we built models beginning with the simplest possible model [$\phi'(.),p'(.)$] (Lebreton et al. 1992). We modeled all AHY plovers as a single age class and introduced increasing complexity by allowing either ϕ' or p' to vary among periods [e.g. $\phi'(t)$ or $p'(t)$]. After determining the best-supported temporal structure for ϕ' and p', we considered models with individual covariates for monitoring effort, breeding status, and band type by sequentially adding each covariate to the best-supported temporal model. These models allowed logit-transformed apparent survival and detection probabilities to vary as a linear function of the covariate(s).

We used banding and resighting data from 1993 – 2008 in a second Cormack-Jolly-Seber model to estimate the influence of each form of nest loss on apparent annual survival (ϕ) of AHY plovers. For this analysis, each annual breeding season represented a single occasion and individual birds were coded as detected if they were observed at any time during the breeding season. We conducted 1,000 bootstrap simulations using model [$\phi(t),p(t)$] and estimated $\hat{c} = 0.96$, which we left as 1 (Burnham and Anderson 2002, Cooch and White 2008). We assigned year-specific covariates indicating forms of nest loss experienced by each individual plover during each of the 1993 – 2007 breeding seasons: these included apparent disappearance of a nesting or brood-rearing plover (disappeared), mate of a plover that apparently disappeared (widowed), nest abandonment where both plovers were subsequently observed (deserted), nest loss due to flooding (flooded), or nest loss due to clutch predation (depredated). Plovers received a covariate value of 1 during years when they had a nest failure for one of these particular reasons; otherwise they received a covariate value of 0. As for the within-season analysis, we built models sequentially using the design matrix and beginning with the simplest possible model [$\phi(.),p(.)$]. We modeled all AHY plovers as a single age class and introduced increasing complexity by allowing φ and p to vary annually [i.e., $\phi(\mathrm{t})$ and $p(\mathrm{t})$]. We also considered models that allowed ϕor p to vary as a linear function of year (covariate: trend; (Dinsmore 2008)). After finding the best temporal structure for φ and p, we sequentially added year-specific covariates describing different forms of nest loss: disappeared, widowed, deserted, flooded, and depredated and retained any covariates that led to reductions in AIC_c (Burnham and Anderson 2002:131).

The age distribution of 297 nesting plovers with individual-specific band combinations was determined for each year from 1993 – 2007. If a plover was AHY when first banded (n = 99), we assumed it was one-year-old and incremented the age by one year for each subsequent breeding season (hence, these values represent minimum known ages). These distributions were summed across years to determine the frequency with which plovers aged 1 to 13 years old nested in the Great Lakes. The age distribution of the 31 plovers that disappeared were estimated similarly (19 were of known age), but were not partitioned by year. Age distributions of nesting and disappeared plovers were compared in aggregate and for each sex separately, using a Kolmogorov-Smirnov test in program R version 2.6.2 (CRANS 2006). We compared the sex ratio of disappeared plovers against a 50:50 distribution using a likelihood-ratio χ^2 test.

RESULTS

Approximately 16% of monitored clutches laid by Great Lakes plovers from 1993 – 2007 were lost prior to hatching (recall that virtually all nests were protected by predator exclosures). Abandonment was the most common cause of nest loss, comprising 50% of all nest losses, but predation (31%) and flooding (19%) were also important (Table 1). Among abandoned nests, 70% were abandoned concurrent with the disappearance of one or both members of the nesting pair, whereas 30% of abandonments appeared to be desertions based on subsequent resightings of both pair members. Predation and desertion occurred at consistently low levels each year, losses due to flooding tend to occur sporadically, and losses due to disappearances have become more common since 2002 (Table 1).

The best-approximating models of within-season resighting rates (p') included effects of time period, monitoring effort, and breeding status (Table 2). Resighting probability increased from late April through late May and remained high through late July (Fig. 2). The mean resighting rate for nesting plovers during 27 April to 15 July was $p' = 0.908$ (SE = 0.025) and for non-nesting plovers it was $p' = 0.791$ (SE = 0.045). There was ≥ 0.97 probability of resighting a nesting plover at least once if it was still alive and remained on the nesting grounds for ≥ 20 days following nest failure and ≥ 0.92 probability if it remained on the breeding grounds for ≥ 10 days, except at the very beginning or end of the nesting season. Cumulative resighting probability was somewhat lower for non-nesting plovers, but exceeded 0.95 for plovers remaining on the breeding grounds for ≥ 20 days, except near the very beginning or end of the nesting season.

The best-approximating model of apparent annual survival included linear trends for both survival and detection probability and individual covariates for plovers that disappeared or deserted their nests (Table 3). Detection probability averaged 0.939 and increased over time, ranging from 0.851 (SE = 0.047) in 1994 to 0.986 (SE = 0.006) in 2008. Apparent survival exhibited a negative trend over time (Fig. 3; $\beta_T = -0.066$, SE = 0.021). None of the 31 AHY plovers coded as disappeared were ever observed again and model-based estimates of their survival were < 0.001. Estimated annual survival of plovers that deserted their nests was 0.570 (SE = 0.019), whereas plovers that did not desert or disappear during nesting had apparent annual survival of 0.771 (SE = 0.013). There was no evidence that plovers whose mates disappeared or lost nests to flooding or predation experienced lower apparent survival. To estimate the amount of annual mortality associated with nest abandonment we solved the top-approximating model at observed mean annual values for proportions of plovers that disappeared and deserted and we compared these to model-based estimates where we set these covariate values to 0 (Fig.3). Suspected causes of disappearance included 19 losses to avian predators, 2 cases of botulism, 1 weather-related mortality (a hailstorm), and 9 unknown causes, with Merlins (*Falco columbarius*) implicated as the likely avian predator in 15 cases.

The age distribution of plovers that disappeared differed significantly from that of plovers nesting in the Great Lakes from 1993 – 2007, ($P < 0.01$, two-sided Kolmogorov-Smirnov test). The median age of nesting males and females was 3.0 years of age (Fig. 4a); whereas the median age of males and females that disappeared was 5.0 ($P = 0.01$, one-sided Kolmogorov-Smirnov test) and 3.5 years ($P = 0.02$, one-sided Kolmogorov-

Smirnov test), respectively (Fig. 4b). Females tended to disappear more often than males (20/146 vs. 11/151; likelihood-ratio $\chi^2 = 2.69$, $P = 0.10$).

DISCUSSION

Our study demonstrated that most nest failures of Great Lakes Piping Plovers attributed to abandonment during 1993-2008 were actually cases of unrecognized adult mortality. The frequency of these events has increased dramatically since 2002 (Fig. 3) and currently accounts for approximately one fifth of annual adult mortality. Attendant plover disappearances occurred during a roughly one month period characterized by high resighting rates; thus, disappearances were not due to detection failure. Plovers that disappeared during the breeding season were older than the overall nesting population, tended to be females, and were likely killed by avian predators.

If Great Lakes Piping Plovers were not individually color banded and monitored on a near-daily basis by a large contingent of volunteers, we likely would have concluded that nest abandonment resulted from behavioral decisions to curtail parental investment. We may have even assumed that many of these abandoned nests were replaced by renests, because Piping Plovers are known to renest (Elliott-Smith and Haig 2004). Although some authors have speculated that nest abandonment may be due to mortality of the attendant adult (Yorio and Boersma 1994, Cohen et al. 2006), we found very few studies that quantified parental mortality as the likely cause of unattended nests. Wiktander et al. (2001) documented 16 abandonments in Lesser Spotted Woodpeckers (*Dendrocopos minor*), 14 of which resembled disappearances as described in our study, including three cases where carcasses were found. Neuman et al. (2004) identified parental mortality as the likely cause of nest abandonment at 35 of 1,410 (2.5%) Snowy Plover nests over a 16-year period.

Detection probability—Individual plovers had a very high probability of being seen, both within and between breeding seasons. In 2008, detection probability for breeding plovers was >0.90 during each 10-day period from mid May through early July, and the cumulative probability of being seen at least once for plovers spending at least 20 days at breeding sites approached 100%. Plovers with nests and young are generally tied to a particular stretch of beach for the duration of the incubation/rearing periods (Haffner et al.2009). Thus, the likelihood of observing a nesting plover during a detection period in May through early June, but never again, was essentially zero assuming the plover was still alive and available for detection. Detection probabilities were somewhat lower for non-breeding plovers (Fig. 2), but cumulative detection probabilities for plovers that remained at breeding sites for at least 30 days also approached 100%. This indicates that breeding plovers that disappeared from nesting beaches during early or mid nesting season have almost certainly died or emigrated from the monitoring areas.

Detection probabilities were also extremely high in our among-year analysis, averaging 0.94 over our entire study period. Detectability approached 100% during each of the last 5 years when most disappearances were recorded. Thus, disappearances were not likely due to temporary emigration from breeding sites, because among-year detection probabilities can be used as surrogates for measuring temporary emigration (Arnold and Clark 1996). Combining within- and among-year detection probabilities can allow investigators to formally distinguish between detection failure and temporary emigration by using a robust design mark-resighting model (Dinsmore 2008); however, we could not employ this methodology in our study because within-season resighting information was rigorously recorded during only one field season. We recommend that future monitoring efforts for similar studies record band combinations on at least a weekly basis throughout the breeding season to enable within- and among-season analyses.

Apparent Annual Survival—None of the 31 plovers noted as having 'disappeared' during the breeding season were ever observed again, and mark-resighting analysis suggests these disappearances were deaths. Cormack-Jolly-Seber analysis cannot formally distinguish death from permanent emigration (Cooch and White 2008), and the adjective 'apparent' is usually used to denote that individuals could have permanently emigrated to another unmonitored location. However, we regularly document breeding dispersal events exceeding 50 km (J. Kroese et al., unpubl. data) and we obtain frequent resightings of our color-banded Great Lakes Piping Plovers from the wintering grounds (LeDee 2008), and none of the plovers that disappeared during the breeding season were seen again during winter or at other Great Lakes nesting sites. Plovers that deserted their nests also had lower survival prospects, and our analysis suggests that they suffered about 20% additional mortality (apparent annual survival averaged 0.77 for plovers that did not disappear or desert, versus 0.57 for plovers that deserted their nests). We suspect that some of the abandonments that were coded as desertions due to insufficient evidence were actually disappearances. Alternatively, plovers that desert their nests may be of lower quality or in poorer nutritional condition than non-deserting individuals (Arnold et al. 1995), and that the same factors that predispose plovers to desert their nests also place them at greater risk of mortality during the coming year. In contrast, plovers that lost nests to other factors did not show evidence of decreased survival, nor did widow(er)s of disappeared plovers have lower survival.

Our best-supported model of annual apparent survival indicated that since 2002, observed losses during the breeding season have averaged 5.7% of the adult breeding population per year. This model also included a declining linear trend in annual survival when abandonment-related mortality was excluded, and together these two factors have contributed to much lower estimates of annual survival in recent years (Fig. 3). Most adult disappearances occurred during a relatively short time period spanning approximately 34 days (June 2nd ± 17 days), which is approximately twice the mortality rate one would expect were mortality events distributed evenly throughout the annual cycle.

Unless birds are radiomarked, causes of mortality are usually unknown. In our study, evidence of mortality was usually indirect, but for eight cases where death was confirmed, avian predators were implicated in six. The species most frequently identified by nest monitors was the Merlin. Beginning in 2005, the consecutive loss of breeding adults at two of the more populous nesting sites in the Great Lakes resulted in a federal effort to selectively remove Merlins observed hunting the shoreline and active nests. This is not the first time Merlins have been implicated in plover mortality; Neuman et al. (2004) also attributed the loss of nine breeding Snowy Plovers to Merlin predation. Plovers that disappeared were disproportionately older than the Great Lakes nesting population at large, and this pattern tended to be stronger within males than within females (Fig. 4). Nearly twice as many female plovers as males disappeared during breeding, suggesting that costs associated with egg laying may predispose females to higher desertion and mortality rates (Yorio and Boersma 1994).

We encourage other investigators to consider parental mortality as a potentially important cause of nest abandonment. Failure to equate mortality with nest abandonment may result in its misinterpretation as a behavioral decision. Although radiotelemetry is probably the easiest way to document such mortality (Devries et al. 2003), we demonstrate here that combined analysis of nesting histories and mark-recapture studies can also shed light on nest abandonment as an indicator of adult mortality. These approaches are especially important for rare birds where concerns about deleterious marking effects will likely preclude the use of radiotelemetry. Recovery efforts for rare ground-nesting species often include the use of protective exclosures to curtail nest depredation, but this strategy has been criticized as incurring greater mortality risk on nesting adults (Murphy et al. 2003, Neuman et al. 2004, Isaksson et al. 2007). Our results support the suspicion of previous investigators that many nest failures attributed to parental desertion should be reinterpreted as adult mortality (Neuman et al. 2004) and suggest that apparent abandonment can be used as an indicator of breeding-season mortality.

TABLE 1. Annual number of Great Lakes Piping Plover nests lost due to disappearance of an attendant adult, desertion by attendant adults, predation, and flooding, versus total number of nests initiated. In addition, we list the number of uniquely marked male (M) and female (F) birds affected by each form of nest loss. For all categories of nest loss, blank spaces or values <*n* indicate M or F that were not uniquely banded.

TABLE 1.

		Abandonment						Egg predation			Flooding		
		Disappearance[1]			Desertion								
Year	Nests	*n*	M	F	*n*	M	F	*n*	M	F	*n*	M	F
1993	19	2			1	1		1	1	1	0		
1994	21	1		1	0			2	2	2	0		
1995	23	0			0			2	2	2	0		
1996	23	2		1	1	1	1	2	2	1	0		
1997	25	1		1	1	1	1	1		1	0		
1998	26	0			0			1	1	1	0		
1999	39	0			1	1	1	2	2	1	4	4	3
2000	34	2	1	1	0			4	1	1	0		
2001	36	1		1	0			4	2	2	0		
2002	56	5	1	5	2	1	2	4			2	1	2
2003	51	1	1		2	1	2	1	1	1	0		
2004	59	3	3	1	2	1		1	1		4	2	2
2005	58	7	3	1	1	1	1	1	1	1	1	1	
2006	60	4	1	3	1	1	1	3	2	2	3	3	2
2007	69	5	2	4	3	3	1	1		1	4	4	1
Total	599	34	12	19	15	12	10	30	18	17	18	15	10

TABLE2. Top-ranking models describing the effects of monitoring period (c denotes constant; t denotes interval-specific temporal variation), band type (band), site-by-period specific monitoring effort (monitor), and breeding activity (breed) on apparent survival (ϕ') and detection probabilities (p') of Great Lakes Piping Plovers during 10-day intervals throughout the 2008 nesting season. Parameters having additive relationships are joined by +.

ϕ'	p'	$\Delta QAIC_c$ [a]	w_i [b]	K [c]	QDeviance
c + band	t + monitor + breed	0.00	0.56	13	546.24
c	t + monitor + breed	2.69	0.15	12	550.99
t + band	c + monitor + breed	3.01	0.12	13	549.24
c	t + band + monitor + breed	4.25	0.07	13	550.49

[a] $QAIC_c$ for the top ranking model = 572.70, $\hat{c}$ = 1.96

[b] Model weight; 5 additional models accounted for the remaining 0.10 model weight.

[c] Number of parameters

TABLE3.Models describing the effects of year (c denotes constant; t denotes fully-temporal annual variation, T denotes linear trend) and different forms of nest abandonment (disappeared, deserted) on apparent annual survival (ϕ) and annual detection probabilities (*p*) of Great Lakes Piping Plovers during 1993-2008.Parameters having additive relationships are joined by +.

ϕ	p	ΔAIC_c[a]	w_i[b]	K[c]	Deviance
T + disappeared + deserted	T	0.00	0.70	6	1018.43
T + disappeared	T	1.69	0.30	5	1022.15
T + deserted	T	72.51	0.00	5	1092.97
T	T	73.11	0.00	4	1095.60
t	T	80.48	0.00	17	1076.21
T	t	82.99	0.00	17	1078.73
t	t	89.12	0.00	30	1057.17
c	c	90.78	0.00	2	1117.30

[a] AIC_c of top-ranking model = 1030.53; $\hat{c}$ = 0.96

[b] Model weight

[c] Number of parameters

Fig.1. Distribution of Great Lakes nesting sites that participated in Piping Plover detection surveys during April – July of 2008. Circles represent sites with monitors that reported band combinations observed throughout the 2008 breeding season. Observations occurred on a near daily basis at CV, ES, GM, GU, IP, LI, LU, NM, PI, SL, and SB.

Fig. 1.

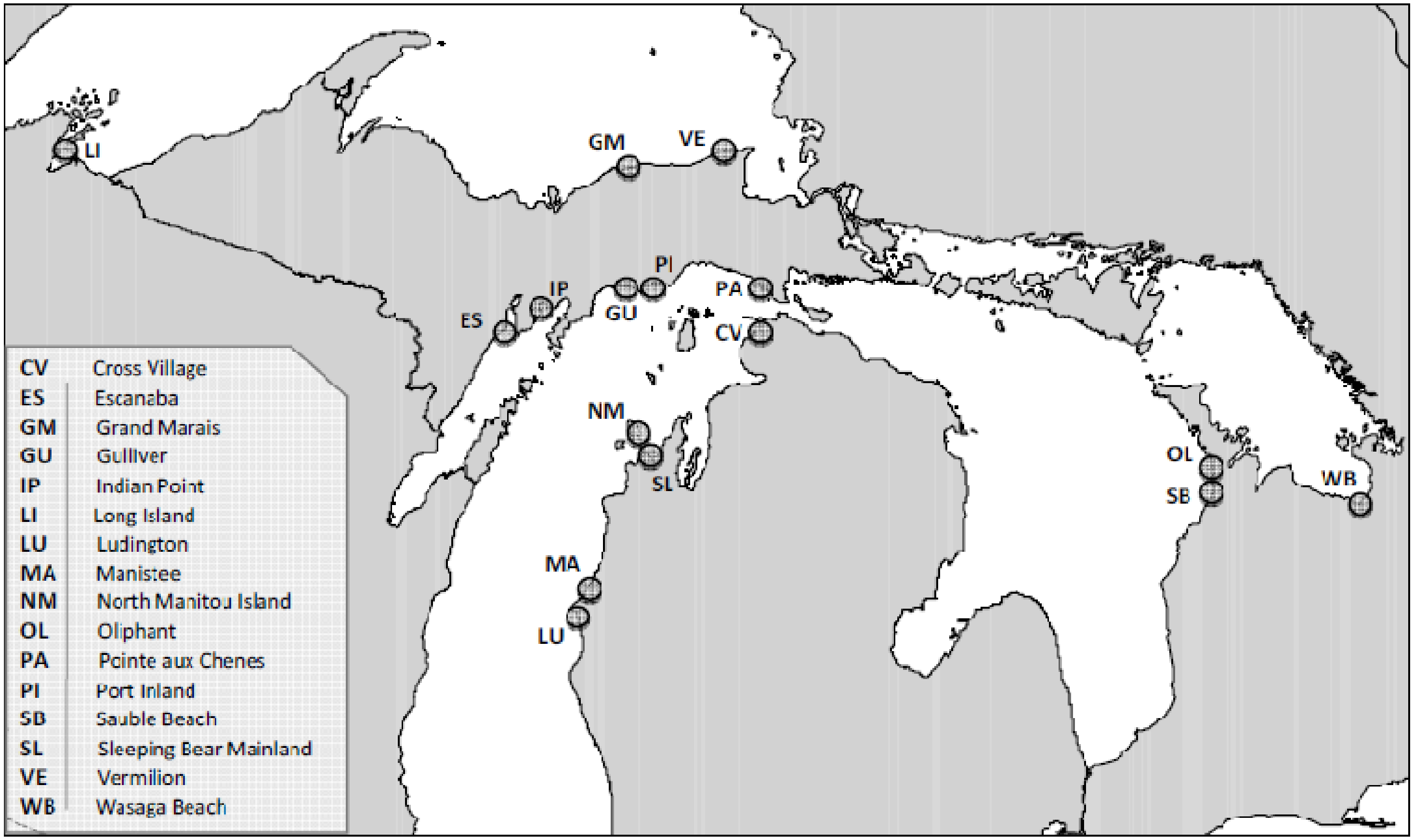

LI
GM
VE
PI
IP
PA
ES
GU
CV
NM
SL
OL
SB
WB
MA
LU
CV Cross Village
ES Escanaba
GM Grand Marais
GU Gulliver
IP Indian Point
LI Long Island
LU Ludington
MA Manistee
NM North Manitou Island
OL Oliphant
PA Pointe aux Chenes
PI Port Inland
SB Sauble Beach
SL Sleeping Bear Mainland
VE Vermilion
WB Wasaga Beach

Fig.2.Model-based detection probabilities of breeding (solid line) and non-breeding (dashed line) Piping Plovers during 10-d detection periods in the 2008 breeding season relative to the frequency with which plovers have disappeared during those periods 1997 - 2007 (gray bars, left axis). Error bars on detection probabilities represent 95% confidence intervals.

Fig. 2.

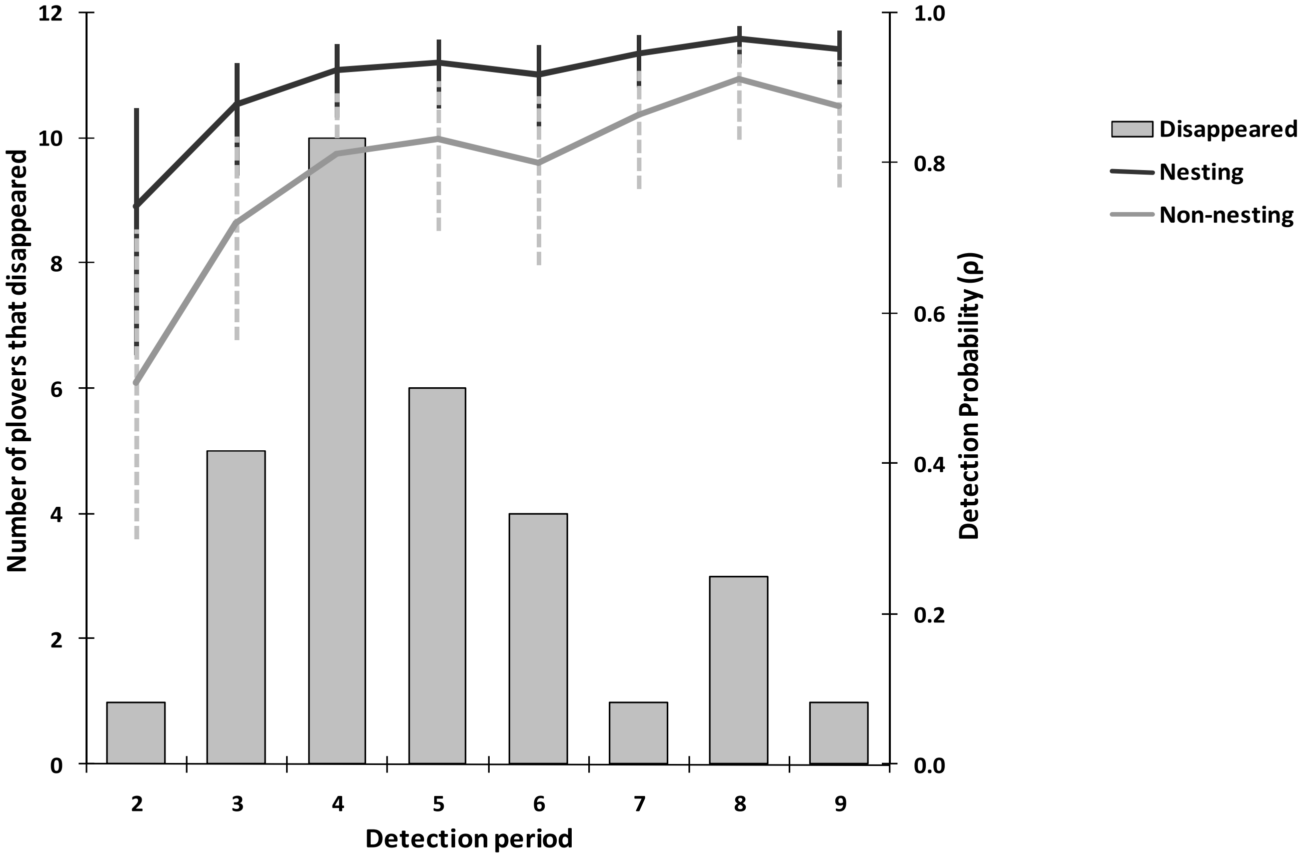
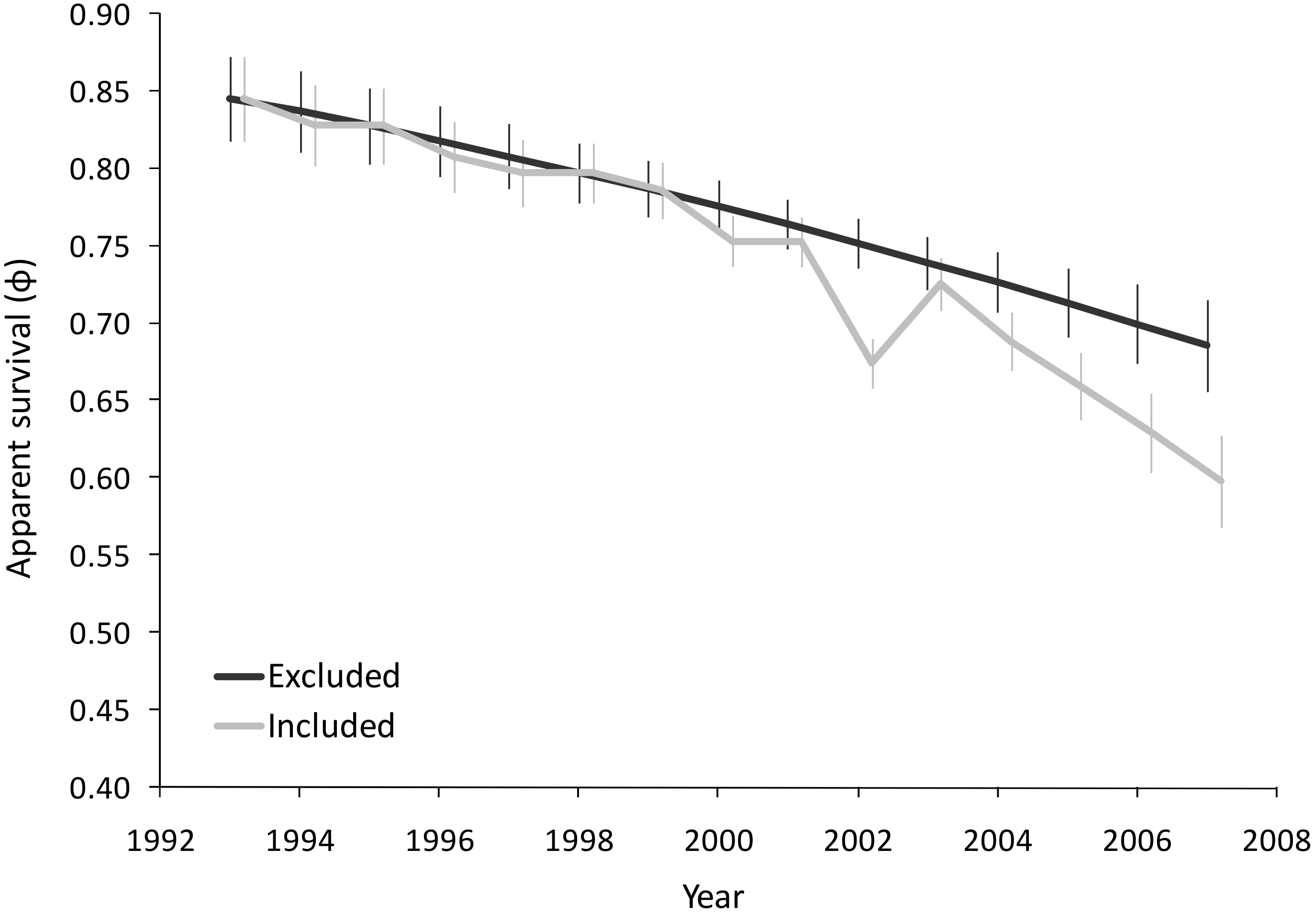

Number of plovers that disappeared
0
2
4
6
8
10
12
Detection Probability (ρ)
0.0
0.2
0.4
0.6
0.8
1.0
Detection period
2
3
4
5
6
7
8
9
Disappeared
Nesting
Non-nesting

Fig.3. Model-based estimates and 95% confidence intervals of annual survival of Great Lakes Piping Plovers when average annual losses due to disappearance and desertion are included (gray lines) versus excluded (black lines) from calculations, as based on the best-supported model from Table 3.

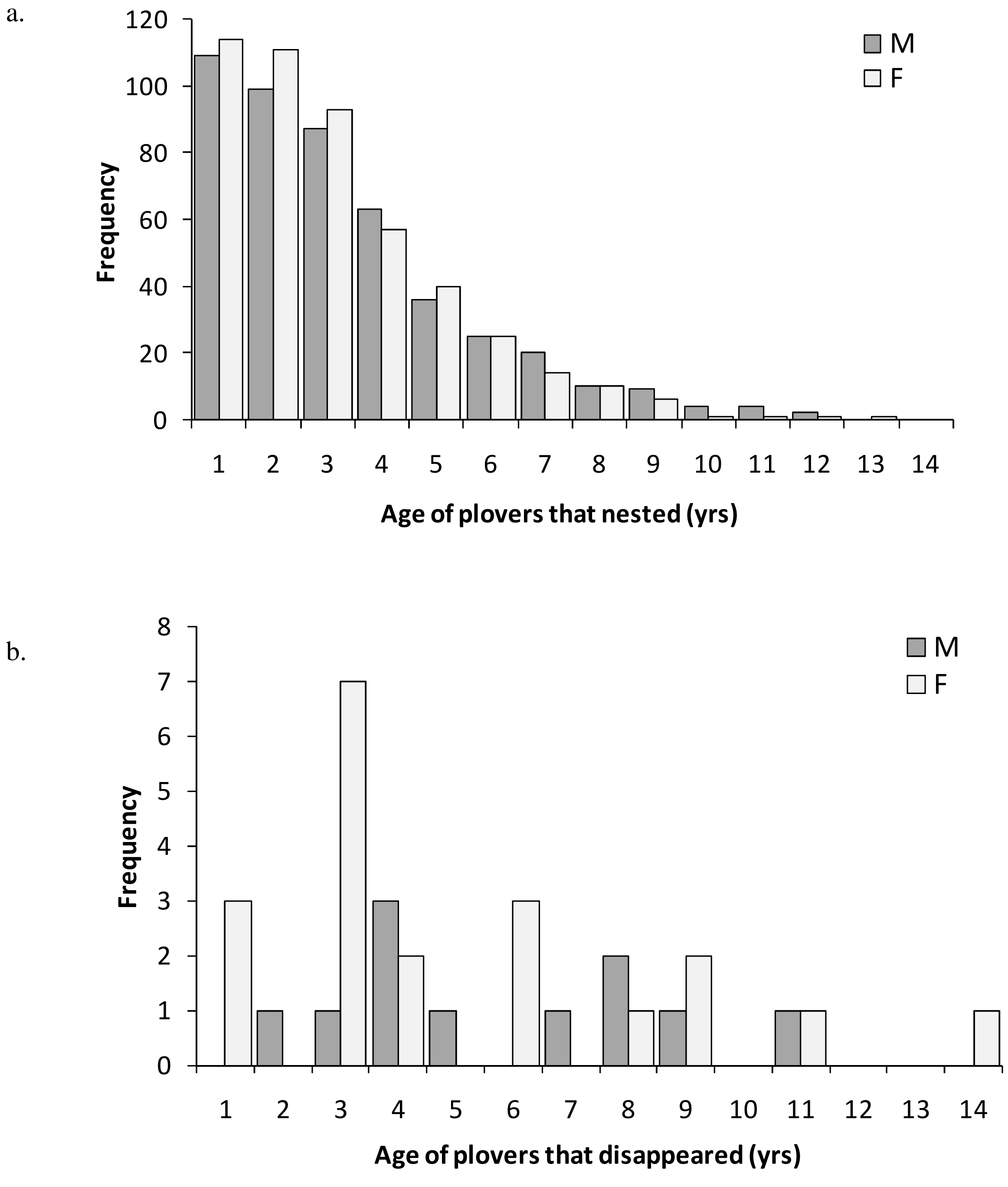
Fig. 3.



0.90
0.85
0.80
0.75
0.70
0.65
0.60
0.55
0.50
0.45
0.40
Apparent survival (Φ)
1992
1994
1996
1998
2000
2002
2004
2006
2008
Year
Excluded
Included

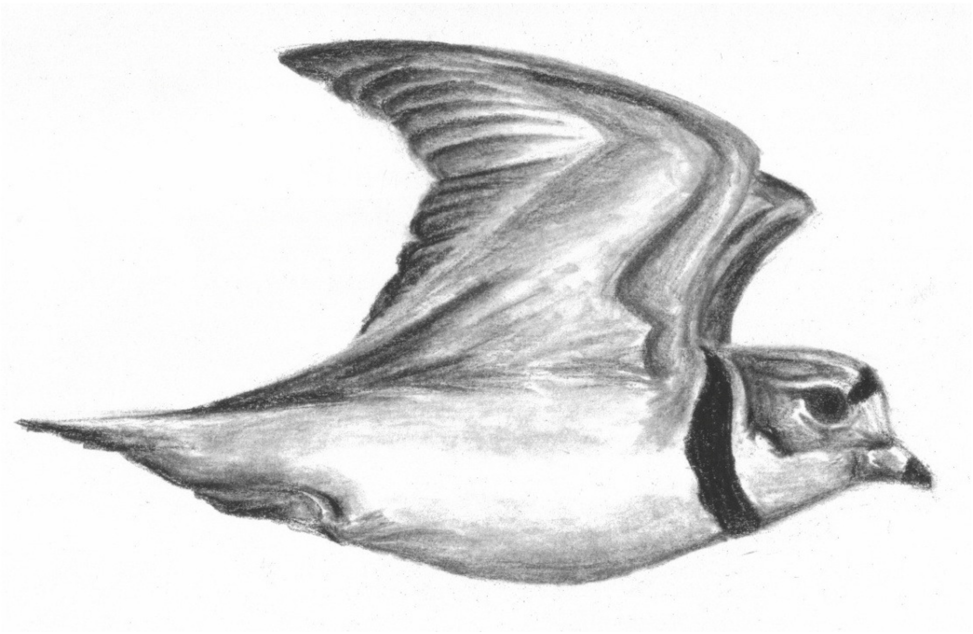
Fig.4. Age distribution of the Piping Plover population nesting in the Great Lakes 1993 – 2007, (n_M = 151, n_F = 146). 3b. Age distribution of Piping Plovers suspected to have disappeared 1997 – 2007, (n_M = 11, n_F = 20). Since many plovers were first banded as adults of unknown age, these represent minimum age distributions.

Fig. 4.


a.
120
100
80
60
40
20
0
Frequency
M
F
1
2
3
4
5
6
7
8
9
10
11
12
13
14
Age of plovers that nested (yrs)
b.
8
7
6
5
4
3
2
1
0
Frequency
M
F
1
2
3
4
5
6
7
8
9
10
11
12
13
14
Age of plovers that disappeared (yrs)

Chapter 2

Partitioning the annual survival of Great Lakes Piping Plovers



Introduction

Migration is a behavioral process that occurs within varied taxonomic groups, and although the method of locomotion may limit the distances traversed, numerous species of birds, mammals, fish, reptiles and even insects are known to exhibit annual migrations. These species are characterized by a highly dichotomous annual cycle wherein they reside at different locations during different seasons (Webster *et al.* 2002). Migration presumably evolved because different locations confer greater reproductive success or greater survival, but individual locations either provide only one of these benefits, or the benefits are only available for part of the year due to strongly seasonal environments. Hypothesized benefits of migration include various combinations of decreased competition, decreased predation or increased photoperiods and food resources (Cox 1985), but these benefits must be weighed against the costs associated with the migratory process, such as increased energetic requirements for travel and increased mortality risks while traversing unfamiliar habitats.

Birds provide an especially good model for studying migration because they traverse immense distances, are easily markedand are widely observed by a wide network of researchers, wildlife managers and volunteers. There is extensive evidence suggesting migration is energetically stressful for birds (Liechti 2006, Gordo 2007). Morever, migrants may experience elevated predation risk during or immediately after migration resulting from deteriorated flight performance due to molt and excess energy reserves required for migration, as well as depleted energy reserves upon arrival (Lank *et al.*

2003). Cross-seasonal effects (i.e. events occurring during one season that influence reproduction or survival in a subsequent period) can further influence migratory successas well as subsequent reproductive success through variation in the level of nutrient reserves that individuals carry when they arrive at their breeding or wintering destinations (Myers 1981, Rappole & Warner 1986, Nebel & Lank 2003). However, it remains unclear whether increased mortality risk is actually associated with migration. For example, Sandercock & Jaramillo (2002) found no difference in survival among sparrow species of varying migratory propensity, whereas Sillett & Holmes (2002) found evidence for decreased survival during migration in black-throated blue warblers (*Dendroica caerulescens*).

Weather conditions (e.g. temperature, precipitation, wind speed) are known to heavily influence timing of migration, especially among the smaller-bodied species including shorebirds (Charadriidae) (Lank *et al.* 2003, Gordo 2007). Inclement weather conditions can increase energetic costs of maintenance and thermoregulation, reduce food availability (especially for insectivorous birds), and increase the energetic costs of migration (Gordo 2007). Catastrophic mortality due to severe weather has been recorded when conditions shift rapidly during periods when migrants have largely depleted their energy reserves (Jehl 1993). In addition, there are several large-scale climactic phenomena believed to drive many of the global annual patterns in precipitation and temperature experienced by migratory organisms (Gordo 2007). Along the southern Atlantic Coast of North America, the North Atlantic Oscillation (NAO), driven by alternating high and low pressure zones in the Azores and Icelandic regions, is largely responsible for years of mild wet (+ NAO years) or severe dry winters (- NAO years) (Ottersen *et al.* 2001). Although the influence of the NAO is well documented for seabirds and migratory European species and is known to have a pronounced influence on weather patterns along the North American Atlantic coastline,little is published on its effect on North American migrants. A heightened understanding of the influence of weather patterns on migratory survival will yield clues to how the survival of migratory species may respond to global climate change.

Previous studies investigating a survival cost associated with migration have focused on cross-taxa comparisons and revealed some evidence to suggest migratory species have higher annual survival rates than non-migratory species (reviewed by Sherry & Holmes 1995, Sandercock & Jaramillo 2002). However, as they often compare unrelated organisms, it may be that cross-taxa comparisons do not adequately reveal species-specific costs of migration. To assess a species-specific cost of migration one must either: i) compare stationary to migratory populations within a single species or ii) within a migratory population, partition the annual survival among seasons and compare survival rates between stationary and migratory periods (Sillett and Holmes 2002).

Telemetry has been used to estimate survival of migratory species during segments of their annual cycle (e.g., lesser scaup, *Aythya affinis*: Herring & Collazo 2004; Henslow's sparrow, *Ammodramus henslowii*: Thatcher *et al.* 2006; piping plover, *Charadrius melodus*: Drake et al. 2001), and such data have also been combined with annual estimates of survival based on band recovery data to estimate survival during the remainder of the year (e.g. mallard, *Anas platyrhynchos*: Hoekman et al. 2002), but only a few studies have used telemetry to partition estimates of survival throughout the entire annual cycle (e.g. emperor goose, *Chen canagica*: Hupp *et al.* 2008). Collecting telemetry data across the entire annual cycle requires either a network of observers with appropriate equipment at all major breeding, wintering and migratory areas or else satellite transmitters that can be reliably monitored wherever an organism goes. These techniques remain prohibitive due to their expense, and until very recently, size restrictions on transmitters have precluded their use on smaller species. With the exception of Sillett & Holmes (2002), who elegantly stitched together the mark-recapture histories of two different populations of the black-throated blue warbler to find higher survival variability during migratory periods, studies using mark-recapture methodologies throughout the annual cycle have been similarly biased in focus on large-bodied waterfowl (i.e. geese, swans) that have been marked with neck collars.

Here we estimate seasonal survival of after hatch year (AHY) piping plovers, a small migratory shorebird species endemic to North America. The Great Lakes population of piping plovers is federally endangered (U.S. Fish and Wildlife Service 1986), breeds along shorelines of Lakes Superior, Michigan and Huron and resides along the US Atlantic and Gulf coastlines during the non-breeding season (Stucker *et al.* 2010). Spring migration begins in late March and extends through mid-May, although journeys of individual birds generally occur in less than two-weeks (Elliott-Smith and Haig 2004). Fall migration is more protracted and begins in early July with the departure of female plovers from the breeding grounds and terminates in September with the departure of young of the year. A population wide mark-recapture program begun in 1993 has facilitated estimates of annual survival for this population, but aside from evidence that about 20% of the annual mortality is associated with loss of nesting adults (Roche *et al.* 2010), there is little indication of where in the annual cycle that most mortality occurs. However, estimates of mortality during non-migratory periods suggest that piping plovers experience little mortality while on their wintering grounds (Drake *et al*. 2001, Cohen *et al.* 2008) or breeding areas (Roche *et al.* 2010), suggesting that variability in annual survival may be driven by mortality during the migratory periods.

We used the extensive mark-recapture data on Great Lakes piping plovers observed on both breeding and non-breeding areas to estimate seasonal survival during 2000-2009. We took this approach in order to 1) identify when mortality occurs and which periods are the most variable, and 2) to identify potential correlates of annual variation in survival within each period. Possible sources of variation we investigated included the influence of mean minimum winter temperature, mean number of degree-days (i.e. number of days during which temperature was high enough for insect development), and annual winter NAO index.

Methods

STUDY SYSTEM AND FIELD METHODS

The Great Lakes piping plover is a ground-nesting migratory shorebird endemic to North America; of the three recognized breeding populations, the Great Lakes is the smallest

(71 pairs in 2009) and federally endangered (USFWS 1985). Piping plovers reside at nesting sites along Lake Michigan, Superior, and Huron shoreline from mid-April through July. Plovers migrate south during July or August to spend the non-breeding period on the southern US Atlantic Coast. Most of the Great Lakes population is concentrated along shoreline in North Carolina (NC), South Carolina (SC), Georgia (GE), and both the Atlantic and Gulf coasts of Florida (FL) (Stucker *et al.*2010, Gratto-Trevor *et al.in press*).

Since 1993, nesting plovers have been captured using modified Potter traps (Lincoln 1947) and marked with unique combination of US Geological Survey (UGSG) metal bands and up to four Darvic plastic color bands (Avinet Inc., Dryden, NY, USA), which facilitate the identification of individual plovers without recapture. Since 2005, plovers nesting in the Great Lakes have been banded with an orange plastic flag that distinguishes these individuals as Great Lakes breeders. Chicks hatched in the Great Lakes (annually95% banded) are caught by hand and banded prior to fledging with a combination of USGS metal bands and a brood-specific combination of up to three Darvic plastic color bands. Since 2005, an orange band (signifying the Great Lakes population) has been placed above the tibiotarsal joint on all chicks. At the end of the 2009 breeding season, ~ 78% of the breeding population was uniquely marked.

The population is well monitored while on the breeding grounds, with volunteers and collaborators making frequent surveys of historical and contemporary nesting habitat in April and May (Roche *et al.* 2010). Once breeding pairs are discovered, monitoring of pairs occurs on a near daily basis from the end of May through July when chicks fledge.

When visiting an active or historical nesting site, monitors record the date and band combinations of plovers encountered to facilitate creation of capture-recapture histories. During the non-breeding season (August - March), volunteers in NC, SC, GA and FL make opportunistic sightings of Great Lakes piping plovers. If these birds are uniquely color banded, volunteers record the date, band combination and often take photos. This information is then reported to and compiled by researchers at the University of Minnesota (LeDee *et al. in press*, Stucker *et al.*2010). Although most sightings are not compiled during structured surveys, there is significant overlap in the non-breeding sites visited by volunteers as these sites correspond with local birding hotspots.

DATA ANALYSIS

Encounter Histories

We compiled breeding and non-breeding period sightings of after-hatch year (AHY) piping plovers with unique band combinations from winter 1999 through summer 2009. We did not include earlier data because reports of plovers on the non-breeding grounds were infrequent prior to 1999 (LeDee et al. *in press*). As we do not mark piping plovers uniquely in their hatch year we limited our analysis to AHY plovers only (Larson 2000, Roche et al. 2008). We divided the year into 4 recapture periods, two during breeding (b1: 12 April –6 June, b2: 7 June – 16 July) and two during the non-breeding period (nb1: 1 July – 30 November, nb2: 1 December– 30 April), (Table 1) so as to estimate the intra-seasonal survival of AHY piping plovers. There was some overlap between nb2/b1 and b2/nb1 because plovers migrated asynchronously, such that some individuals were seen on the breeding grounds in spring before other plovers had left the wintering grounds, and vice versa in the fall. Because we were interested in risks of migration, where a plover was sighted during migrational periods was more important than when it was sighted. If a plover with a unique band combination was observed at least once within a period this was treated as a ‘recapture’ event. Because plovers that may have emigrated from monitored areas on the breeding grounds were still susceptible to being detected on the wintering grounds, our estimates of survival are “true survival” and not the more typical “apparent survival” where mortality is confounded with permanent emigration (i.e., our analysis shares many similarities with a Barker model; Barker 1997, LeDee et al. *in press*).

Covariates

Sex. The sex of Great Lakes piping plovers has been determined via observation of relative plumage dimorphism within pairs (e.g. darker breast and head bands on males) in addition to breeding season behaviors (e.g. territorial and aerial displays, copulation) since unique banding began in 1993. We included sex as a covariate to explain variability in detection probability as previous studies have found an effect of sex on wintering latitude and detection probability while plovers are on the non-breeding grounds (Stucker et al. 2010, LeDee et al. *in press*).

Global weather.We used seasonal indices of NAO magnitude as covariates representing the influence of global weather patterns on seasonal survival. Principle component based estimates of NAO magnitudes were available for 1999 – 2009 at http://www.cgd.ucar.edu/cas/jhurrell/indices.html. These measurements were available in three-month intervals that we used as covariates for seasonal survival as follows: winter (September-October-November, **SON NAO**; December-January-February, **DJF NAO**), spring (March-April-May, **MAM NAO**), fall (June-July-August, **JJA NAO**). We did not include an NAO covariate for summer survival because there was no evidence to suggest the NAO influenced inland North American climate during the summer months.

Regional weather. We compiled minimum daily temperature (°C) and precipitation (cm) data for the breeding and non-breeding grounds during the winter of 1999 through 2008 (weather data are not yet available for 2009). We collected data available online (http://cdiac.ornl.gov/epubs/ndp/ushcn/access.html) from weather stations located at sites near to the five primary locations where Great Lakes piping plovers were observed during the non-breeding season (winter and spring seasonal survival): Tarpon (Gulf Coast FL), Titusville (Atlantic Coast, FL), Brunswick (GA), Charleston (SC), and Morehead (NC). We used data collected from a weather station in Cheboygan (MI) to represent conditions on the breeding grounds (summer and fall seasonal survival). Of the piping plovers observed on the non-breeding grounds during this period, 194 plovers were observed in what we considered five primary regions (a few individuals were observed in multiple regions): Gulf Coast FL (n = 48), Atlantic Coast FL (n = 18), GA (n = 65), SC (n = 50), and NC (n = 36). We created seasonal temperature covariates (covariate: **temperature**) by averaging minimum daily temperature data across the relevant survival window: winter (15 September – 13 February), spring migration (14

February – 8 May), breeding (8 May – 25 June) and fallmigration(26 June – 14 September). We created seasonal precipitation covariates (covariate: **precipitation**) by summing daily precipitation that occurred during the same intervals. Because plovers inhabit a rather wide range during the non-breeding period (p_{nb1} and p_{nb2}), we created single temperature and precipitation covariates representative of all regions. We averaged all daily minimum temperatures and summed all daily precipitation for winter and spring intervals in each region. We then used these values to create a weighted mean for the non-breeding grounds based on the percentage of plovers found within a given region (e.g. 30% of all plovers were sighted in GA, so mean daily temperatures were multiplied by 0.3). For survival analysis we standardized all local weather covariates to a mean of zero and standard deviation of one.

Predation. We incorporated two covariates intended to represent predation risk by merlins during summer and winter. A substantial portion of nest abandonments during the breeding season are due to predation by merlins (*Falco columbarius*) on incubating adult plovers (Roche et al. 2010), so we used the annual number of nests suspected to have been abandoned due to adult mortality (covariate: **abandoned)** to represent relative predation risk during the summer in 2000-2009. The annual fall migration of merlins occurs between September and December, after most plovers have already arrived on their non-breeding grounds. Thus, we postulated that counts of fall migrating merlins would be most likely to influence winter survival of plovers. To estimate merlin abundance we used annual migration data collected at Hawk Mountain (PA) (www.hawkcount.org)during September – December 1999 – 2008 (covariate: **merlins**).

We standardized all predation covariates to a mean of zero and standard deviation of one.

Model selection

To estimate seasonal survival and detection likelihoods for piping plovers we used the Cormack-Jolly-Seber recaptures-only model in program MARK (White and Burnham 1999). For this analysis, each of our 40 encounter occasions represented a single detection period during: the first (nb1) or second (nb2) half of the non-breeding period or the first (b1) or second (b2) half of the breeding period. Individual birds were coded as detected only if they were observed in the appropriate part of their range within a specific detection period.

Our most highly parameterized model [ϕ({winter, spring, summer, fall}*t), *p*({nb1,nb2,b1,b2}*t)] included 78 parameters, estimating 38 unique survival rates, 38 unique detection rates, and 1confounded estimate of final survival times resighting rate (Lebreton et al. 1992). To assess goodness of fit, we conducted 1,000 bootstrap simulations using this global model. Our estimate of overdispersion ($\hat{c}$) was 1.09, indicating little evidence for lack of fit, but we neverthelessused Akaike's information criterion corrected for small samples and overdispersion ($QAIC_c$) to rank models based on (Burnham and Anderson 2002).

We used a hierarchical modeling approach to estimate seasonal survival and assess the potential effect of environmental covariates on Great Lakes piping plovers. In brief, we: 1) attempted to reduce model complexity in resighting rates (*p*) to facilitate better estimation of survival processes (Lebreton *et al.* 1992), 2) built simple models to test whether seasonal survival was supported, 3) partitioned model variance to determine how much variation in seasonal survival could be attributed to ‘real’ process variation, 4) ranked the influence of various covariates in affecting variation in survival within individual seasons (while holding survival for the other three seasons constant) and finally 5) built a ‘full’ model incorporating results from the top seasonal models and made sure that predictions of this model were robust to alternate parameterizations of survival and detection probabilities.

Detection probabilities. Because the same monitoring teams were present throughout the entire breeding season and monitoring effort was therefore consistent between b1 and b2 each year, we constrained breeding season detection probabilities (p_{b1} and p_{b2}) to a common intercept, but allowed them to vary annually ($p_{\mathrm{b*t}}$). Non-breeding season detections (p_{nb1} and p_{nb2}) were collected largely by volunteers and effort may have varied between periods and so we included two separate intercepts and allowed detection probabilities to vary annually independently of breeding season detection probabilities. This model, hereafter referred to as *p*(reduced), resulted in a net reduction of 46.2 QAIC_c units relative to our global model. We examined subsets of this 61 parameter model to investigate causes of variation in seasonal survival.

Seasonal survival. To test whether there was evidence for seasonal differences in survival, we simplified the fully parameterized model ϕ(season*t) by building constant (ϕ.), year (ϕ_{year}) and seasonal (ϕ_{season}) models. To build ϕ_{season} we constrained each season to a separate intercept (i.e., we estimated separate survival rates for summer, fall, winter and spring, but these seasonal survival estimates did not vary among years). As there was strong support for seasonal differences in survival, we preceded to determine if there was evidence of annual variation in these estimates. Such variation would be evident if the model $\phi_{season*year}$ had greater support (i.e. lower $QAIC_c$) than model ϕ_{season}, but the simpler model could be ranked higher simply because it has many fewer parameters (i.e., 4 vs. 38).

Variation in survival estimates is composed of real demographic variance, commonly referred to as process variation, as well as sampling varianceor statistical 'noise'. To determine whether the differences in seasonal survival estimates were a result of real demographic variance or noise, we used intercept-only random effects models in program MARK to estimate the proportion of total variance in survival that was attributable to process variance. A substantial amount of process variance indicates that seasonal survival varies annually, and supports the use of environmental covariates in attempt to understand the potential causes of this variation.

To assess the influence of environmental covariates on seasonal survival we built models where seasonal survival was fully temporal(e.g. $\phi_{winter*t}$),constant (ϕ_{winter}) and a linear function of specific covariates ($\phi_{winter+covariate}$) for each season of interest; survival probabilities in all other seasons were held constant (i.e. intercept only). We used *p*(reduced) to model detection probabilities. We built seasonal models according to our *a priori* list (Table 2), ranked models via $QAIC_c$, and estimated the total deviance explained by each covariate by comparing it to the amount of deviance explained by the fully temporal model: [QDev ϕ_{null}– QDev $\phi_{covariate}$] / [QDev ϕ_{null} – QDevϕ_t]. This approach can only be applied to total deviance (process + noise) and is analagous to examining proportions of variation explained by the sum of squares used in multiple regression (Fredriksen *et al.* 2008).

Finally, we used the results of our season-specific covariate models to inform the creation of our final composite model. This model was comprised of all top-ranked model structures (lowest $QAIC_c$) from the season-specific models as well as *p*(reduced). We used this model to generate seasonal survival estimates for all four seasons concurrently. We converted all estimates of survival to weekly rates by dividing by the number of weeks between the mid-points of each detection period (Table 1).

Results

Detection probabilities. The probability of detecting AHY piping plovers was highest during the breeding period ($p_{\mathrm{b1\ \&\ b2}}$), when rates were typically at or above 90% (Figure 1). Detection probabilitites were higher during the first half of the non-breeding period (p_{nb1}) than during the second half (p_{nb2}), but much lower than during the breeding period (Fig. 1). Detection probabilities exhibited greater annual variability during the non-breeding period than during the breeding period (Figure 1). Finally, female piping plovers were had higher rates of detection than males ($\beta_{\mathbf{sex}}$ = 0.2322, 95% CI: -0.0122, 0.4766); although this was modeled as an additive effect over all 4 seasons, it was most apparent during the non-breeding season.

Seasonal survival.Among simple models including only year or season effects, there was greater support for seasonal variation than for annual variation (Table 3). The best-supported model without covariates recognized constant survival in summer, fall and winter and temporally-varying survival in the spring. Nevertheless, random-effects models recognized substantial annual process variation during all four seasons, with the greatest amount of process variation occurring in spring and the least occurring in summer (Table 4). We therefore examined potential covariates for all four seasons.

There was strong support for a positive effect of minimum temperature on spring survival ($\beta_{\mathbf{temperature}}$ confidence interval did not overlap 0), whereas NAO, abandoned nests and precipitation were associated with negative effects on survival during winter and summer anda positive effect on fall survival, respectively (Table 3). Although these latter 3 effects were all supported by lower $QAIC_c$ values, confidence intervals overlapped zero indicating weaker support.

In our best-supported combined model, weekly survival probabilities of AHY piping plovers were highest and least variable during the summer and lowest and most variable in spring; survival probabilities in winter were high but variable and during fall they were lower but less variable (Fig. 2). This model (and models nested immediately within it) accounted for 95% of the Akaike model weights and explained 33% of the deviance attributable to annual variation within seasons using only 11% as many parameters as the full model $\varphi_{\text{season*year}}$. During summer, survival decreased with increasing levels of nest abandonment ($\beta_{\mathbf{abandoned}}$ = -0.5631, 95% CI: -1.1487, 0.0224). There was week evidence suggesting Fall survival rates were positively influenced by increased precipitation on the breeding grounds ($\beta_{\mathbf{precipitation}}$ = 0.2005, 95% CI: -0.3311, 0.7321) and were less annually variable than winter or spring survival rates (Fig. 2 & 4). During winter, weekly survival rates were highly variable (Fig. 2) and were negatively correlated with the NAO index ($\beta_{\mathbf{SON\ NAO}}$ = -0.8083, 95% CI: -2.2177, 0.6012), (Fig. 5). Weekly survival rates in spring were the most variable and there was strong support for a positive correlation with spring minimum temperatures ($\beta_{\mathbf{Temperature}}$ = 0.7922, 95% CI: 0.2550, 1.3294) (Fig. 6).

Discussion

Annual survival of reproductive adults is a key driver of population viability for most avian and mammalian species (Sæther & Bakke 2000). We believe that partitioning annual survival estimates into seasonal components is a necessary next step towards understanding population dynamics as it enables the investigation of specific environmental factors affecting survivorship during each major component of the annual cycle. Using this information we were able to identify spring and fall migration as periods of highest vulnerability, as well as identify specific environmental factors influencing survival during each of the four seasons.

SURVIVAL DURING STATIONARY PERIODS

Stationary periods for Great Lakes piping plovers occur during the winter and summer periods (generally 15 September – 14 February, 9 May – 26 June), although some birds are still migrating at the beginning of the winter period (e.g., young of the year) and end of the summer period (e.g. failed nesters or females that have abandoned their broods).

Estimates of seasonal survival during winter and summer were higher than during the spring and fall migratory periods (Table 4).

Winter

Past studies of winter survival in piping plovers have indicated this is not a period of great vulnerability. Telemetry studies of 49 individuals during August 1997 – April 1998 at Laguna Madres, Texas (Drake *et al.* 2001) and 7 individuals during December 2005 – March 2006 at Oregon Inlet, North Carolina (Cohen *et al.* 2008) detected zero mortalities. Our estimate of average winter survival was 0.964 over 22 weeks, which equates to an expectation that about 1 in 28 radiomarked plovers would be predicted to die during the winter. Although winter survival was high in our study, it was also the second most variable among years, a factor that would not have been revealed in the previous cited studies as they occurred over a single year.

In contrast to piping plovers, winter survival rates have been identified as limiting factors among several species of birds.. For relatively large-bodied game species, such as ruffed grouse (*Bonasa umbellus*), northern bobwhites (*Colinus virginianus*), and wild turkeys, radio telemetry studies have revealed low survival rates during the fall/winter period (Kurzejeski *et al.* 1988, Burger *et al.* 1995, Humberg *et al.* 2009). Small-bodied non-migrants have shown similar vulnerability, with juvenile willow tits experiencing highly variable winter survival rates and Carolina wren (*Thryothorus ludovicianus*) population dynamics heavily influenced by the winter period (Lahti *et al.* 1998, Link *et al*. 2007).

We found only one study in which winter was identified as a period of low survival for a migratory species and in this case the cause was anthropogenic; Gauthier *et al*. (2001) believed low winter survival in snow geese (*Chen caerulescens*) was due to winter harvests. Although Jones *et al*. 2004 indicated the non-breeding season (which included winter) was a period of low survival for cerulean warblers (*Dendroica cerulea*), this interval also included migration and thus lower survival rates are not necessarily associated with winter. However, the overwhelming majority of studies estimating winter survival for large and small-bodied migratory species suggests this is not a particularly sensitive time. Winter-only radio telemetry studies of lesser scaup and Henslow's sparrows revealed high survival rates, although for the latter this was only at sites of high quality; both studies concluded winter was not a period of high vulnerability (Thatcher *et al.* 2006, Herring *et al*. 2004). While seasonal survival in emperor geese, greater white-fronted geese (*Anser albifrons*) and greater snow geese has been shown to be either relatively high (Schmutz & Ely 1999, Hupp *et al*. 2008) or simply the same as the rest of the annual cycle (Menu *et al.* 2005) during the winter period.

Weekly piping plover winter survival rates were more influenced by the NAO index during September – November (SON NAO) than any of the other environmental covariate investigated; years of more negative SON NAO values were associated with higher winter survival. Most effects of NAO on migratory species (both survival and migration timing) have been documented for European species, wherein positive NAO indices (associated with wetter and more milder winters in Europe and the US Atlantic Coast) are associated with higher survival (Grosbois *et al.* 2005, Sandvik et al. 2005, Flockhart *et al.* 2008) and early spring migration (Forchhammer *et al.* 2002, Huppop & Huppop 2003, Stervander *et al.* 2005, Vahatalo *et al*. 2004). Thus, our results, of increased weekly winter survival with more negative SON NAO indices run counter to previous findings and local climate changes (i.e. temperature and precipitation) had little influence on winter survival. This is somewhat surprising because local climate strongly influences the survival of both stationary and migrant species. Temperature, particularly bouts of 'severe temperatures' have resulted in decreased survival in willow tits (*Poecile montanus*), the European dipper (*Cinclus cinclus*), cerulean warblers, and greater sage grouse (Lahti *et al*. 1998, Loison *et al.* 2002, Jones *et al*. 2004, Moynahan *et al.* 2006), as has total number of days of snowfall (Link *et al.* 2007).

Summer

There are few studies focusing exclusively on breeding season survival of piping plovers, as the summer has generally been believed to be a period of low vulnerability (citations?). However, several studies have pointed to occurrences where incubating adults have gone missing, and raptors have often been implicated in these disappearances (Murphy *et al*. 2003, Cohen *et al.* 2006, Roche *et al.* 2010). Most evidence suggests summer is not a particularly vulnerable time period for birds and it has been demonstrated to be the season with the highest survival in numerous migratory and non-migratory species (Jones *et al.* 2004, Hupp *et al*. 2008, Atlwegg *et al.* 2009). In fact, only one study of a migratory species indicated summer was a period of vulnerability; Kirby *et al.* (1986) pinpointed incubation as a period of high vulnerability. Our results support this general understanding of summer as a season of relatively high survival.

Summerwas the only season during which we found no effect of weather on survival. This was not a particularly surprising result given that most of the literature does not link summer survival to climate. In one of the few studies that did draw this connection, Stokke *et al.* (2005) determined that temperature experienced during the breeding season influenced the survival of juvenile common-house martins (*Delichon urbicum*) presumably through the influence of temperature on aerial insect abundance. Results of this study supported our previous conclusions that nest abandonment resulting from the disappearance of breeding adults was an important predictor of annual survival (Roche *et al.* 2010), and in the present study we were able to further pinpoint the timing of these events and verify that they were affecting summer survival rates.

SURVIVAL DURING MIGRATORY PERIODS

Although the migration of individual piping plovers may last from 1-2 weeks (during the spring migration north) to slightly > 2 weeks (during the fall migration south) (Eliott-Smith and Haig 2004), the ‘migratory period’ occurs over a wider interval. During spring, adult males are the first to migrate, with older males arriving on the breeding grounds as early as mid-April. Older females arrive approximately a week after the males, and the spring migration is usually completed by about mid-May with the arrival of younger birds. Thus, movement is really only occurring towards the end of the spring interval defined by this study (14 February – 9 May), although the beginning of the interval may be important for the acquisition of resources prior to migration. In the fall, migration may begin as early as late June with the departure of adult females and it continues through mid-September with departures of young of the year. Although this migration overlaps the fall interval defined by this study, the movement of uniquely marked individuals (adult female and male plovers) occurs primarily from late June through early August and thus really only occurs during the first half of the fall interval (26 June– 15 September). Similar to Sillett *et al.* (2002), our averaged annual estimates of seasonal survival were substantially lower during the migratory periods (spring and fall) than during the stationary summer and winter periods (Table 4), suggesting a potential cost associated with migration. Although we acknowledge that our fall and spring periods include long intervals when individual plovers were sedentary, the most parsimonious explanation for lower survival during fall and spring is costs associated with migration.

Spring

There have been no previous estimates of spring survival for piping plovers, although LeDee (2005) postulated that lowered survival of Great Lakes piping plovers might be lower during the non-breeding season, due to mortality during spring migration. In our study, weekly estimates of spring survival were the lowest and most variable of all seasons, with most (~76%, Table 4) represented by real demographic variation rather than noise due to sampling imprecision. Spring is a season of low survival rates in several non-migratory species including the snail kite (*Rostrhamus sociabilis*), Carolina wren, and wild turkey (Bennetts *et al*. 1999, Link *et al*. 2007, Humberg *et al.* 2009), but few studies have examined survival during this period specifically; even fewer have focused on species unaffected by hunting. This is also true for migratory species. Sillett & Holmes (2002) demonstrated that apparent survival of black-throated blue warblers was lower during 'movement' periods, but their approach did not allow them to differentiate fall from spring migration. We found no studies that specifically estimated survival during the spring period formigratory non-game species. Hupp *et al*. (2008) estimated low spring survival in emperor geese; however, subsistence hunting was occurring during this period.

We found that piping plover spring apparent survival was most influenced by minimum temperatures experienced on the non-breeding grounds during the spring interval. We ran a post-hoc analysis to determine whether minimum temperatures during one particular month were more likely than another to influence apparent survival rates and found the strongest relationship was with March minimum temperatures. One mechanism by which temperatures might play an important role in spring survival could be through the availability of food prior to migratory departure. Piping plovers feed predominantly on marine invertebrates (e.g. marine worms, beetles, and flies) whose development is impeded by prolonged bouts of low temperatures (e.g. below 8°C). Failure to acquire sufficient energy prior to or during spring migration could result in higher incidents of mortality during migration. For example, in red knots (*Calidris canutus*), low survival and breeding success was associated with poor body condition at spring stopover sites (Morrison *et al.* 2007). However, most documented effects of temperature on survival have focused on the influence of winter weather (e.g. snowfall and temperature) for non-migratory species (Lahti *et al.* 1998, Loison *et al.* 2002, Moynahan *et al*. 2006), or in the case of migratory species such as the cerulean warbler, isolated severe weather events (Jones *et al*. 2004). Our study is the first to present evidence for a pronounced survival effect of prolonged low minimum temperatures in a migratory species.

Fall

As with spring survival, there have been no previous estimates of fall survival made for piping plovers, and very few estimates of fall survival among birds in general. In our study, weekly estimates of fall survival were the second lowest of all seasonal estimates, although they were much less variable than spring survival estimates. Fall apparent survival probabilities were not as variable as spring survival estimates, and actually had the least amount of variability that could be attributable to the environment (process variation ~ 66%, Table 4) of any season measured. There is some evidence fall may be a relatively high risk season for non-migratory species such as ruffed grouse and willow grouse (*Lagopus lagopus*) (Kurzejeski *et al.* 1998, Smith and Willebrand 1999), but very little evidence suggesting this is the case for migratory species. Hupp *et al*. (2008) demonstrated August was a period of low survival for emperor geese, but as was the case in May, this was a period during which the geese were experiencing a subsistence harvest. Similarly, although Menu *et al*. (2005) found survival rates in juvenile greater snow geese were lowest during the fall migration period, but this coincided with the birds' first hunting season and it was unclear if this apparent 'cost of migration' would have extended to non-hunted populations.

A demonstrated relationship exists between the timing and route of the southward (fall) shorebird migration and the fall falcon migration, presumably because shorebird survival is contingent upon lack of overlap between the two (Lank *et al.* 2003). We did not find a relationship between fall survival of piping plovers and merlin abundance, but we were unable to obtain a measure of merlin abundance from habitats directly used by our plover population. Fall survival was most influenced by the amount of precipitation that fell on the breeding grounds during the fall interval, but this relationship was not robust. For Great lakes piping plovers, increased fall precipitation led to increased fall apparent survival, an effect most similar to the results of Altwegg *et al*. (2009) who postulated this effect could be explained if increased precipitation resulted in increased food availability.

CONCLUSIONS

Our study supports the conclusion of Sillett & Holmes(2002) that survival during migratory periods is lower than during stationary periods. Unlike Sillett &Holmes(2002), we directly measured survival rates during migratory periods using data from a single well-monitored population. In addition, by testing the influence of annually varying environmental factors, we offer several potential explanations for observed annual patterns in seasonal survival. Our results indicate piping plovers are particularly susceptible to periods of low temperatures on their non-breeding grounds immediately prior to spring migration. If this relationship is driven by food availability prior to migration, it would reinforce the importance of migratory connectivity between the non-breeding and breeding ranges: while survival on the non-breeding grounds may be relatively high, degraded habitat or severe temperatures may decrease food availability, resulting in decreased survival of breeding adults during the energetically-demanding spring migration period.

Table 1. Timing and length of intervals used to estimate seasonal Great Lakes piping plover detection and survival (1999 – 2009). Also listed is the number of uniquely identifiable piping plovers observed during each detection period.

	Detection Periods				Survival Intervals			
	p_{nb1}	p_{nb2}	p_{b1}	p_{b2}	ϕ_{winter}	ϕ_{spring}	ϕ_{summer}	ϕ_{fall}
Start	1-Jul	1-Dec	12-Apr	7-Jun	15-Sep	14-Feb	9-May	26-Jun
End	30-Nov	30-Apr	6-Jun	16-Jul	14-Feb	9-May	26-Jun	15-Sep
Days	153	151	56	40	152	84	48	81
Weeks	21.9	21.6	8.0	5.7	21.7	12.0	6.9	11.6
Plovers	*99*	*77*	*250*	*257*	-	-	-	-

Table 2. List of *a priori* models.

*A priori*ϕ **models**	**Description**
Simple	
.	survival is constant among season and years
season	survival varies by season but is constant among years
year	survival varies by year but is constant among seasons
t	survival varies by season and year
- for below models survival varies by season but remains constant among years except as noted -	
Winter	
winter + **merlins**	merlin abundance during their fall migration influences winter survival
winter + **temperature**	average winter minimum temperatures influence winter survival
winter + **precipitation**	total winter precipitation influences winter survival
winter + **DJF NAO**	the NAO index during December, January, and February influences winter survival
winter*t	winter survival varies annually
Spring	
spring + **temperature**	average spring minimum temperatures influence spring survival
spring + **precipitation**	total spring precipitation influences spring survival

spring + **MAM NAO**	the NAO index during March, April, and May influences spring survival
spring + **DJF NAO**	the NAO index during December, January, and February influences spring survival
spring*t	spring survival varies annually
Summer	
summer + **abandoned**	the number of abandoned nests per breeding season influences summer survival
summer + **temperature**	average summer minimum temperatures influence summer survival
summer + **precipitation**	total summer precipitation influences summer survival
summer*t	summer survival varies annually
Fall	
fall + **temperature**	average fall minimum temperatures influence fall survival
fall + **precipitation**	total fall precipitation influences fall survival
fall + **JJA NAO**	the NAO index during June, July and August influences fall survival
fall*t	fall survival varies annually

Table 3. Models describing the effects of season, year and environmental covariates on seasonal survival (ϕ) for Great Lakes piping plovers observed during 2000 - 2009. Akaike's information criterion (AIC) values were calculated based on quasi-deviance (QDev), number of parameters (K), overdispersion ($\hat{c} = 1.09$) and effective sample size and models were ranked according to $\Delta QAIC_c$ values and Akaike model weights (w_i). Parameters having additive relationships are joined by **+** and multiplicative relationships by *****. The word 'season' designates an intercept-only model for the four seasons (wherein the terms spring, summer, fall, winter represent the season-specific intercepts with no annual variation), whereas 't' designates separate intercepts for each year. For all models of φ, detection probabilities are modeled as $\boldsymbol{p}(\{p_b*t, [p_{nb1}, p_{nb2}] + t\} + sex)$**.**

Model (ϕ)	**Δ QAIC$_c$**	**w$_i$**	**K**	**QDev**
winter + **SON NAO**, spring + **temperature**, summer + **abandoned**, fall + **precipitation**	0.00	0.72	30	2687.81
winter, spring + **temperature**, summer, fall	2.37	0.22	27	2696.40
winter, spring*t, summer, fall	6.30	0.03	35	2683.68
winter, spring, summer + **abandoned**, fall	9.15	0.01	27	2703.18
winter, spring, summer, fall + **precipitation**	10.34	0.00	27	2704.37

winter + **SON NAO**, spring, summer, fall	11.06	0.00	27	2705.09
season	11.25	0.00	26	2707.36
winter + **temperature**, spring, summer, fall	12.29	0.00	27	2706.33
winter, spring **MAM NAO**, summer, fall	12.68	0.00	27	2706.71
winter, spring + **precipitation**, summer, fall	12.83	0.00	27	2706.87
winter, spring, summer + **precipitation**, fall	13.07	0.00	27	2707.11
winter, spring + **DJF NAO**, summer, fall	13.13	0.00	27	2707.17
winter, spring, summer, fall + **JJA NAO**	13.24	0.00	27	2707.27
winter + **precipitation**, spring, summer, fall	13.24	0.00	27	2707.27
winter, spring, summer, fall + **temperature**	13.28	0.00	27	2707.32
winter, spring, summer + **temperature**, fall	13.32	0.00	27	2707.35
winter + **merlins**, spring, summer, fall	13.32	0.00	27	2707.35
winter + **DJF NAO**, spring, summer, fall	13.32	0.00	27	2707.36
winter, spring, summer*t, fall	13.47	0.00	35	2690.85
winter*t, spring, summer, fall	14.58	0.00	35	2691.96
winter, spring, summer, fall*t	22.23	0.00	35	2699.61

t	26.33	0.00	61	2648.37
.	28.37	0.00	23	2730.67

[*] $QAIC_c$= 2749.00

Table 4. Estimates of seasonal survival (φ), associated standard errors (SE) and estimated amount of variance attributable to annual process variation (σ^2), where % process variance = σ^2/SE^2. Estimates are from random-effects models fit in Program MARK.

Season (ϕ model)	**φ**	**SE (φ)**	**σ (process)**	**% process**
Winter	0.9638	0.0255	0.0182	50.9
Spring	0.9284	0.0359	0.0314	76.5
Summer	0.9844	0.0085	0.0062	53.2
Fall	0.9380	0.0234	0.0154	43.3

Fig. 1. Annual probability of detecting (*p*) [male/female] Great Lakes piping plovers on the non-breeding grounds during July - November (p_{nb1}) and December – April ($\mathrm{p}_{\mathrm{nb2}}$) and on the breeding grounds during April - July ($p_{\mathrm{b1\&b2}}$). Thick lines represent annual detection probabilities (solid black = $p_{\mathrm{(b1\ \&\ b2)}}$, dashed gray = p_{nb1}, solid gray = p_{nb2}); thin lines of matching color and pattern represent the corresponding upper and lower confidence intervals.

Figure 1.

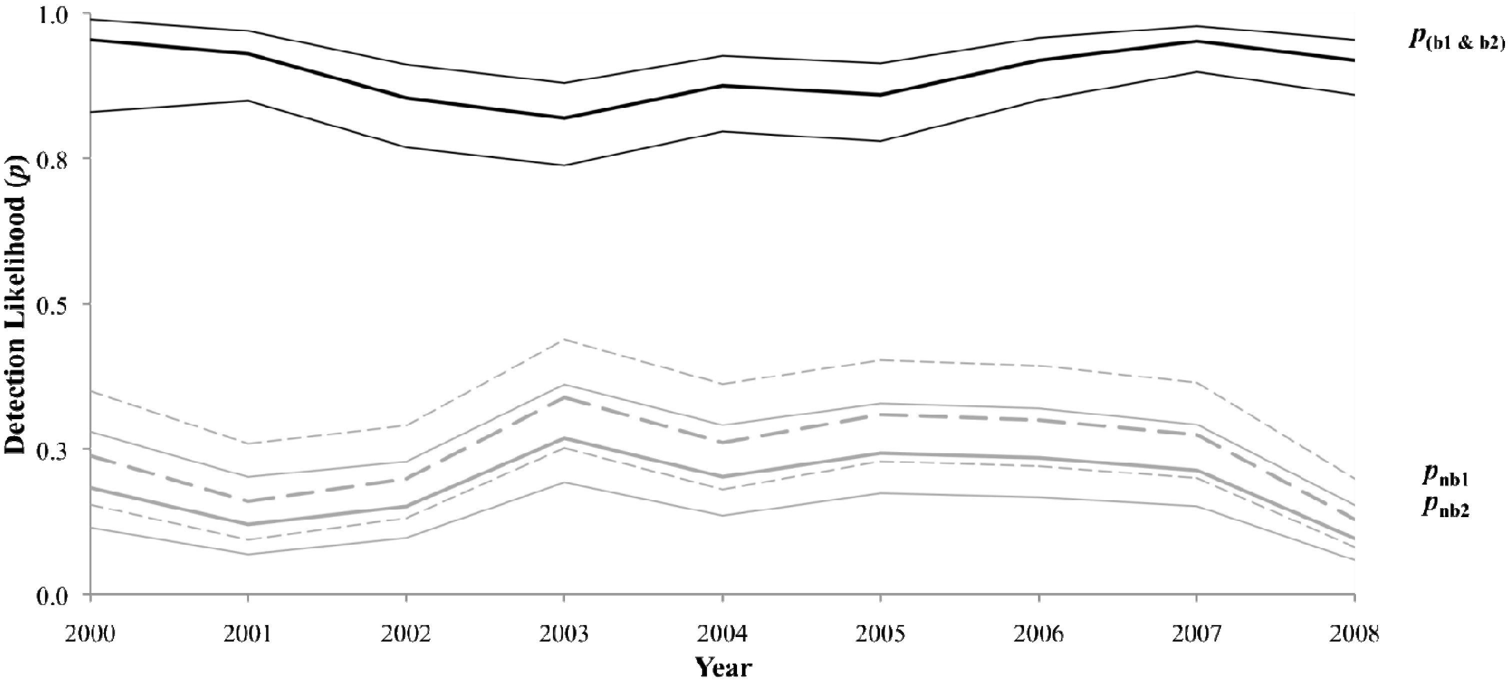

1.0
0.8
0.5
0.3
0.0
Detection Likelihood (p)
2000
2001
2002
2003
2004
2005
2006
2007
2008
Year
$p_{(b1\ \&\ b2)}$
p_{nb1}
p_{nb2}

Figure 2. Estimates of weekly survival (ϕ) for after hatch year Great Lakes piping plover by season and year (2000 – 2009) generated by top model ϕ(winter + **SON NAO**, spring + **temperature**, summer + **abandon**, fall + **precipitation**), ***p***([(p_{b1}, p_{b2})*t], [p_{nb1}*t], [p_{nb2}*t]).

Figure 2.

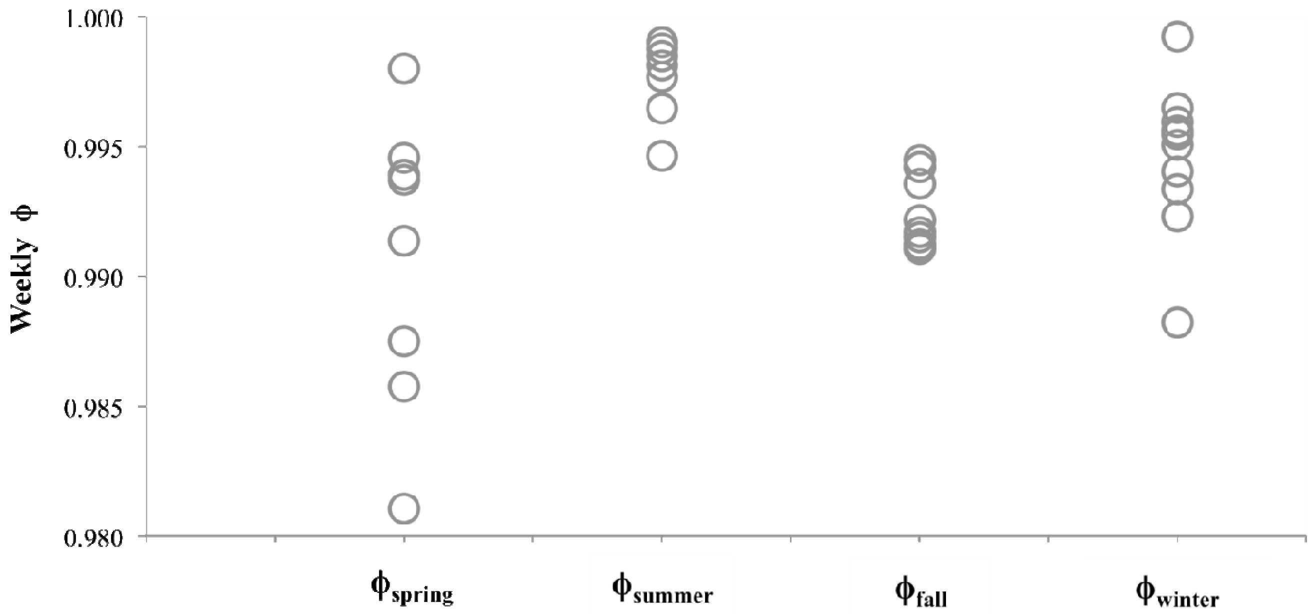
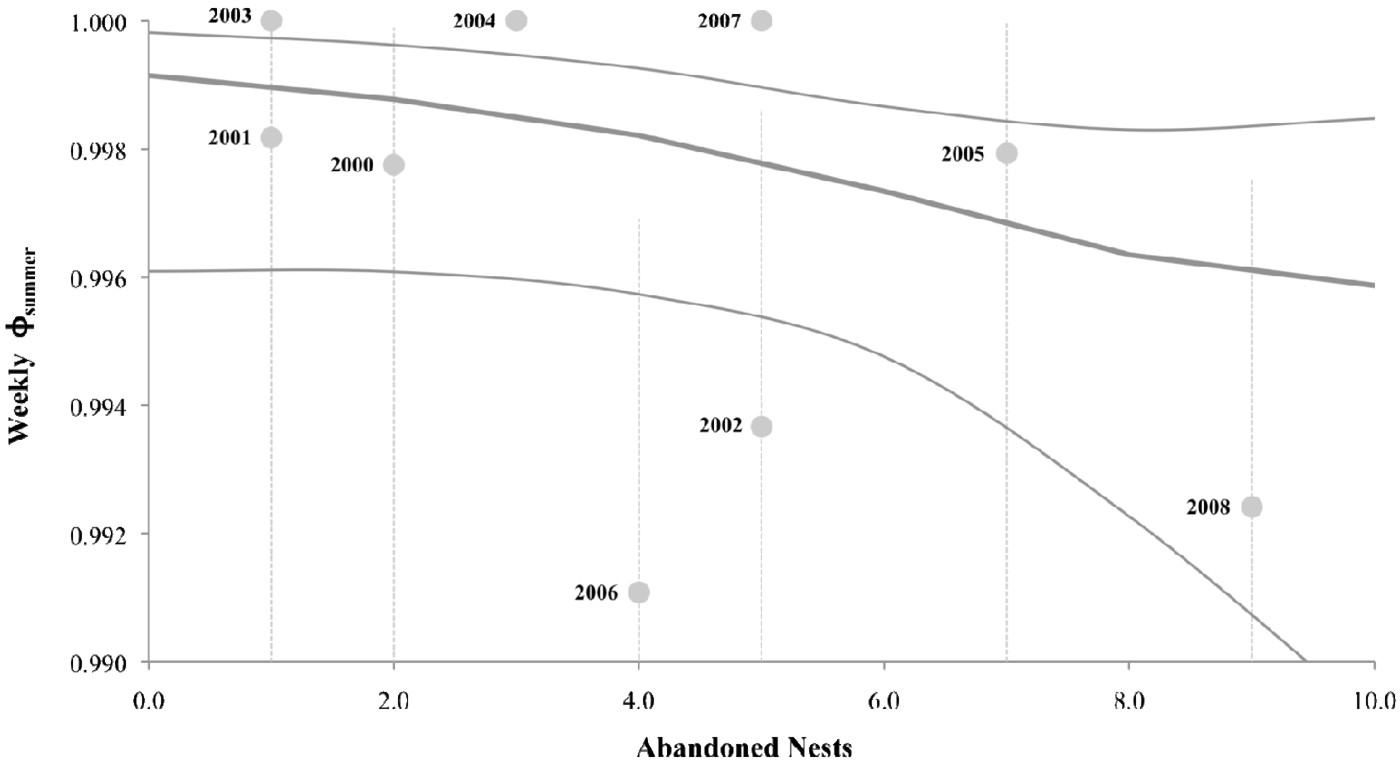

1.000
0.995
0.990
0.985
0.980
Weekly ϕ
ϕspring
ϕsummer
ϕfall
ϕwinter

Fig. 3. Weekly estimates of survival (ϕ) during summer (thick gray line) for after hatch year Great Lakes piping plovers in relation to annual number of nests abandoned during 9 May – 25 June (2000 – 2009) generated by top model ϕ(winter + SON NAO, spring + temperature, summer + abandon, fall + precipitation), ***p***([(p_{b1}, p_{b2})*t], [p_{nb1}*t], [$\mathrm{p}_{\mathrm{nb2}}$*t]). The thin gray lines represent the upper and lower 95% confidence intervals. The circles represent 'raw' estimates of weekly survival derived from model ϕ(t), ***p***(reduced) with upper and lower 95% CI (vertical dashed gray lines) for the labeled year and associated number of abandoned nests.

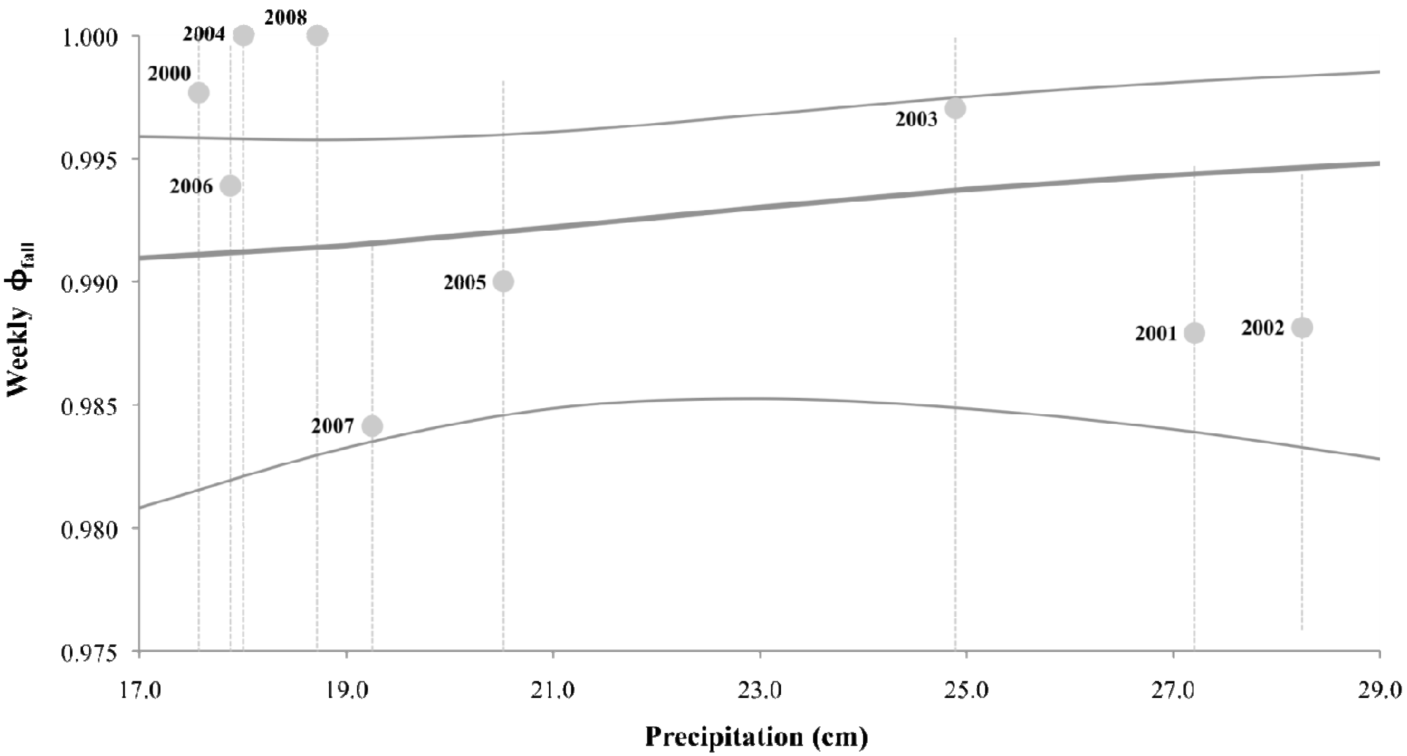
Figure 3.



2003
2004
2007
2001
2000
2005
2002
2008
2006
1.000
0.998
0.996
0.994
0.992
0.990
Weekly Φ_{summer}
0.0
2.0
4.0
6.0
8.0
10.0
Abandoned Nests

Fig. 4. Weekly estimates of survival (ϕ) during fall (thick gray line) for after hatch year Great Lakes piping plovers in relation to total precipitation during 26 June – 14 September (2000 – 2009) generated by top model ϕ(winter + SON NAO, spring + temperature, summer + abandon, fall + precipitation), ***p***([(p_{b1}, p_{b2})*t], [p_{nb1}*t], [p_{nb2}*t]). The thin gray lines represent the upper and lower 95% confidence intervals. The circles represent ‘raw’ estimates of weekly survival derived from model ϕ(t), ***p***(reduced) with upper and lower 95% CI (vertical dashed gray lines) for the labeled year and associated total precipitation.

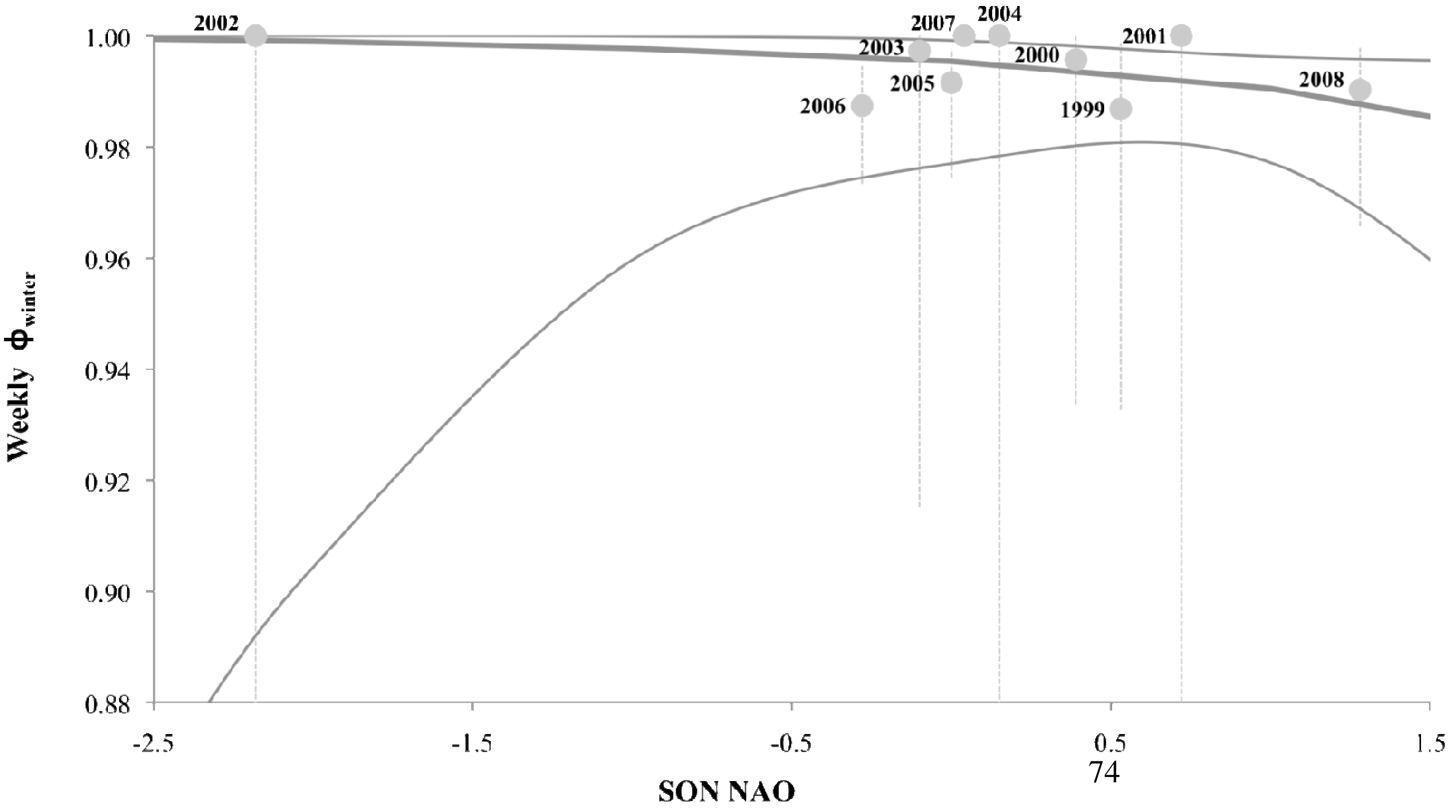
Figure 4.



1.000
0.995
0.990
0.985
0.980
0.975
Weekly Φ_{fall}
17.0
19.0
21.0
23.0
25.0
27.0
29.0
Precipitation (cm)
2000
2004
2008
2006
2003
2005
2001
2002
2007

Fig. 5. Weekly estimates of survival (ϕ) during winter (thick gray line) for after hatch year Great Lakes piping plovers in relation to SON NAO index during 15 September – 13 February (1999 – 2008) generated by top model ϕ(winter + SON NAO, spring + temperature, summer + abandon, fall + precipitation), ***p***([(p_{b1}, p_{b2})*t], [p_{nb1}*t], [p_{nb2}*t]). The thin gray lines represent the upper and lower 95% confidence intervals. The circles represent 'raw' estimates of weekly survival derived from model ϕ(t), ***p***(reduced) with upper and lower 95% CI (vertical dashed gray lines) for the labeled year and associated SON NAO index.

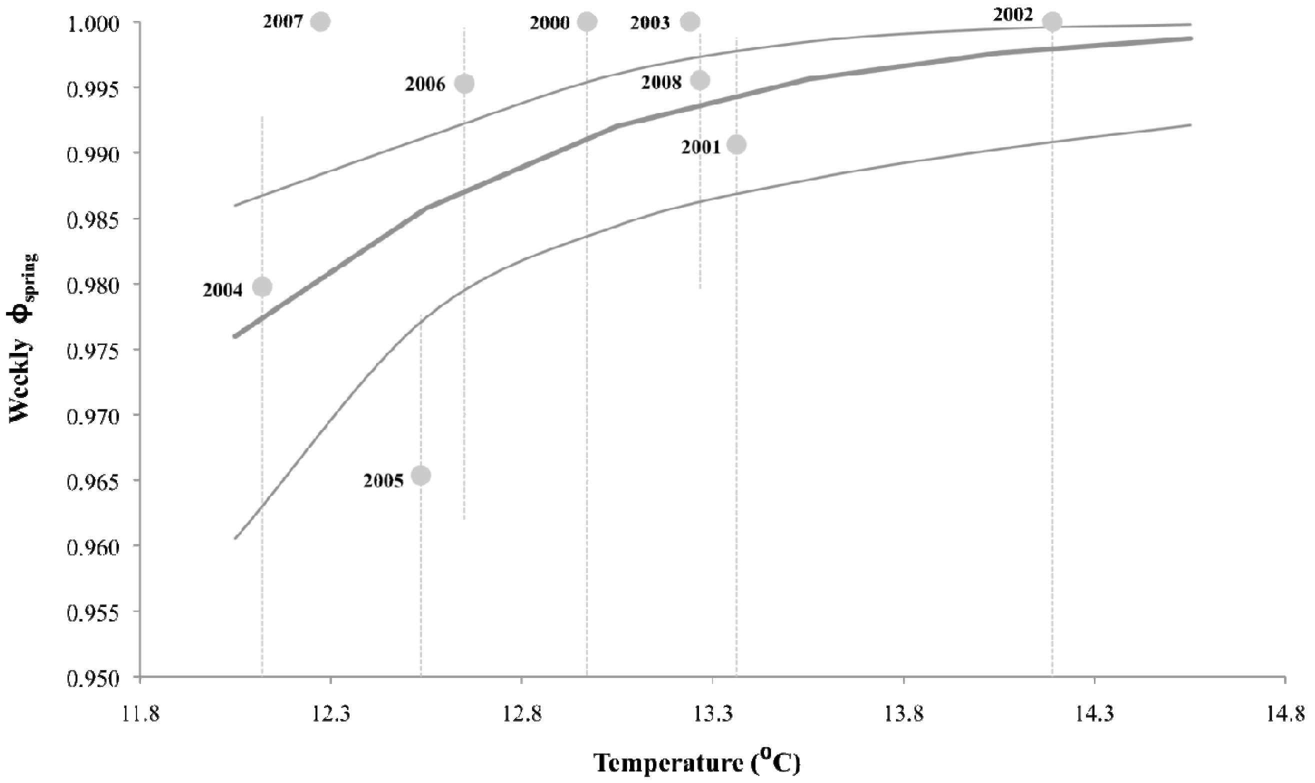
Figure 5.



2002
2007
2004
2003
2000
2001
2005
2008
2006
1999
1.00
0.98
0.96
0.94
0.92
0.90
0.88
Weekly Φ_{winter}
-2.5
-1.5
-0.5
0.5
1.5
SON NAO

Figure 6. Weekly estimates of apparent survival (ϕ) during spring (thick gray line) for after hatch year Great Lakes piping plovers in relation to average minimum temperatures during 14 February – 8 May (2000 – 2009) generated by top model **ϕ(**winter + SON NAO, spring + temperature, summer + abandon, fall + precipitation)**,** ***p***([(p_{b1}, p_{b2})*t], [p_{nb1}*t], [p_{nb2}*t]**)**. The thin gray lines represent the upper and lower 95% confidence intervals. The circles represent 'raw' estimates of weekly

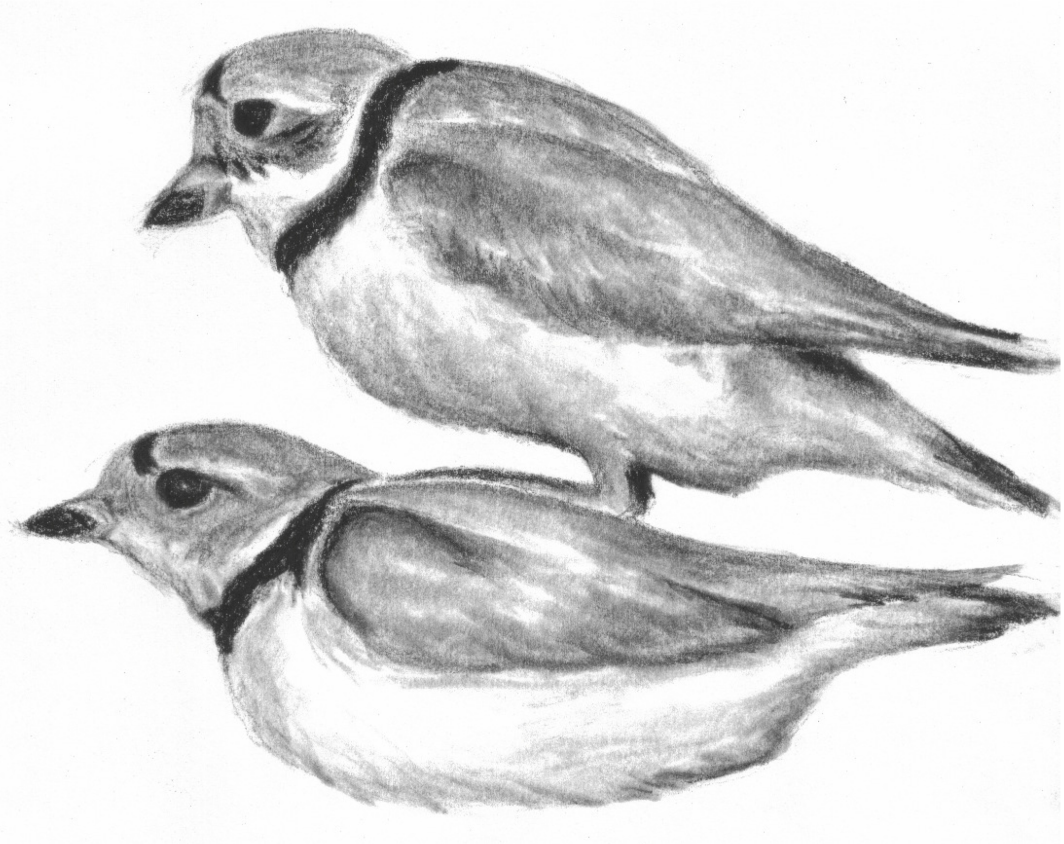
Figure 6.



1.000
0.995
0.990
0.985
0.980
0.975
0.970
0.965
0.960
0.955
0.950
Weekly Φ_{spring}
11.8
12.3
12.8
13.3
13.8
14.3
14.8
Temperature (°C)
2007
2000
2003
2002
2006
2008
2001
2004
2005

Chapter 3

Minimal Evidence for Inbreeding Depression in an Endangered Population of Piping Plovers (*Charadrius melodus*)



1. INTRODUCTION

Mating between close relatives leads to increased population homozygosity, thereby exposing deleterious recessive alleles and ultimately leading to a reduction in fitness, a phenomenon commonly known as inbreeding depression (Keller & Waller 2002). Inbreeding depression is a frequently cited concern for threatened and imperiled populations, and although reduced fitness is often difficult to document in the wild, there is widespread acknowledgement that inbreeding depression is a potentially important issue for conservation (Charlesworth & Charlesworth 1987; Lande 1988; Frankham 1995; Keller & Waller 2002; Brook *et al.* 2002; O'Grady *et al.* 2006; Leberg & Firmin 2008). Deleterious effects of inbreeding have been documented in captive populations (Ralls *et al.* 1988; Laikre & Ryman 1991) and in wild populations by several experimental and observational studies (Jiménez *et al.* 1994; Saccheri *et al.* 1998; Westemeier *et al.* 1998; Kruuk *et al.* 2002; Liberg *et al.* 2005). However, only a few studies have documented the effects of inbreeding depression in already imperiled populations (Daniels & Walters 2000; Jamieson *et al.* 2007; Ewing *et al.* 2008; Räikkönen *et al.* 2009). Our study tests theory with data procured from a wild population to estimate the frequency of inbreeding and its impacts on the fitness of an endangered North American population, the piping plover (*Charadrius melodus*), which passed through a bottleneck of < 20 pairs 25 years ago.

The effects of inbreeding depression in wild populations are more pronounced early in development (Keller & Waller 2002) and are more likely to influence population vital rates than morphological traits (DeRose & Roff 1999). Studies investigating the effects of inbreeding on fitness in birds have documented deleterious effects on hatching success (Spottiswoode & Møller 2004), body size (Kruuk *et al.* 2002) and juvenile survival (Jamieson *et al.* 2007). Less frequently documented are deleterious effects on probability of recruitment and lifetime reproductive success (Szulkin *et al.* 2007). Such negative effects are commonly cited as a conservation concern for threatened and imperiled populations, which may remain small (an effective population size of < 100) for several generations, exacerbating the probability of further inbreeding (Keller & Waller 2002). Because these populations are already demographically stressed, genetic factors are likely to further affect population viability prior to extinction (Spielman *et al.* 2004); any reduction of fitness due to inbreeding depression only serves to further handicap their ability to overcome these demographic threats (Caughley 1994).

The piping plover (*Charadrius melodus*) is a ground nesting, migratory shorebird endemic to North America (Elliot-Smith & Haig 2004). Of the three recognized breeding populations, the Great Lakes population is the smallest and listed as federally endangered (U. S. Fish and Wildlife Service 1985). The population consisted of approximately 17 breeding pairs in 1985, but increased to 71 breeding pairs by 2009 (Cuthbert & Roche 2009). Despite over two decades of growth, small size and a recent bottleneck place the population at risk of inbreeding depression. Since 1993, Great Lakes piping plovers have been uniquely marked with color bands. Extensive banding and resighting data have facilitated the compilation of a 16-year pedigree (1993 – 2008), from which inbreeding coefficients may be calculated. We used these pedigree data to 1) estimate the frequency of mating between close relatives ($f \geq 0.125$) within the Great Lakes population and 2) test for an association between level of inbreeding and deleterious effects on five fitness characteristics: hatching success of eggs, chick body mass at banding, and survival of piping plovers during three life stages (hatch to fledging, fledging through one year of age and subsequent adult survival). Finally, we built a stochastic population model to simulate the effect size (number of pairs) at which inbreeding depression would have a detectable effect on recruitment rates (i.e. survival through the second year) given our understanding of present inbreeding levels and presence of inbreeding depression among the five fitness characteristics that we measured.

2. METHODS

(a) Field sampling

Beginning in late Aprilsurveys for Great Lakes piping plovers are conducted by technicians at contemporary nesting locations throughout Michigan. When pairs with nests are discovered, nesting habitat is protected via partial beach closures (Melvin *et al.* 1992) and nests are covered with wire mesh exclosures (Rimmer & Deblinger 1990; Melvin *et al.* 1992) to exclude avian and mammalian predators. Nests are monitored regularly throughout incubation and egg fates are recorded as hatched, depredated (missing or destroyed), flooded or unhatched (incubated to term but failing to hatch). Since 1993, nesting plovers have been captured during incubation using single-chambered Potter traps (Lincoln 1947) and banded with unique combinations of US Geological Survey (USGS) aluminum bands, up to three Darvic (Avinet Inc., Dryden, NY, USA) color bands and an orange Darvic plastic flag, which facilitates future identification of banded individuals without recapture. At most sites with nesting pairs, plover monitors make regular visits through mid-July to check on the status of nests and chicks and to confirm the identity of adult plovers observed at each location. Chicks are banded before fledging with USGS aluminum bands and up to three Darvic bands and are weighed using a spring scale (± 0.5 g) prior to receiving bands. If plovers survive and recruit into the breeding population as nesting adults (most typically at one year of age for females or two years for males), they are recaptured and marked with a full combination of color bands. Adults that have not been recaptured still retain chick bands, which provide limited ability to identify individuals based on resighting information (Roche *et al.* 2008). Since 1993, ~ 78% of all breeding plovers have carried full color band combinations which allows for individual identification based on resighting only; >90% wore metal leg bands and 2-3 color bands allowing for full identification upon capture and limited identification based on resighting. We used breeding sites at which monitoring and nesting of multiple pairs was relatively consistent throughout this time period, including 1) Benzie and Leelanau County (Sleeping Bear Dunes National Lakeshore), 2) Emmet County, 3) Mason and Manistee County, 4) Schoolcraft County, 5) Mackinaw County, 6) Alger and Luce County, and 7) Delta County, Michigan.

(b) Pedigree compilation

Low sample sizes and incomplete information on relatedness make detecting inbreeding depression a difficult task in wild populations (Keller & Waller 2002). However, pedigree analysis, in which inbreeding coefficients are directly calculated via ancestry lineages, is recognized as a reliable technique in species where the behavioural and genetic mating systems are concordant (Pemberton 2004; Pemberton 2008). Throughout much of the 1980s, the Great Lakes population numbered between 10 – 20 breeding pairs. Despite recent increases (i.e., 71 documented breeding pairs in 2009), inbreeding depression remains a risk (Briskie & Mackintosh 2004). Banding data indicate that at least 70% of the current breeding population is descended from the 17 known breeding pairs present at the time of federal listing (U. S. Fish and Wildlife Service 1985). The remaining individuals are either the descendents of unbanded individuals within these lineages or progeny of additional pairs breeding at unknown locations. We considered all adults banded during 1993-1995 to be unrelated 'founding' members of the population when constructing the Great Lakes pedigree (Pemberton 2008). Each plover hatched and/or banded during 1993 -2008 was assigned a unique identification number and entered into the pedigree. If ancestry could not be traced back to a single brood, we recorded paternity and maternity as 'unknown' in which case these individuals were treated as founders ($f = 0$). Piping plovers are socially monogamous within each nesting attempt, extra-pair copulations are infrequent and conspecific brood parasitism has not been observed (Elliott-Smith and Haig 2004). DNA fingerprinting studies have not been conducted on this species, but in the closely related Kentish plover (*Charadrius alexandrinus*) <4% of young exhibited evidence of extra-pair paternity (Küpper *et al.* 2004). Given that snowy plovers have a more polygamous mating system than piping plovers (Page *et al.* 2009) the expected rate of paternity exclusions in piping plovers is even lower.

We used the "pedigreemm" package in program R (Vazquez *et al.* 2010) to create a pedigree and estimate inbreeding coefficients (*f*) for the Great Lakes population. Inbreeding coefficients were calculated using a 'direct' algorithm according to a method developed by Sargolzaei and Iwaisaki (2005). Pedigree-generated inbreeding coefficients are minimum estimates of true inbreeding as they only represent inbreeding that has occurred since 1993, the year unique banding of nesting adults first occurred. If the founding members of the population were highly inbred, true levels of inbreeding could be much higher.

To estimate the frequency with which inbreeding occurred within the Great Lakes populations during 1993 – 2008, we restricted frequency estimates to individuals where complete pedigrees were known for at least 2 generations (Pemberton 2004). We summed occurrences of moderate ($0.125 \leq f < 0.25$, indicative of pairing between first cousins) and close inbreeding ($f \geq 0.25$, indicative of full sib or parent-offspring pairings) in the pedigrees of individuals where the identities of all parents and grandparents were known (Marshall *et al.* 2002; Pemberton 2004).

(c) Statistical analyses

To ensure sufficient pedigree depth for analysis of inbreeding coefficients (i.e. at least two generations) we excluded data on eggs laid and chicks hatched prior to 2000. We built generalized linear models regressing hatchability, chick weight and chick survival on inbreeding coefficients and other relevant covariates in program R (CRANS 2009). For all regressions, we began with a full model and sequentially removed covariates that were the least explanatory, based on absolute values of β/SE. We compared the Akaike

Information Criterion (AIC) value of the reduced model upon removal of each term and accepted the new model only if the AIC value was lower than the model it was nested within.

(i) *Hatching success*

Hatching success was measured as the percentage of eggs (n = 1132) incubated to term (i.e. not depredated, abandoned or broken) that actually hatched (Table 1). We modeled individual egg fate as a binomial function (link = logit) of four covariates: inbreeding coefficient (f), nest initiation date, year and breeding site. Year and site were treated as categorical variables. We accounted for potential non-independence of eggs within clutches by treating clutch as a random effect on the intercept.

(ii) *Body mass*

We treated the mass (g) of each chick (n = 727) banded during 2000 – 2008 as a continuous response variable influenced by six covariates: inbreeding coefficient (f), hatch date, days of age at banding (both linear and quadratic), year and breeding site. We accounted for non-independence among brood mates by treating brood as a random effect on both the intercept and the slope of the age covariate (i.e. brood-specific hatchling mass and growth rates, respectively).

(iii) *Survival*

We estimated chick survival (n = 1070) using Shaffer's (2004) logistic exposure model, where the fate of a chick was treated as a binary response for each day [lived = 1, died = 0]. Interval length was a single day for chicks that lived to a known age (t) and a series of n days for chicks that died at an unknown age between two successive sightings separated by >1 day. This model uses maximum likelihood methods to estimate the age at which chicks died with a user defined link function [logexp = $\log(\mu^{1/t}/(1-\mu^{1/t}))$] (Shaffer 2004). We built our full logistic model to regress chick survival against five covariates: inbreeding coefficient (f), age (t), hatch date, year and breeding site. We originally used a quasibinomial model to accommodate extra-binomial variation, which could occur if survival was correlated among siblings. However, because there was no evidence of overdispersion ($\hat{c} = 1.007$) we built the regression as a simple binomial. We generated estimates of fixed effects along with 95% confidence intervals for the best-supported model.

We estimated post-fledging survival using a Cormack-Jolly-Seber recaptures only model in program MARK (White & Burnham 1999) using band resighting data from 566 color-banded fledglings marked during 2000 – 2007 and resighted during 2001 – 2009. We modeled age-specific variation in annual apparent survival using two age classes (ϕ_1 = survival from banding until 1 year old, ϕ_{2+} = annual survival for each subsequent year) and age-specific variation in detection probability using four age classes (p_1, p_2, p_3 and p_{4+} represent the probability of a living plover being seen as a 1, 2, 3 or ≥4 year old) (Roche *et al.* 2008). We introduced increasing temporal complexity by allowing ϕ and p to vary among years [i.e., ϕ(t) and p(t) describe models in which there are different estimates of $\phi$and p for each year]. We also considered trend models that allowed ϕ or p to vary as a logistic function of year (Dinsmore 2008). Our most highly parameterized model of age and temporal effects ($\phi_{\mathrm{Age}[1,2+]*\mathrm{t}}$, $p_{\mathrm{Age}[2,3,4,5+]*\mathrm{t}}$) included 47 parameters and estimated 15 unique survival rates, 26 unique resighting rates and six confounded estimates of final survival times final resighting rate (Lebreton *et al.* 1992). This global model was used to test for overdispersion ($\hat{c}$) using a bootstrap goodness-of-fit test (Cooch & White 2008). Our estimate of $\hat{c}$ was 1.06, and we used Akaike's information criterion corrected for small samples and overdispersion (QAIC$_c$) to rank all competing models. After finding the best-supported temporal structure for ϕ and p (model with lowest QAIC$_c$), we determined if $\phi_1$or ϕ_{2+}were affected by inbreeding (f) by adding this covariate to the design matrix in MARK.

(iv) *Simulation*

Inbreeding might have several minor effects that seem unimportant individually, but together create a substantial decline in reproductive success. To assess the potential influence of inbreeding on total fitness, we wrote a stochastic simulation model in program R to estimate recruitment, which we define as the number of offspring from each breeding pair that survive to their second year (SY). We estimated recruitment per breeding pair rather than per egg or nest because piping plovers will renest following total clutch failure, and we measured recruitment at age two rather than age one because male offspring typically enter the breeding population as two-year olds (E. A. Roche, unpublished data).

For each breeding pair we generated an inbreeding coefficient for all offspring by sampling from a beta distribution with mean = 0.021, SD = 0.063, $\alpha = 0.0878$ and $\beta = 4.092$. Clutches were randomly assigned 3 or 4 eggs at probabilities of 0.05 and 0.95, respectively (clutches of 1, 2 and 5 eggs occur at frequencies < 0.01 and were ignored). First nesting attempts had a 0.73 probability of nest success (A. Claassan, unpublished data), which we defined as the probability of having at least one tended egg survive throughout the typical 28-day incubation period. If the first nest was unsuccessful, we simulated a 0.53 probability of renesting, with a 0.60 probability that the renesting attempt would be successful (A. Claassan, unpublished data). Most nest failures are due to flooding or to predation on eggs or breeding adults (Roche et al. 2010), therefore the probability of successfully hatching a nest was modeled as independent of inbreeding coefficients. If a pair failed to hatch a nest, it was assigned a recruitment of 0.

We modeled hatchability, chick survival, first-year survival and second-year survival using models derived from our analyses described immediately below. If the top-supported model did not include inbreeding, we added it back into the model to obtain an estimated effect of inbreeding for our simulation model. Our rationale was that inbreeding might have subtle and nonsignificant effects on several vital rates, but the collective impact of these incremental effects might be a detectable decline in fitness.

3. RESULTS

During 1993 – 2008, 591 piping plovers from 173 individual broods had pedigrees that were complete for at least two generations (i.e. the identity of both parents and all grandparents were known). From this sample, 27 plovers in 7 broods (4.6%) were moderately inbred ($0.125 \leq f < 0.25$) and 18 plovers in 5 broods (3.0%) were closely inbred ($f \geq 0.25$, maximum = 0.5625 observed in 3 different broods). The entire Great Lakes pedigree consisted of 388 individuals (17.8%) with a detectable level of inbreeding ($f > 0.0$).

Hatching success was not influenced by inbreeding coefficient, but was related to Julian initiation date (JID), declining from an estimated 95.0% among eggs laid on 20 April to 87.4% among eggs laid on 19 June. Although there was evidence that hatching success was non-random among clutches ($SD_0 = 1.96$, 95% CI: 1.73 – 2.19), no other variables affected hatching success.

After adjusting for age, inbreeding coefficient was the most significant predictor of chick weight at time of banding (Figure 1). Weight at 10.2 days old (the average age of chicks at banding) ranged from an estimated 21.1 grams at $f = 0.0$ to 17.6 grams among plovers with $f = 0.25$. Chick weight at banding also varied among broods, with variation on both the intercept ($\alpha_0 = 4.23$, 95% CI: 3.03 – 5.89) and the slope ($SD_{Age} = 0.39$, 95% CI: 0.27 – 0.56). Chick survival from hatch to fledge was influenced by all covariates tested and declined with increasing inbreeding coefficient values. Cumulative survival from hatching until 24 days of age ranged from an estimated 74.9% for plovers with zero inbreeding to 57.5% among plovers with $f = 0.25$ (Figure 2). There was no evidence that inbreeding affected first year survival of piping plovers (ϕ_1) or survival in any subsequent year (ϕ_{2+}) (Table 2).

For modeling purposes, we obtained the following relationships between inbreeding (f) and hatchability, chick survival, first-year survival and second-year survival:

$$\text{Logit(Hatchability)} = -3.834 \pm 1.96(\text{clutch}) + 0.962(f)$$

$$\text{Logit(Daily chick survival)} = 3.680 + 0.071(\text{age}) - 2.623(f)$$

$$\text{Logit(First-year } \phi) = -0.612 + 0.013(f)$$

$$\text{Logit(Second-year } \phi) = 0.926 + 0.013(\text{f})$$

Cumulative chick survival was the product of daily chick survival for chicks aged 1-24 days of age. The results of our stochastic simulation model indicated we would only have 3.3%, 3.5%, 4.8%, and 9.3% power to detect a significant ($\alpha < 0.05$) effect of inbreeding on recruitment of two-year olds into the breeding population if the number of pairs sampled was 50, 100, 500 and 1000, respectively.

4. DISCUSSION

(a) Frequency of Inbreeding

We found moderately high frequencies of inbreeding among Great Lakes piping plovers (7.6% of individuals had $f \geq 0.125$ and 3.0% of individuals had $f \geq 0.25$). The Mauritius kestrel (*Falco punctatus*) and an urban population of American crow (*Corvus brachyrhynchos)* exhibited substantially higher frequencies of inbreeding with 24.3 and 19.0% of the populations having $f \geq 0.125$, respectively (Ewing *et al.* 2008; Townsend *et al.* 2009). Within a reintroduced population of New Zealand North Island robins (*Petroica longipes*), inbreeding between close relatives ($f \geq 0.25$) occurred in 3.1% of all pairings (Jamieson *et al.* 2007), which was similar to what we found for Great Lakes piping plovers. However, inbreeding occurred at much lower frequencies than those demonstrated in the Great Lakes in two other populations of conservation concern. In Mexican jays (*Aphelocoma xdtramari*) only 4.9% of all pairings resulted in offspring with $f \geq 0.125$ (Brown & Brown 1998) and in red-cockaded woodpeckers (*Picoides borealis*) only 2.7% of all pairings produced offspring with $f \geq 0.125$ (Daniels & Walters

2000). Interestingly, the frequency of inbreeding within the red-cockaded woodpecker population was equivalent to that of a decidedly robust great tit (*Parus major*) population (2.5% of $f \geq 0.12$; Szulkin *et al.* 2007).

Cross-taxa comparisons of inbreeding frequency are difficult to make due to the inconsistency of methods, metrics and pedigree depths available for analysis. For example, in takahe (*Porphyrio hochstetteri*), 59% of all pairings were between related individuals (Jamieson & Ryan 2000), but the degree of inbreeding (f) was not reported. In an insular population of house sparrows (*Passer domesticus*) Jensen *et al.* (2007) found that 36.7% of all fledglings had $f > 0$ (Jensen *et al.* 2007) and Keller (1998) found that 72% of song sparrow (*Melospiza melodia*) pairs on Mandarte Island, British Columbia were detectably related, but in these cases the frequency of inbreeding may be high simply because the pedigreeswere deep and thus included small levels of inbreeding that occurred many generations ago.

(b) Inbreeding Depression

We found evidence of inbreeding depression on chick mass and chick survival of Great Lakes piping plovers. Inbreeding depression has been previously detected across a continuum of traits in large wild populations of common organisms such as the great tit (Szulkin *et al.* 2007). However, few studies have documented inbreeding depression on hatch-year or adult survival rates, suggesting that if inbreeding depression occurs it is usually in early life-history stages.

(i) *Hatching success*

A negative relationship between inbreeding and hatching success has been found under controlled laboratory conditions. Established inbred lines of sand crickets (*Gryllus firmus*) and a satyrian butterfly (*Bicyclus anynana*) had decreased hatching success relative to non-inbred lines (Saccheri *et al.* 1996; Roff 1998). In both the great reed warbler (*Acrocephalus arundinaceus*) and blue tit (*Parus caeruleus*), higher genetic similarity (as measured by DNA band-sharing coefficients, d^2) between members of a pair resulted in lower hatching success (Bensch *et al.* 1994; Kempenaers *et al.* 1996). In a review of 99 avian species, Spottiswoode *et al.* (2004) found that as d^2 increased from 0.0 to 0.7, hatching success decreased from 96.2% to 76%; this effect was most pronounced among insular populations and cooperative breeders. Finally, in the great tit, collared flycatcher (*Ficedula albicollis*) and Mexican jay, pedigree generated inbreeding coefficients were used to demonstrate that hatching success decreased with accumulation of inbreeding within pedigrees (Brown & Brown 1998; Kruuk *et al.* 2002; Szulkin *et al.* 2007; Szulkin & Sheldon 2008). In the mid 1990s, an Illinois (USA) population of greater prairie chickens (*Tympanuchus cupido*) became isolated and suffered drastic reductions in hatching success and was salvaged via genetic supplementation with breeding individuals from populations in neighboring states (Westemeier *et al.* 1998). Interestingly, Great Lakes piping plovers did not experience decreased hatching success as inbreeding increased and there was no evidence to suggest this effect has become more pronounced over the years and thus a cause of conservation concern. Overall hatching success of Great Lakes piping plovers is approximately 92%, a level that is consistent with other wild bird populations (Koenig 1982) and suggests no deleterious effects of inbreeding.

(ii)*Body mass*

Most studies have found that inbreeding has no effect on morphological traits such as body mass or tarsus length (Jensen *et al.* 2007; Szulkin *et al.* 2007), but Kruuk *et al.* (2002) demonstrated a significant negative relationship between inbreeding coefficients and tarsus length in collared flycatchers. In mammals, body mass was negatively associated with inbreeding in house mice (*Mus musculus,* Lynch 1977), mandrill (*Mandrillus sphinx,* Charpentier *et al.* 2006) and grey wolf (*Canis lupus,* Laikre & Ryman 1991), but not in ring-tailed lemurs (*Lemur catta,* Charpentier *et al.* 2008). In light of these findings, we were surprised to find a strong negative relationship between weight at banding and inbreeding in Great Lakes piping plovers. Because birds had not reached asymptotic size when we banded them, we are unable to determine if lower body mass is simply indicative of slower growth rates, or if it has lifetime consequences in terms of smaller adult body size (Boag 1987). Fledging mass often has a pronounced impact on first year survival in birds (Pettifor *et al.* 2001), although we found no effect of inbreeding on first-year survival in our data.

(iii) *Juvenile survival*

Effects of inbreeding depression are believed to be most severe early in an organism's life, and have consequently been far more frequently studied during this period than any other. Our results for Great Lakes piping plovers are consistent with previously published studies that found survival rates of inbred individuals are lower early in life than for non-inbred individuals. In mammals, a significant negative correlation between early survival and inbreeding has been reported in brown bears *(Ursus arctos*) and grey wolves (Laikre *et al.* 1996; Liberg *et al.* 2005). In birds, the offspring of closely related great tits, red-cockaded woodpeckers and North Island robins had lower survival to fledging (Schiegg *et al.* 2006; Jamieson *et al.* 2007; Szulkin *et al.* 2007), and the offspring of closely related Mexican jays, song sparrows, American crows and red-cockaded woodpeckers have been shown to have lower first year survival (Brown & Brown 1998; Keller 1998; Daniels & Walters 2000; Townsend *et al.* 2009).

(iv) *Adult survival*

Only a few studies have investigated an effect of inbreeding on survival following the juvenile period. For example, Laikre *et al.* (1996) found that inbred captive brown bears had a lower overall life expectancy, an effect that was not explainable by mortality during early life. Szulkin *et al.* (2007) found non-significant trends towards lower recruitment (both sexes), later breeding (males), and smaller clutches (females) among inbred great tits. Using a robust sample of individually marked piping plovers we found no evidence of an inbreeding effect on survival from fledging through the first year of life (ϕ_1) or from the second year on (ϕ_{2+}) and point estimates of survival actually increased slightly with increased levels of inbreeding. Our results suggest that while inbreeding is mildly deleterious during early life, its effects are negligible for individuals that survive through fledging age.

When inbreeding coefficients and their influence on juvenile survival were modeled using sample sizes much larger than we could ever obtain empirically, we found only slight decreases in fitness associated with inbreeding depression. Despite undergoing a severe population bottleneck (< 20 breeding pairs) and experiencing moderate levels of ongoing inbreeding, life history traits of Great Lakes piping plovers do not appear to be limited by inbreeding depression.

Table 1. Hatching success of eggs laid by Great Lakes piping plovers 2000 – 2008.

	nests	eggs	unhatched	hatching success
2000	19	76	5	0.93
2001	24	95	11	0.88
2002	23	89	12	0.87
2003	32	121	4	0.97
2004	32	127	9	0.93
2005	37	145	11	0.92
2006	41	163	9	0.94
2007	47	183	14	0.92
2008	40	157	15	0.90
Total	295	1156	90	0.92

Table 2. Top-supported models for piping plover survival (2000-2009). Akaike's information criterion (AIC) values were calculated based on quasi-deviance (QDev), number of parameters (K), overdispersion ($\hat{c} = 1.06$), and effective sample size. Models were ranked according to $\Delta QAIC_c$ values and Akaike model weights (w_i). Survival varies as a function of year (. = constant, t = fully temporal, T = temporal trend) and inbreeding coefficient (*f*).

Rank	**Model**	**Δ $QAIC_c$**	**w_i**	**K**	**QDev**
1*	$\phi_{age}.$	0.00	0.48	14	1302.84
2	$\phi_{age} + T$	1.84	0.27	15	1301.94
3	$\phi_{age} + f$	2.07	0.18	15	1302.80
4	$\phi_{age}*T$	3.25	0.09	16	1301.94
5	$\phi_{age}*f$	3.75	0.07	16	1302.45
8	$\phi_{age}*t$	10.47	0.00	29	1281.66

*$QAIC_c$ = 1331.3

Figure 1. Effect of inbreeding coefficient (*f*) on chick weight. Estimates generated for weight at day 10.2 by the top-supported model [Y(Weight) = $(1.802 + \alpha_{\text{intercept}}) + (2.201 + \alpha_{\text{Age}})*\text{Age} + -0.0299*\text{Age}^2 + -14.027*f$]. Thin lines represent lower and upper confidence intervals of chick weight. The symbol α represents the random effect term, (in this case a random number drawn from a normal distribution with a mean = 0 and $\text{SD}_{\text{intercept}} = 4.231$ or $\text{SD}_{\text{Age}} = 0.393$ respectively). Confidence intervals were generated by solving the top-supported model at 10 000 randomly simulated values of α and taking the mean of these iterations. The grey columns represent the sample-size (*n* = number of piping plovers) at each inbreeding coefficient value (note log scale).

Figure 1.

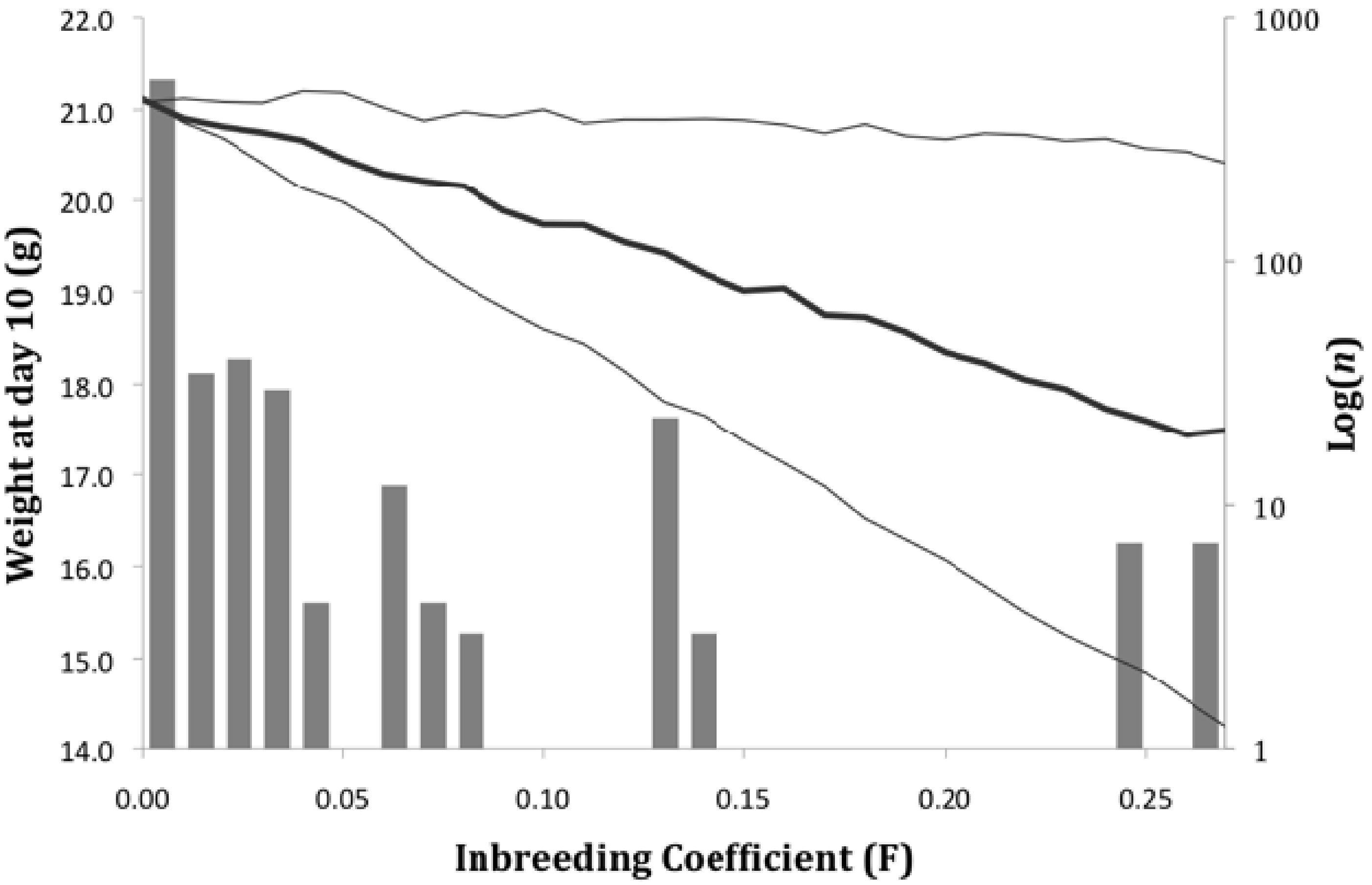
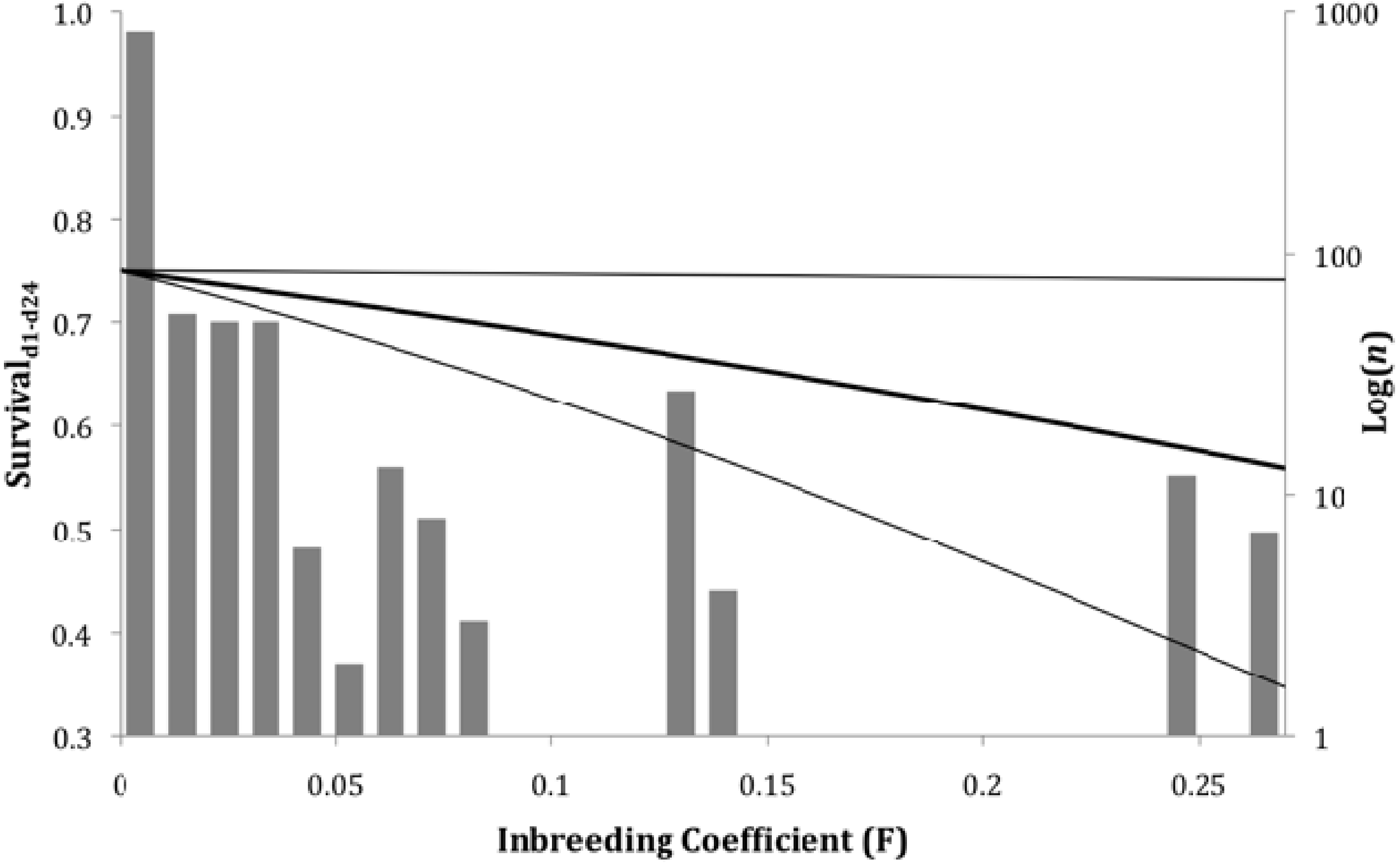

22.0
21.0
20.0
19.0
18.0
17.0
16.0
15.0
14.0
Weight at day 10 (g)
1000
100
10
1
Log(n)
0.00
0.05
0.10
0.15
0.20
0.25
Inbreeding Coefficient (F)

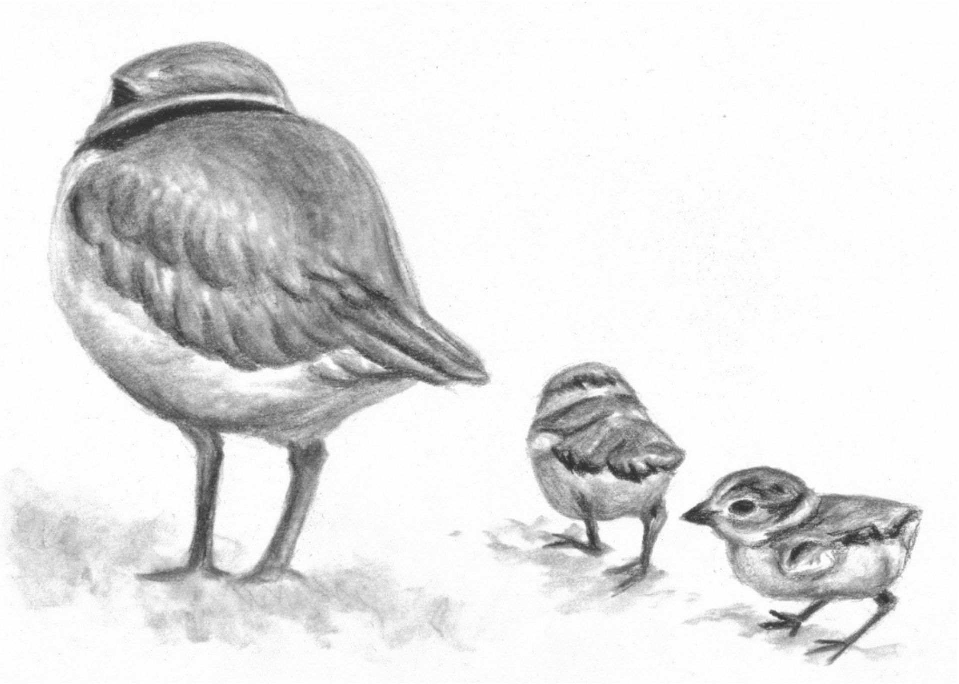
Figure 2. Effect of inbreeding coefficient (*f*) on chick survival through day 24. Estimates generated at mean covariate values for the top-supported model [Y(Chick Survival) = 5.024 + -2.623*f + 0.071*Age - 0.010*HD + 2.429*Year + 0.299*Site]. We solved this equation for all chick ages (days 1 – 24) taking the logit link of the product at each age and then multiplying across all ages. Thin lines represent lower and upper confidence intervals of inbreeding coefficient, generated by repeating the above while solving for the upper and lower 95% confidence interval values of *f*. The grey columns represent the sample-size (*n* = number of piping plovers) at each inbreeding coefficient value.

Figure 2.


1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
Survival$_{d1\text{-}d24}$
1000
100
10
1
Log(n)
0
0.05
0.1
0.15
0.2
0.25
Inbreeding Coefficient (F)

Chapter 4

Age dependent survival and reproduction in Piping Plovers



Introduction

There is substantial evidence from many diverse taxa that differential reproduction is driven by both age- and sex-dependent factors (Finch 1990). This is particularly true of birds, where age-dependent differences in survival and reproduction have been well documented (Curio 1983, Sæther 1990, Martin 1995). It is widely acknowledge that understanding the interplay between age and reproduction is necessary for the proper investigations into evolutionary ecology (Espie et al. 2000). However, the causes and processes underlying age-dependent variation in reproduction and survival have proved elusive due to the limited availability of long-term datasets, the inability to study both sexes, and differential reproductive investment between the sexes (Brown and Roth 2009).

Life history theory suggests that there is a survival cost to reproduction, and that natural selection should favor organisms that balance the effort they place into each reproductive event in order to maximize their lifetime fitness (Charnov and Krebs 1974). This results in a trade-off between current reproduction and future reproduction, leading individuals to optimize their life-history decisions in a manner that may favor long-term reproductive success at the expense of maximizing reproductive success in a given season (Charnov and Krebs 1974, Goodman 1974). One of the most influential factors mediating the seasonal decision to breed is the intrinsic age of the individual (Williams 1966). As evidence for this, young birds typically make up the majority of the non-breeding population in any given year (Newton and Rothery 1997) and breeding performance typically increases with age (Newton 1989, Sæther 1990).

Although younger birds do not generally reproduce as well as older birds, this may occur for different reasons. For example, two very different scenarios may result in individuals nesting at younger ages: these individuals may simply be more fit and thus able to compete for mates at earlier ages, or these individuals may be less fit and precociously engage in reproduction early even though greater reproductive success could be attainted through later recruitment (van de Pol and Verhulst 2006). There is currently no consensus on why birds exhibit age-dependent reproduction and at least four general and non-exclusive hypotheses have been presented to explain the trend towards increasing reproductive success with age (Wooller et al. 1990; Table 1, Fig. 1).

The selection hypothesis (Fig. 1a; Orians 1969, Curio 1983) states that the positive relationship between increased survival and reproductive success with age does not occur on the individual level (i.e. individuals do not get better at surviving and reproducing as they age), but rather individuals who are less good at surviving are also less good at reproducing and are disproportionately eliminated from the population at younger ages. To demonstrate conclusive support for the selection hypothesis, one would need to demonstrate: 1) a positive association between reproductive success and probability of survival within individuals, 2) positive correlations between age and reproductive success and between age and survival at the population level (but not as a result of within-individual correlations), and 3) a reduction in population-level variance in survival and reproductive success with age (Table 1).

The recruitment hypothesis (Fig. 1b; Hamann and Cooke 1987) also posits a positive correlation between reproduction and survival (i.e. good survivors are good reproducers).

However, this hypothesis differs from the selection hypothesis by suggesting that both higher reproductive success and survival occur when age of recruitment (i.e. age at first breeding) is delayed. One may infer that there is a generally negative effect of reproductive effort on survival across individuals and ages and that individuals that delayi reproduction until they are older are presumably better able to shoulder the costs. Detecting effects consistent with the recruitment hypothesis would require demonstrating that both survival and reproductive success are positively influenced by delayed recruitment age and that there is an association between decreased survival and increased reproductive effort (Table 1).

The restraint hypothesis (Williams 1966, Charlesworth 1980, Curio 1983), depicted in Figure 1c, is the only one of the four hypotheses in which a senescent effect on survival is required. Under this hypothesis, survival is projected to decrease as age increases and reproductive effort (although not necessarily reproductive success) is projected to increase at these older ages. Again, tacit in this hypothesis is a negative effect of increased reproductive effort on survival, which is ostensibly why reproductive effort is not increased until survival probability is already diminished. Detecting effects consistent with the restraint hypothesis would require demonstrating that survival decreases with increasing age and reproductive effort increases with increasing age. Additionally, evidence that increased reproductive effort is associated with decreased survival at any age would offer further support for this hypothesis (Table 1).

Finally, the constraint hypothesis (Curio 1983, Nol and Smith 1987), depicted in Figure 1d, predicts that both reproductive effort and reproductive success increase as age increases due to maturation or acquisition of skills or social status. According to this hypothesis, change occurs within individuals (rather than cohorts) as they become better parents with age. Detecting effects consistent with the constraint hypothesis would require demonstrating that reproductive effort and success increase with age within individual organism (Table 1).

The processes underlying these hypotheses are clearly different, as evidenced by the selection and recruitment hypotheses, which operate on the 'population level', versus the constraint and restraint hypotheses, which operate on the level of the individual (Cam et al. 2000). Thus, focus of studies on age-dependent breeding performance should be to determine how much may population-level age-dependent trends be explained by inadequate experience within individuals versus differential mortality among individuals (Espie et al. 2000). Here we use 17 years of survival and fecundity data (1993 – 2009) from a marked-population of piping plovers (*Charadrius melodus)* nesting along the US Great Lakes to assess the evidence in favor of each of the four age-dependent hypotheses just discussed. The piping plover is a migratory ground-nesting shorebird endemic to North America. There are three legally recognized breeding populations, of which the Great Lakes population is the smallest and federally endangered (USFWS 1986). We used the extensive dataset on both sexes of this marked population to 1) determine whether piping plovers exhibit evidence of age-dependent survival, 2) identify factors influencing reproductive effort and success including the effect of age, and in lieu of our results from our first two objectives, 3) evaluate which, or which combination, of the four hypotheses best describes the interplay of survival and reproductive patterns in piping plovers.

Methods

Field methods.

Historical, recent and potential nesting habitat was surveyed at the beginning of each breedingseason to locate nesting pairs (1993 – 2009) along the shorelines of Lake Michigan, Lake Superior, and Lake Huron. When pairs with nests were discovered, nesting habitat was protected via partial beach closures (Melvin et al. 1991) and nests were protected with covered wire exclosures (Rimmer and Deblinger 1990, Melvin et al. 1992). Breeding piping plover pairs were monitored from nest initiation through chick fledging. Since 1993, nesting plovers have been captured during incubation using single-chambered Potter traps (Lincoln 1947) and banded with unique combinations of US Geological Survey (USGS) aluminum bands and Darvic (Avinet Inc., Dryden, NY, USA) color bands, which facilitated future identification of banded individuals without recapture. At most sites with nesting pairs, plover monitors made regular visits through mid-July to check on the status of nests and chicks and to confirm the identity of plovers observed at each location. Chicks were banded before fledging with USGS aluminum bands and up to three Darvic bands. If they survived and recruited into the breeding population, they were marked with a full combination of up to 5 color bands upon first recapture. Adults that were not recaptured retained chick bands, which provided for limited ability to identify individuals based on resighting information (Roche et al. 2008).

Statistical Analysis.

We used a combination of mark-recapture based Cormack-Jolly-Seber (CJS) survival analysis and general linear mixed-models (GLMM) to address the influence of age on survival, reproduction, and the interplay between them. For both CJS and GLMM analyses, we represented reproductive effort as: 1) the total number of nests initiated, and 2) the total number of eggs tended by an individual plover in each year it was known to breed. We represented reproductive success as 1) the total number of chicks hatched and 2) the total number of chicks fledged by an individual plover in each year it was known to breed.

Testing the four different age-dependent hypotheses required a synthesis of results from both our CJS and GLMM analysis. In Table 1, we detail the specific aspects of each analysis used to test each hypothesis as well as the predicted results of each hypothesis.

Survival analysis

We used a Cormack-Jolly-Seber recaptures-only model in program MARK (White and Burnham 1999) to estimate the age-specific apparent survival of piping plovers of known age. We included all piping plovers banded in their hatch year 1993-2009 and individuals were recorded as ‘detected’ if they were banded or resighted within a specific breeding season (April-August), resulting in a model with 17 encounter occasions. Our most fully parameterized model $[\phi(\text{Age}*\text{t}), p([p_2,p_3,p_4,p_{5+}]*\text{t})]$ allowed survival rates to vary by year for each age class, through a possible maximal age of 17 years (i.e. the age of a bird hatched in 1993 who lived through 2009), and allowed resighting rates to vary by year for four age classes (based on results from Roche et al. 2008). The fully parameterized global model included 194 parameters, estimating 125 unique apparent survival rates, 54 unique resighting rates, and 15 confounded estimates of final survival times final resighting rate (Lebreton et al. 1992). We conducted 1,000 bootstrap simulations using this global model and estimated overdispersion ($\hat{c}$). Our estimate of $\hat{c}$ was 1.34 and used Akaike's information criterion corrected for small samples and overdispersion ($QAIC_c$) to rank models based on (Burnham and Anderson 2002). We followed a hierarchical modeling approach to estimate age-specific survival by: 1) reducing model complexity in detection probabilities (p) (Lebreton et al. 1992), 2) testing for age-dependence in apparent survival rates, and 3) including reproduction-related covariates to ascertain the relationship between survival and reproductive effort or success.

We used the design matrix to reduce model complexity in p (Lebreton et al. 1992), exploring models that constrained our four detection age classes (p_2, p_3,p_4, and p_{5+}, hereafter collectively referred to as STAGES) to 1) constant detection rates across years with separate detection rates for each age class [p(STAGES.)], 2) separate detection rates for each age class varying in the same manner annually [p(STAGES+t)], 3) separate detection rates for each age class, with each age class following an independent log linear trend through time [p(STAGES*T)], and 4) separate detection rates for each age class varying according to the same log linear trend [p(STAGES+T)]. Of these, the best-supported model, [p(STAGES+T)], resulted in a net reduction of 72.62$QAIC_c$ relative to our global model. Finally, we investigated the additive (+) and multiplicative (*) influence of sex (covariate: SEX) on resighting probability. Our best-supported model included a sex-effect on the resighting probability of second year piping plovers (p(STAGES + T+ SEX_{p2})) and resulted in a further reduction of 2.62 QAIC_c. We then examined subsets of this 142 parameter model to investigate age-specific apparent survival (Lebreton et al. 1992).

To test whether there was evidence for age-dependence in piping plover apparent survival, we simplified the fully parameterized model for apparent survival by building: constant (.) and age dependent (AGE) models. We began by reducing the fully parameterized model for apparent survival to test the number of age classes supported. Past survival models have supported the division of apparent survival into two age classes: hatch year (HY) and after hatch year (AHY) (Larson et al. 2000, Roche et al. 2008). We held apparent survival constant across years and tested (via QAIC_c) whether anything from one to four age classes were better supported. The best-supported model (8 parameters and resulting in a reduction of 183.58 QAIC_c) included only two age-classes: HY and AHY. However, the three age-class model, which included separate age classes for HY, second year (SY), and after second year (ASY) was only slightly less well supported (with only one additional parameter it was still within 2 QAIC_c of the best-supported model) indicating the addition of another age class did explain some of the variability in apparent survival. We used the model with two age-classes to investigate whether there was an influence of age within AHY survival rates. To do so, we included an additional parameter which constrained the AHY age-class to a logistic age trend such that within the constant intercept for AHY, plovers of older ages would follow different survival rates according to a logistic trend. This 9 parameter model [ϕ(HY., AHY+AGE),p(4-AGES+T+SEX$_{p2}$))] was best-supported and led to an additional reduction of 0.31 QAIC$_c$.

We used this best-supported model of age, year, and sex effects on apparent survival and detection probabilities to explore the relationship between apparent survival and reproduction in male and female plovers, thus testing the four age-dependent hypotheses mentioned earlier. To determine whether male and female piping plovers experienced differential age-related survival probabilities we added the covariate: SEX to our best-supported model and an interaction term between SEX and AGE. We then included the following reproduction-related covariates to our best-supported model [ϕ(HY., AHY+AGE),p(STAGES+T+SEX$_{p2}$)]. For each reproductive covariate we tested for main effects as well as interactions with AGE and SEX(Table 2); for example, we predicted that survival costs associated with egg production would be born disproportionately by females whereas costs associated with chick rearing would be born disproportionately by males. To test whether earlier recruitment into the breeding population influenced apparent survival, we included the covariate: second year nest (SYN). This individual covariate was categorical and represented whether a piping plover was known to nest (1) or not (0) in their second year. To test whether the amount of reproductive effort expended was related to apparent survival, we included the following covariates: number of nests initiated (NESTS) and number of eggs tended (EGGS). To test whether reproductive success and apparent survival were related, we included the final two covariates: number of chicks hatched (CHICKS) and number of chicks fledged (FLEDGLINGS).

As our objective was to determine whether there was support for an effect of each covariate individually on survival, we compared model-support only within nested subsets of models that included the same covariate. We selected the top-supported models (via $QAIC_c$) to best represent the influence of each individual reproductive covariate on apparent survival. However, we did not compare model rankings among apparent survival models featuring different reproductive covariates nor did we attempt to create a universal 'top-model' including all reproduction covariates because we were interested in the individual effect of each on survival.

General Linear Mixed-Models

We used general linear mixed-modeling (GLMM) to ascertain the influence of age and individual variability on reproductive effort and success in piping plovers. We built regressions for measures of reproductive effort and success using GLMMs following Poisson distributions in program R (CRANS 2009). We used the number of nests initiated (nests) as a response variable to measure reproductive effort, and we used the number of chicks hatched (chicks) and chicks fledged (fledglings) as response variables to measure reproductive success. When regressing variables related to reproductive effort, we included only individuals for whom an original nest failed in our dataset; individuals who did not fail would have had no opportunity to initiate multiple nests as piping plovers are not multi-brooded (Elliott-Smith and Haig 2004). When regressing variables related to reproductive success, we included all known age-individuals with reproductive histories in our dataset. For all regressions, we began with a full model and sequentially removed covariates that were the least explanatory, based on absolute values of β/SE (i.e., Z-scores). We compared the AIC value of the reduced model upon removal of each term and accepted the new model only if the AIC value was lower than the model it was nested within. We calculated AIC values using 2Loglikelihood – 2k (where 'k' is the number of parameters in the model). Once we had arrived at a top model through elimination of terms, we tested whether adding the random-effect of individuals onto the intercept or slope terms decreased model AIC values using R-package lme4 (Bates and Maechler 2009). Our analysis of the influence of age on reproduction in piping plovers was initially based on a sample of 257 uniquely banded individuals with known ages and reproductive histories. However, missing data for several of the covariates included in our analyses changed these sample sizes depending on the reproductive response variable investigated and thus we report specific sample sizes for each model.

Julian nest initiation date. Date of nest initiation is an age-dependent factor leading to increased reproductive success in many bird species (citation). Therefore, we used all plovers of known age with reproductive histories (*n* = 249 individuals) to regress the Julian nest initiation date as a linear function of: age, age^2, sex, first, and year. We treated sex as categorical variables and accounted for non-independence among reproducing individuals by treating individual identity as a random effect on the intercept term as well as the slopes of age and age at first breeding.

Nests. The number of nests (*n* = 245 individuals*)* was a measure of the total number of nests a plover initiated during a given breeding season. Only individual plovers that were known to have lost their original nest (and thus had the opportunity to renest) were included in this portion of the analysis. We modeled number of nests initiated as a linear (Poisson) function of: age, age^2, sex, age at first nesting attempt (first), Julian initiation date (jid), year of nest initiation (year), and all two-way interaction terms. We treated sex as a categorical variable and accounted for non-independence among individuals by treating individual identity (band number) as a random effect on the intercept as well as the slopes of age at first breeding, initiation date, and age.

Chicks. The number of chicks (n = 249 individuals) was a measure of the total number of chicks hatched by a plover during a given breeding season. All plovers of known age with reproductive histories were included in this portion of the analysis. Our analysis was identical to that reported for Nests.

Fledglings. The number of fledglings (n = 249 individuals) was a measure of the total number of chicks surviving to the age of fledging (i.e. the age at which flight is acquired) during a given breeding season. All plovers of known age with reproductive histories were included in this portion of the analysis..

Results

Age-dependent survival.

Our analysis was based on a sample of 1,335 uniquely-banded hatch-year piping plovers and our results suggested strong support for an influence of age on survival. Our best-supported model included separate intercepts for ϕ_{HY} and ϕ_{AHY} as well as an additional parameter representing a linear senescent decline in AHY survival as a function of increasing age (Fig. *; β_{AGE} = -0.076, 95% CI: -0.173-0.021). Describe this effect using endpoints: predicted survival for 1-year-old plovers was 0.75, whereas it declined to 0.61 for 10-year old plovers. We found no evidence for an influence of sex or sex by age interaction on apparent survival (Table 2).

Age-dependent reproduction.

We used the number of nests initiated and eggs tended to represent the reproductive effort undertaken by breeding piping plovers. Our analysis of the factors influencing the numbers of nests initiated annually revealed a quadratic influence of plover age (Table 3, Figure 2a); older individuals tended to initiate more nests. In addition, there was a positive relationship between age at first breeding and the annual number of nests initiated, suggesting that individuals recruiting into the breeding population at later ages were more likely to renest than individuals recruiting at younger ages (Table 3).

Number of chicks hatched was positively related to plover age, but the relationship between age and fledging success differed between the sexes (Table 3). Older females had a higher likelihood of fledging more chicks, whereas older males were less likely to fledge as many chicks as younger males or same-aged females (Figure 2b). However, males that began breeding at earlier ages were less likely to fledge as many chicks as males that delayed their age at first breeding (Figure 2c). Plovers fledged more young if nests were initiated earlier in the breeding season (Table 3). In addition, a notable degree of variability in fledging success was due to heterogeneity among individuals, as evidenced by a large random effect on the intercept term (SD = 1.003).

Finally, older plovers were more likely to initiate nests early in the breeding season than younger individuals (Figure 2d). There was model support for a random effect of the individual piping plover for the intercept term (SD = 3.874), indicating the variation in timing of nest initiation was partly driven by individual variation (Table 3).

Reproduction and survival.

Based on the sample of 257 known-aged individuals for which we had reproductive histories, we investigated the effects of reproductive effort and reproductive success on age- and sex-dependent variation in apparent survival. We found evidence for additive effects of all reproductive covariates on apparent survival, evidence for interactive effects between age and all reproductive covariates, and evidence for interactive effects between sex and measures of reproductive success (e.g. Chicks and Fledglings; Table 2).

Individuals capable of hatching more chicks experienced higher apparent survival rates ($\beta_{CHICKS} = 0.256$, CI: 0.044 – 0.468). This effect was especially prominent among females, who experienced apparent survival rates ~30% higher if they hatched four chicks rather than zero (Figure 3a). Similarly, there was both sex- and age-dependent variation in apparent survival in relation to number of chicks fledged. Individuals capable of fledging more chicks experienced higher apparent survival rates ($\beta_{FLEDGLINGS} = 0.219$ CI: 0.009 – 0.429), and this trend was more pronounced among females than males

(Figure 3b).

Piping plovers that nested as 1-year olds had higher apparent survival throughout life for both sexes. In addition, individuals nesting in their second year, were more likely to experience low apparent survival rates if they were less successful at hatching or fledging chicks (Figure 3c and 3d). Piping plovers capable of initiating more nests experienced higher rates of apparent survival (β_{NESTS} = -0.934 CI: -1.98 – 0.115), and older individuals capable of initiating multiple nests experienced higher apparent survival rates than younger individuals capable of initiating multiple nests, ($\beta_{NESTS*AGE}$= 0.263 CI: -0.039 – 0.56) (Figure 4a). Finally, older individuals that hatched or fledged more chicks experienced higher apparent survival rates than similarly aged individuals with lower reproductive success ($\beta_{CHICKS*AGE}$ = 0.080 CI: -0.004 – 0.163 and $\beta_{FLEDGLINGS*AGE}$ = 0.066 CI: -0.018 – 0.150)) (Figure 4b).

Discussion

Older piping plovers have higher reproductive success but lower survival. However, these seemingly straightforward relationships are complicated by several factors, rendering simple explanations untenable. For example, the age of breeding individuals was unrelated to their reproductive effort, but a greater degree of reproductive effort was associated with increased survival. Additionally, despite the positive association between age and reproductive success and the negative association between age and survival, individuals capable of greater reproductive success also experienced higher survival probabilties. Finally, although reproductively successful plovers of both sexes experienced increased survival rates with increased reproductive success, the magnitude of this effect was much stronger for females. Reproductively unsuccessful females were less likely to survive than males while successful females were more likely to survive than males. Here we discuss how the relationship between the particular components of age-dependent reproduction and survival in piping plovers compares to that of other species and how these results should be interpreted in light of the predications of the selection, recruitment, restraint, and constraint hypotheses.

Reproductive Effort.

The number of nests initiated by piping plovers, our metric of reproductive effort was significantly positively related to the date of nest initiation in a given breeding season and weakly associated with age; younger and older individuals initiated fewer nests than middle aged individuals. This specific relationship has been previously documented for wood thrush (*Hylocichla mustelina*), in which females of middle age had a greater likelihood of initiating more nesting attempts than the youngest or oldest individuals (Brown and Roth 2009). However, what has been more commonly found is that the likelihood of renesting increases monotonically with parental age (Becker et al. 2001, Green 2001, Altwegg et al. 2007). Although in the case of female brown thornbills (*Acanthiza pusilla*) researchers suspected this effect was linked to the greater propensity among elder females to nest earlier (Green 2001), our results, which suggested the number of nesting attempts was more associated with nest initiation date than age, appeared to be in the minority.

We found that reproductive effort was closely associated with the date of nest initiation; individuals that nested earlier were capable of greater annual reproductive effort. In many birds, date of nest initiation is positively related to age, with younger individuals more likely to nest later than older birds (Blums et al. 1997, Espie et al. 2000, Murphy 2004). In piping plovers, the date of nest initiation was best explained by a quadratic effect of age representative of senescence, with young breeders initiating nests later than those of older ages. A similar senescent type effect was documented in both female wood thrush and mute swans (*Cygnus olor)*, where females of middle age were more likely to nest earlier than the youngest and older individuals (McCleery et al. 2008, Brown and Roth 2009). The variability in piping plover nest initiation dates was also associated with heterogeneity among individuals, suggesting individuals did not change nest initiation dates throughout their lifetimes. Several other studies have determined that the trend towards earlier nest initiation dates occurs within individuals, rather than through selective loss of late breeding individuals or acquisition of early breeding individuals among older cohorts. For example, Krüger (2005) found that the date of first breeding advanced with age within individual female Goshawks (*Accipiter gentilis*) and Murphy (2004) documented that age-dependent advances in nest initiation dates in Eastern kingbirds (*Tyrannus tyrannus*) also occurred within individuals. Perhaps most applicable for comparison to piping plovers, McCleery et al. (2008) found that the tendency of middle-age female swans to nest earlier than the youngest and oldest individuals was also influenced by individual heterogeneity, concluding that this pattern was likely caused by a combination of individual improvement and population level selection processes.

Reproductive success.

Both measures of piping plover reproductive success, number of chicks hatched and number of chicks fledged, were positively correlated with parental age. This was particularly true for the number of chicks hatched, where reproductive success increased with parental age and there was no evidence that this relationship varied between sexes or among individuals. Relatively few studies have documented a similar effect of age on hatching success. In brown thornbills there was no evidence for an influence of age on hatching success, whereas in barn owls (*Tyto alba*) only males demonstrated increased hatching success with age (Green 2001, Altwegg et al. 2007). In Leach's storm petrel (*Oceanodroma leucorhoa*), Mauck et al. (2004) documented pronounced increases in hatching success between the first through fourth years of breeding, but found that hatching success reached a plateau after 4 years of breeding experience. However, common terns (*Sterna hirundo*) seemed to display a relatively similar pattern to piping plovers with hatching success increasing as a linear function of age (Nisbet et al. 2002).

The relationship between age and fledging success was far more complicated than for number of chicks hatched. Our results suggested that as female plovers aged they had a higher probability of fledging more young, whereas in male plovers, fledging more young was more closely associated with the age at which an individual was first observed breeding; with males recruiting later fledging more young. There are several studies that document a positive association between fledging success and age, but none explicitly suggesting age at recruitment played a role in reproductive success. In Montagu's harrier (*Circus pygargus*), older females laid larger clutches and raised larger broods than younger females, young male brown thornbills were less likely to fledge as many young as older males, adult male common terns were more likely to fledge young than younger individuals, and in both sexes of goshawks the number of young produced increased with increasing age (Lozano et al. 1997, Green 2001, Kruger 2005, Arroyo et al. 2007). Although Lee et al (2008) detected a senescent effect among older common murres (*Uria aalge*), fledging success increased from younger ages into middle age. These studies did not report contrasting patterns between the sexes either because they were not present or the studies did not investigate patterns in both sexes. However, there is some precedent to suggest reproductive strategies may differ between the sexes (Brown and Roth 2009). In their study of barn owls, Altwegg et al. (2007) found that fledgling success increased with female age, but for males they could only report that males of higher age-classes fledged more young than lower age-classes. If the older male age-classes were composed of individuals that recruited at a later age, these results would be similar to what we report for piping plovers.

Survival

There was evidence for a negative linear effect of age on survival, but no evidence for a quadratic effect suggestive of accelerating senescence; however, samples sizes became extremely small beyond 6 years of age, and so it would have been difficult for us to detect an accelerating effect of senescence that occurred beyond this age class. In addition, there was no strong evidence of sex-dependent survival among after hatch year plovers suggesting that both sexes experienced the same survival trend with increasing age. We found no studies for which a similar age-dependent trend (decreasing survival with increasing age) was documented for both sexes. Altwegg et al. (2007) found no evidence for reduced survival at older ages in barn owls, while Brown and Roth (2009) documented a senescent effect of age on the survival of male wood thrush but no evidence of age-dependent trends in female wood thrush. The only studies for which similar age-dependent trends in survival were documented was for female willow tits (*Poecile montanus*), in which female survival significantly declined after five years of age, and female goshawks for which survival systematically declined with age (Orell and Belda 2002, Krüger 2005).

Interestingly, taking into account whether or not a plover was known to have nested during its second year (i.e. at one year of age) was strongly associated with survival probability throughout life. Individuals that postponed reproduction until after their second year had higher survival probabilities than individuals that began nesting as one year olds. This effect occurred in both sexes, although more females (##%) began nesting as 1-year olds than males (##5). The same trend has been documented for blue petrels (*Halobaena caerulea*) and kittiwakes (*Rissa tridactyla*), in which survival was lowest among first-time breeders and in the case of kittiwakes was unrelated to the degree of individual breeding experience (Cam et al. 2000, Barbraud et al. 2004).

There was only weak evidence to suggest the reproductive effort of either sex was associated with changes in survival probability. Plovers that were capable of initiating more nests in a given breeding season experienced higher survival probabilities, and the magnitude of this effect increased with age, but the model projecting these associations was not well supported. Studies documenting associations between survival and reproductive effort (generally measured as the size of eggs or clutches) have produced mixed results. McCleery et al. (2008) found that individual mute swans laying the largest clutches also had the longest lifespans. However, in red-billed choughes, Reid et al. (2003) found nearly the opposite; females that laid the smallest clutches during their early years of breeding lived the longest. Finally, González-Solís et al. (2004) found return rates were lower for common terns that laid smaller eggs.

There was a strong positive association between piping plover survival and reproductive success for both sexes, whether reproductive success was measured by number of chicks hatched or number of chicks fledged. However, there were strong sex differences in the relationship of reproductive success with survival. Female plovers with greater reproductive success experienced survival probabilities ~30% greater than females with low reproductive success. The influence on male survival was less drastic, with only a 10% increase in survival for male plovers experiencing high reproductive success relative to low reproductive success. There are few studies that have directly incorporated some aspect of reproduction success directly into survival analysis (but see Cam et al. 2000 and Barbarud et al. 2005 for the effect of breeding experience), leaving us few equivalent studies to compare our results. Some studies have indirectly examined this relationship by assessing the association of reproductive success and longevity. In

Leach's storm petrel, individuals with the highest reproductive success are also the longest lived (Mauk et al. 2004). Whereas for the common guillemot, individuals who experienced intermediate reproductive success during early life underwent slower rates of reproductive senescence (i.e. experienced greater reproductive longevity) (Reed et al. 2008). Although they did not explicitly test the association of reproduction with survival, Brown and Roth (2009) found patterns similar to what we found in piping plovers; declining reproductive success and survival in aging females, while increasing reproductive success and survival in aging males through middle age.

Conclusion.

The combined results of this analysis of age- and sex-dependent reproduction and survival in piping plovers provide sufficient evidence to reject both the restraint and constraint hypotheses. While survival declined with age, reproductive effort did not further decrease survival and reproductive effort did not increase with age. Past studies have found evidence from both when concluding in favor of the restraint hypothesis (Reid et al. 2003, Reed et al. 2008). Predictions of the constraint hypothesis indicate reproductive success should increase with age due to the enhancement of parenting skills through experience. Many studies have documented individual improvement in reproductive success with experience (McCleery et al. 2009, Brown and Roth 2009). And recent evidence presented by Limmer et al. (2009), who documented increased foraging and chick-feeding efficiency with increased age and experience in common tern, indicates individual improvement is likely a very real phenomenon.

We believe the strong sex-effect on reproductive success suggests patterns observed for males and females are best explained by the recruitment and selection hypotheses respectively. The selection hypothesis predicts there is a positive association between increased reproductive success and increased survival. There is pronounced evidence for this in female piping plovers, which experience substantially elevated survival rates when capable of greater reproductive success. There is substantial precedent set by past studies for the presence of differential selection resulting in age-dependent reproductive success, in specifically females (Espie et al 2000) and both sexes alike (Cam et al. 2000, Mauk et al. 2004, Barbraud et al. 2005). However, it should be noted that this hypothesis does not exclude an additional effect of individual experience on reproductive success (McCleery et al. 2008). In male piping plovers there was a less pronounced selection effect (i.e. the capability of fledging more offspring was not associated with substantially increased survival probability). Instead, males who nested for the first time in their second year experienced lower survival throughout life and were less likely to produce as many fledglings annually as individuals who began breeding at last ages. These patterns fit with those predicted by the recruitment hypothesis, for which there is less support in the literature. This effect has perhaps been best demonstrated in the lesser snow goose, where physiological maturation was measurable in the increasing size of eggs, and thus reproductive success, with age (Robertson et al. 1994).

Table 1. Predictions of the four hypotheses of age-specific variation in reproductive success on variation in survival and reproduction (effort and success). The red arrows indicate what will happen to the response variables (i.e. either survival or reproduction) given the directionality of the pertinent independent variables (black arrows). I indicate which covariates are pertinent to each analysis for reproduction (lower case) and survival (upper case) as well as the response variables that will be used in all reproduction analyses. For further clarification of the analyses used and covariate definitions please refer to the methods section. [CJS = Cormack Jolly Seber analysis, GLMM = General Linear Mixed-Models analysis, AGE/age = age of a plover during a given breeding attempt, first = age of a plover at its first breeding attempt, SYN = whether or not a plover nests in its second year, CHICKS/chicks = number of chicks hatched annually, FLEDGLINGS/fledglings = number of fledglings hatched annually, individual* = random effect of an individual plover].

Table 1

Hypothesis	**Fig**	**Survival**(CJS)		**Reproduction**(GLMM)		
		prediction	*covariates*	*prediction*	*response*	*covariates*

Selection	1a	↑: ↑age ↑: ↑reproductive success	AGE CHICKS FLEDGLINGS	↑ success: ↑age	chicks fledglings	age
Recruitment	1b	↑: ↑ age at first breeding ↓: ↑ reproductive effort ↓: ↑ reproductive success	AGE SYN NESTS CHICKS FLEDGLINGS	↑ success: ↑ age at first breeding	chicks fledglings	age first
Restraint	1c	↓: ↑age ↓: ↑ reproductive effort	AGE NESTS EGGS	↑ effort: ↑ age	nests eggs	age
Constraint	1d	NA	NA	↑ effort: ↑age ↑ success: ↑age	nests eggs chicks fledglings	age first individual*

Table 2. Set of a priori models used to estimate apparent survival of piping plovers, 1993-2009 in relation to age, sex and reproduction. Models are differentiated according to the type of reproductive covariate tested. Parameters having independent (i.e. factorial) relationships are joined by * (e.g., AGE*SEX), whereas parameters having parallel (additive) relationships are joined by + (e.g., AGE + SEX). Akaike's information criterion (AIC) values were corrected for effective sample size (1,773) and overdispersion ($\hat{c} = 1.34$), yielding quasi-AIC (QAICc) values. ΔQAICc values, model weights (w_i), quasi-deviance (QDev), and parameter counts (K) were used to compare among competing models. For all models, HY apparent survival was held constant [φ_{HY}.] and detection probability was represented by p(STAGES+T+SEX_{p2}).

Model (ϕ)	**QAIC_c**	**$\Delta\mathrm{QAIC}_c$**	**w_i**	**K**	**QDev**
AHY + AGE	**1962.09**	**20.24**	**0.000**	**9**	**1943.99**
AHY	1962.39	20.76	0.000	8	1946.31
AHY + AGE + SEX	1962.73	20.89	0.000	10	1942.61
AHY + AGE + AGE^2	1964.05	22.20	0.000	10	1943.92
AHY + AGE + SEX + AGE*SEX	1964.75	22.91	0.000	11	1942.60
AHY + AGE + SYN	**1958.18**	**16.33**	**0.000**	**10**	**1938.05**
AHY + SYN	1958.71	16.87	0.000	9	1940.61
AHY + AGE + SYN + AGE*SYN	1959.49	17.30	0.000	11	1937.34
AHY + AGE + SEX + SYN	1961.27	19.42	0.000	11	1939.12
AHY + AGE + SEX + SYN + SEX*SYN	1963.24	21.39	0.000	12	1939.06
AHY + AGE + SEX + SYN + NESTS	**1960.03**	**18.18**	**0.000**	**12**	**1935.85**

AHY + AGE + SYN + NESTS +SYN*NESTS	1961.03	19.19	0.000	12	1936.85
AHY + AGE + NESTS + AGE*NESTS	1962.96	21.11	0.000	11	1940.81
AHY + AGE + NESTS	1964.02	22.17	0.000	10	1943.90
AHY + AGE + SEX + NESTS	1964.74	22.90	0.000	11	1942.59
AHY + AGE + SEX + NESTS + SEX*NESTS	1966.00	24.16	0.000	12	1941.82
AHY + AGE + SYN + CHICKS + SYN*CHICKS	**1941.85**	**0.00**	**0.444**	**12**	**1917.67**
AHY + AGE + SYN + SEX + CHICKS + SYN*CHICKS	1941.98	0.13	0.415	13	1915.77
AHY + AGE + CHICKS + AGE*CHICKS	1948.99	7.14	0.028	11	1926.84
AHY + AGE + SEX + CHICKS + SEX*CHICKS	1949.34	7.49	0.010	12	1925.16
AHY + AGE + SEX + CHICKS	1949.83	7.99	0.1008	11	1927.68
AHY + AGE + CHICKS	1950.91	9.07	0.005	10	1930.79
AHY + AGE + SYN + FLEDGLINGS + SYN*FLEDGLINGS	**1947.05**	**5.21**	**0.033**	**12**	**1922.88**
AHY + AGE + SYN + SEX + FLEDGLINGS + SYN*FLEDGLINGS	1947.41	5.57	0.027	13	1921.20
AHY + AGE + SEX + FLEDGLINGS + SEX*FLEDGLINGS	1948.60	6.76	0.015	12	1924.43
AHY + AGE + FLEDGLINGS + AGE*FLEDGLINGS	1949.08	7.23	0.027	11	1926.93
AHY + AGE + SEX + FLEDGLINGS	1949.62	7.78	0.021	11	1927.47
AHY + AGE + FLEDGLINGS	1949.70	7.85	0.009	10	1929.57

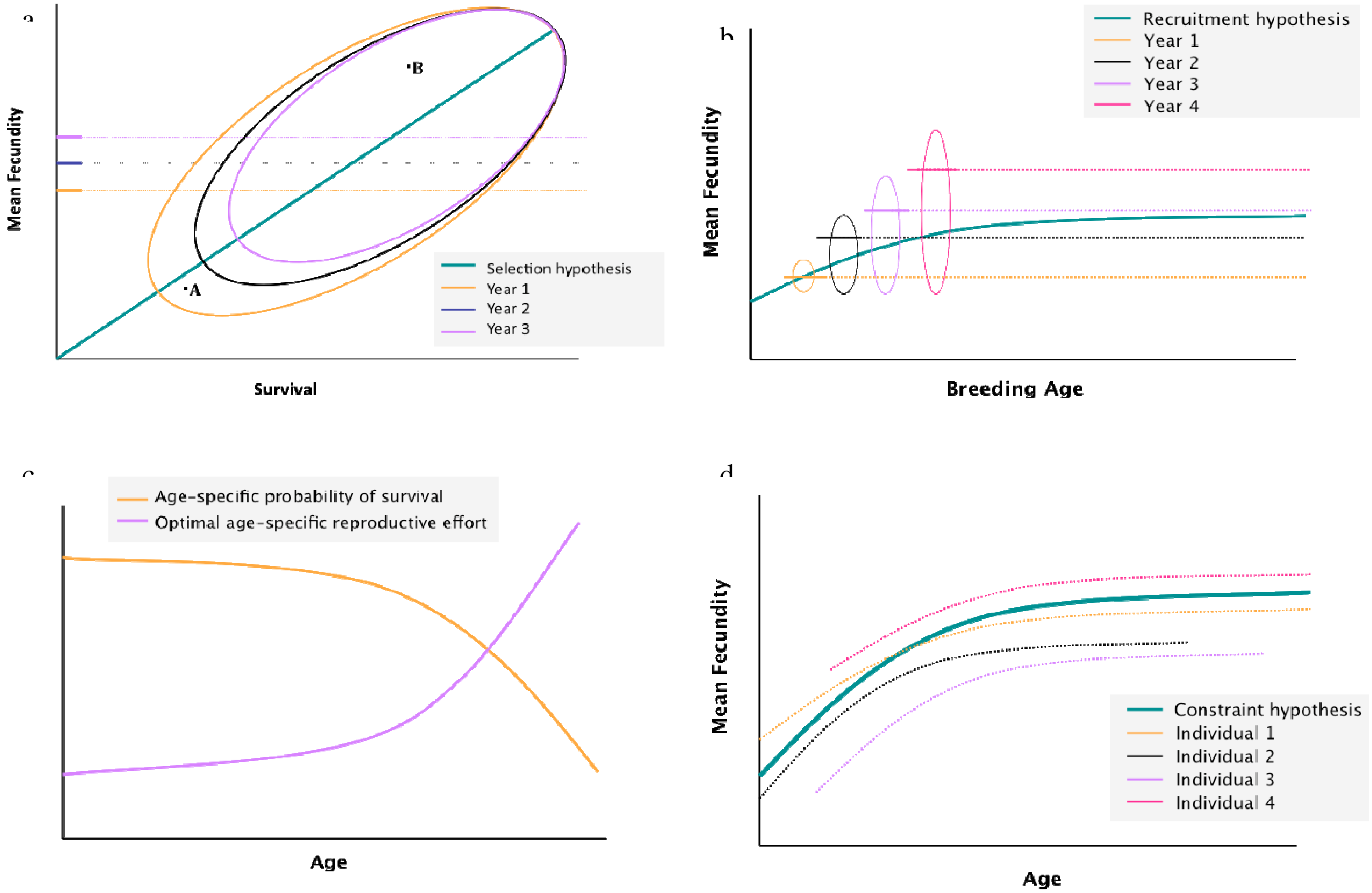
Table 3. Results of the regression analysis of factors influencing reproductive effort and success in piping plovers. Beta-estimates (β) generated by the top-supported models are presented for all included covariates along with their 95% lower (LCI) and upper (UCI) confidence intervals. We have additionally reported the F-statistic and associated P-values generated by performing analysis of variance on all top-models prior to the addition of random effects.

	β	**LCI**	**UCI**	**F-Stat.**	**P-value**
Nests					
intercept	8.039	-36.264	52.342		
year	-0.004	-0.026	0.018	1.43	0.231
sex	-0.165	-2.141	1.810	0.14	0.703
jid	-0.004	-0.015	0.006	6.06	0.014**
first	0.153	0.072	0.235	0.83	0.363
age^2	-0.002	-0.013	0.010	3.46	0.063
sex : jid	0.002	-0.012	0.015	0.90	0.342
age : first	0.000	-0.059	0.058	0.00	0.951
sex : first	-0.030	-0.237	0.177	0.73	0.394
Chicks					
intercept	1.108	1.028	1.189		
age	0.015	-0.006	0.036	3.69	0.055**
Fledglings					
intercept	-53.692	-87.460	-19.925		
age	-0.018	-0.099	0.063	6.29	0.007**
year	0.029	0.012	0.046	11.73	0.001**
jid	-0.023	-0.035	-0.012	11.52	0.001**
sex	-0.263	-0.549	0.022	0.04	0.856
first	-1.336	-2.183	-0.490	1.07	0.136
age : sex	-0.056	-0.118	0.006	0.53	0.670
first : age	0.029	-0.011	0.069	0.87	0.637
first : sex	0.258	0.098	0.419	6.96	0.005**
first : jid	0.008	0.003	0.014	3.42	0.015**
Random Effect	*Std. Dev.*				
individual	1.003				
Julian Initiation Date					
intercept	154.908	152.061	157.755		

age	-6.609	0.769	-5.101	191.64	< 0.000**
age^2	0.393	0.084	0.557	22.17	< 0.000**
Random Effect	*Std. Dev.*				
individual	3.838				

Figure 1. Predictions of the four age-dependent reproduction hypotheses**. (1a)** The **selection hypothesis** predicts a positive correlation between survival and fecundity among individuals. Individuals with poor fecundity are differentially eliminated early on and the mean fecundity of the population (represented by dashed horizontal lines) increases with age through a reduction in variance (diagonal ellipsoids). For example, individual A is eliminated after 1 year, whereas individual B contributes data all 3 years.**(1b)** The **recruitment hypothesis** predicts that individuals of different quality start breeding at different ages and that early recruitment leads to reduced fecundity (i.e., individuals remain on the horizontal dashed line of their initial recruitment age). The addition of more high-fecundity phenotypes with age causes an increase in the mean fecundity (thick green line) of the population as well as increased variance (vertical ellipsoids).**(1c)** The **constraint hypothesis** predicts mean fecundity (thick green line) increases with age because individuals (thin lines) become better breeders through experience. Each individual is expected to show this same age-dependent increase in individual performance (with some variation) and variance in age-dependent breeding performance does not change with age.**(1d)**The **restraint hypothesis** predicts young individuals withhold maximal reproductive effort in favor of enhanced survival. As the probability of senescent mortality increases (orange line), individuals invest more in reproduction (purple line), leading to enhanced reproductive success in older individuals. Reproductive effort (as measured by allocation of parental investment and risk taking) is expected to increase with age.

Figure 1.


a
Mean Fecundity
Survival
B
A
Selection hypothesis
Year 1
Year 2
Year 3
b
Mean Fecundity
Breeding Age
Recruitment hypothesis
Year 1
Year 2
Year 3
Year 4
c
Age-specific probability of survival
Optimal age-specific reproductive effort
Age
d
Mean Fecundity
Age
Constraint hypothesis
Individual 1
Individual 2
Individual 3
Individual 4

c

Figure 2. Relationship between age, reproductive effort, and reproductive success in piping plovers. Figure 2a) illustrates how the number of nests initiated annually varies by piping plover age, according to model [Nests Initiated ~ year + sex + jid + first + age^2 + sex:JID + age:first +sex:first]. Figure 2b) illustrates how the number of chicks fledged annually varies by piping plover age, according to model [Chicks Fledged ~ age + year + jid + sex + first + age:sex + first:age + first:sex + first:JID]]. Figure 2c) illustrates how the number of chicks fledged annually varies by piping plover age at first breeding, according to model [Chicks Fledged ~ age + year + jid + sex + first + age:sex + first:age + first:sex + first:JID], the dark gray line represents males and the light gray line represents females. Figure 2d) illustrates how Julian nest initiation date varies by piping plover age, according to model [Julian Nest Initiation Date ~ age + age^2, random effect on intercept: individual]. For all figures, dashed lines represent upper and lower 95% confidence intervals, while solid lines represent estimates based on the indicated model solved at mean covariate values. Columns of corresponding line colors represent sample sizes [left vertical axis], while lines represent apparent survival rates [right vertical axis].

Figure 2.

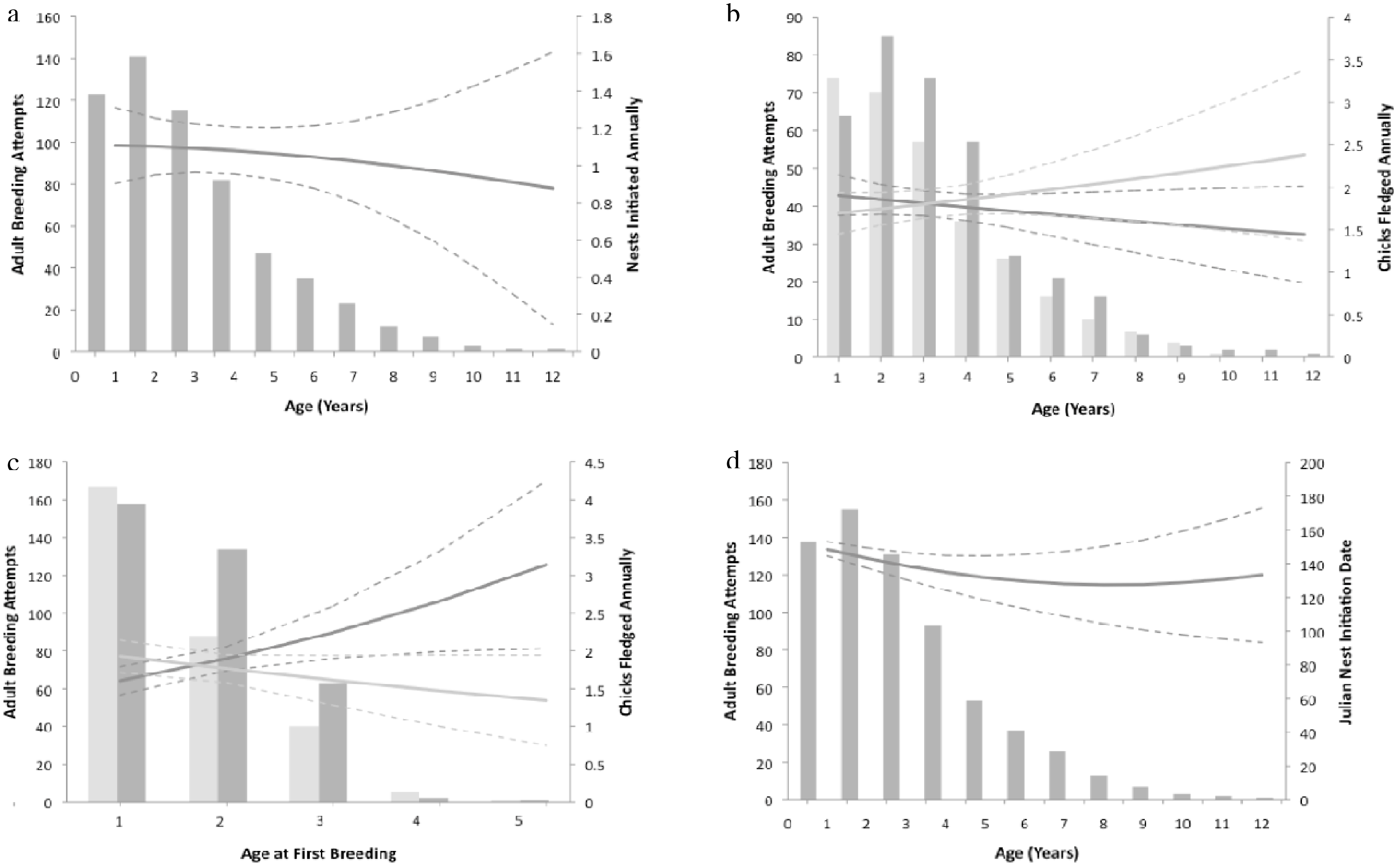

a
Adult Breeding Attempts
Nests Initiated Annually
Age (Years)
0 20 40 60 80 100 120 140 160
0 0.2 0.4 0.6 0.8 1 1.2 1.4 1.6 1.8
0 1 2 3 4 5 6 7 8 9 10 11 12
b
Adult Breeding Attempts
Chicks Fledged Annually
Age (Years)
0 10 20 30 40 50 60 70 80 90
0 0.5 1 1.5 2 2.5 3 3.5 4
1 2 3 4 5 6 7 8 9 10 11 12
c
Adult Breeding Attempts
Chicks Fledged Annually
Age at First Breeding
0 20 40 60 80 100 120 140 160 180
0 0.5 1 1.5 2 2.5 3 3.5 4 4.5
1 2 3 4 5
d
Adult Breeding Attempts
Julian Nest Initiation Date
Age (Years)
0 20 40 60 80 100 120 140 160 180
0 20 40 60 80 100 120 140 160 180 200
0 1 2 3 4 5 6 7 8 9 10 11 12

Figure 3. Relationship between reproduction and annual apparent survival for piping plovers by sex and age at first breeding. Figure 3a) depicts the relationship between the number of chicks hatched annually and apparent survival based on model [ϕ(HY., AHY + AGE + SEX + CHICKS + SEX*CHICKS), *p*(STAGES + t + p_{sex2})]. Figure 3b) depicts the relationship between the number of chicks fledged annually and apparent survival based on model [ϕ(HY., AHY + AGE + SES + FLEDGLINGS + SEX*FLEDGINGS), *p*(STAGES + t + p_{sex2})]. Figure 3c) depicts apparent survival given the number of chicks hatched annually by plovers that did and did not nest in their second year [ϕ(HY., AHY + AGE + SYN + SEX + CHICKS + SYN*CHICKS), *p*(STAGES + t + p_{sex2})]. Dashed lines represent plovers nesting in their second year while solid lines represent plovers nesting for the first time after their second year. Figure 3d) depicts apparent survival given the number of chicks fledged annually by plovers that did and did not nest in their second year [ϕ(HY., AHY + AGE + SYN + SEX + FLEDGLINGS + SYN*FLEDGLINGS), *p*(STAGES + t + p_{sex2})]. Dashed lines represent plovers nesting in their second year while solid lines represent plovers nesting for the first time after their second year. For each figure, light gray represents females while dark gray represents males. Columns of corresponding line colors represent sample sizes [left vertical axis], while lines represent apparent survival rates [right vertical axis].

Figure 3.

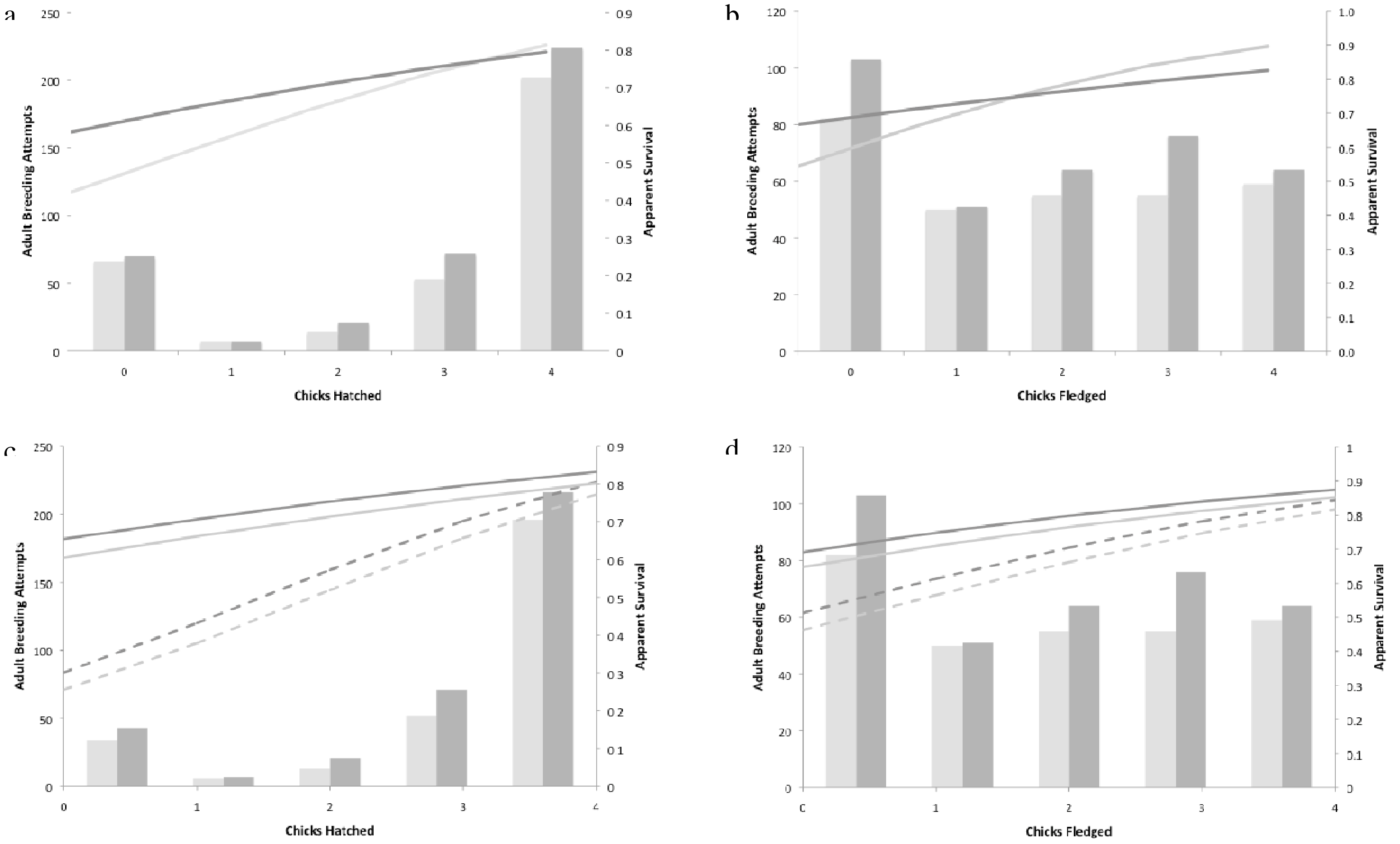
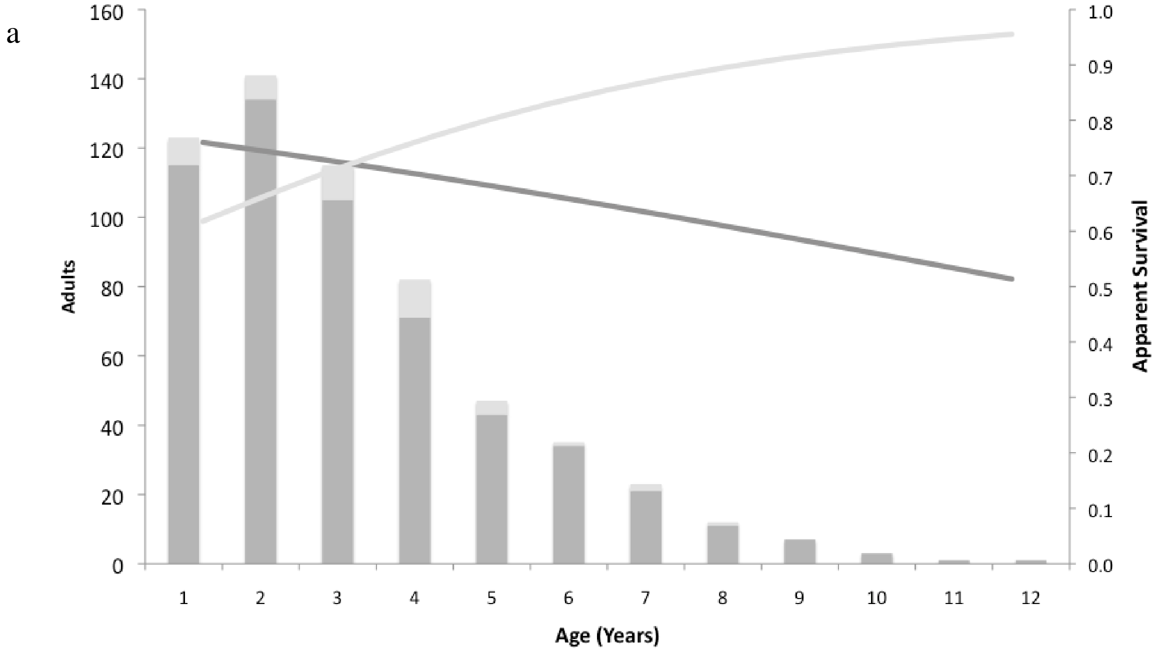
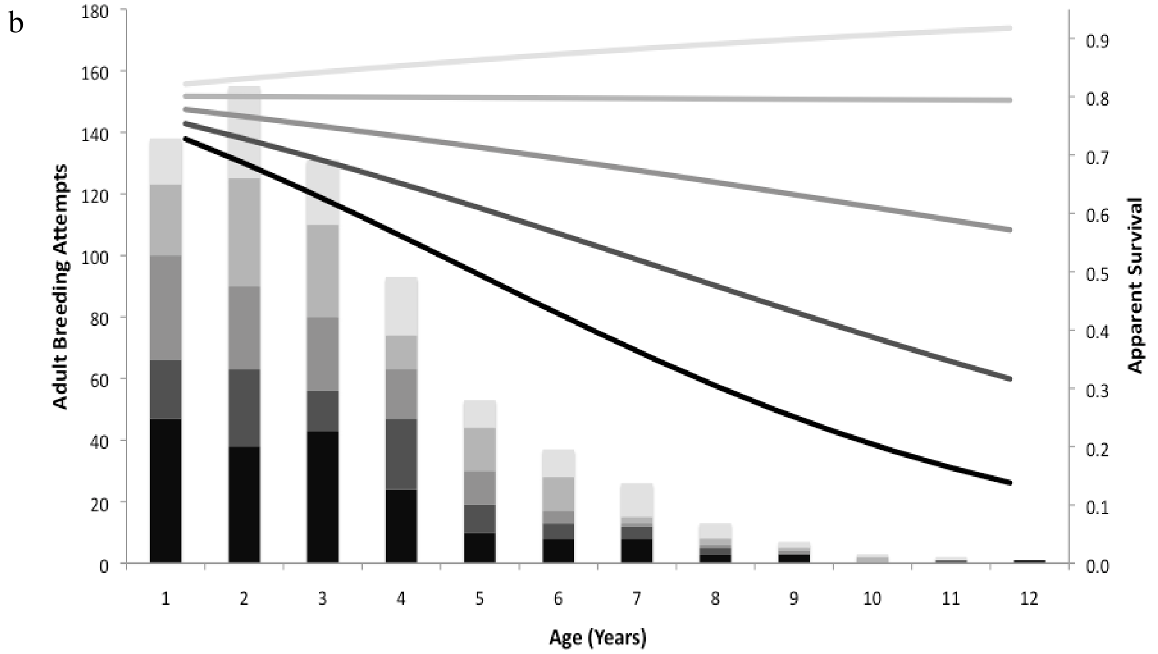

a
250
200
150
100
50
0
Adult Breeding Attempts
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Apparent Survival
0
1
2
3
4
Chicks Hatched
b
120
100
80
60
40
20
0
Adult Breeding Attempts
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Apparent Survival
0
1
2
3
4
Chicks Fledged
c
250
200
150
100
50
0
Adult Breeding Attempts
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Apparent Survival
0
1
2
3
4
Chicks Hatched
d
120
100
80
60
40
20
0
Adult Breeding Attempts
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Apparent Survival
0
1
2
3
4
Chicks Fledged

Figure 4. Relationship between reproduction and annual apparent survival for piping plovers by age.Figure 4a) illustrates how age-dependent apparent survival [right vertical axis] changes with the number of nests initiated (light gray line: 1 nest, dark gray line: 2nests), according to model [ϕ(HY., AHY + AGE + NESTS + AGE*NESTS), p(STAGES + t + p_{sex2})]; columns of corresponding colors depict sample sizes [left vertical axis]. Figure 4b) illustrates how age-dependent apparent survival (right vertical axis) changes with number of chicks fledged (color of lines follow a gradient of 0 to 4 chicks fledged, i.e. black line: no chicks fledged, lightest gray line: 4 chicks fledged), according to model [ϕ(HY., AHY + AGE + FLEDGLINGS + AGE*FLEDGLINGS), p(STAGES + t + p_{sex2})]; columns of corresponding colors depict sample sizes [left vertical axis].

Figure 4.


a
160
140
120
100
80
60
40
20
0
Adults
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Apparent Survival
1
2
3
4
5
6
7
8
9
10
11
12
Age (Years)


b
180
160
140
120
100
80
60
40
20
0
Adult Breeding Attempts
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Apparent Survival
1
2
3
4
5
6
7
8
9
10
11
12
Age (Years)

Chapter 5

Relative fitness of wild and captive-reared Piping Plovers: does egg salvage contribute to recovery of the endangered Great Lakes population?

1. Introduction

Small populations are highly susceptible to stochastic events, genetic bottlenecks, and other factors of an ‘extinction vortex’ that may hasten population decline by reinforcing vulnerability to an original or persistent threat (Gilpin and Soulé, 1986). A well-designed recovery program must identify and nullify the source of population decline while employing strategies intended to enhance the genetic and demographic viability of the existing population (Caughley, 1994). Strategies to remedy external causes of decline may include habitat protection (Nolet and Rosell, 1998; Lafferty et al., 2006) and management of invasive predators (Fritts and Rodda, 1998; Wiles et al., 2003), whereas translocation programs (Caughley, 1994; Westemeier et al., 1998) and captive management (Seddon et al., 2007) may be used to mitigate the effects of small population size. In all cases, establishment of a self-sustaining wild population ultimately defines success (Griffith et al., 1989). Because 15-31% of all species within each major taxon are listed as globally threatened (IUCN, 2004), it will benefit resource-strapped conservationists to adopt complementary recovery strategies. In the Great Lakes, small-scale captive-rearing of piping plover (*Charadrius melodus*) chicks hatched from salvaged abandoned eggs has occurred under the umbrella of a larger and range-wide recovery effort focused on habitat protection, nest monitoring and public outreach. This study examines whether released captive-reared piping plover chicks are capable of surviving and reproducing at rates similar to wild-reared chicks.

The piping plover is a small shorebird endemic to North America and restricted to three breeding populations: the Atlantic Coast, Great Plains, and Great Lakes (Elliott-

Smith and Haig, 2004). The Great Lakes piping plover inhabits coastal dune ecosystems; increases in beach recreation, residential development and watershed management threaten its nesting habitat (Lambert and Ratcliff, 1981). When listed as federally endangered under the U.S. Endangered Species Act in 1986, the Great Lakes piping plover population consisted of ~17 breeding pairs nesting in isolated locations along the coasts of lakes Michigan and Superior (USFWS, 1985). At listing, beach closure, nest monitoring and nest protection were adopted to help the population recover from this critically low size.

Despite intensive management efforts, nest abandonment remained a problem; in the late 1980s research was initiated to investigate the feasibility of cross-fostering or hand-rearing piping plover chicks from eggs salvaged from abandoned nests (Powell et al., 1993; Powell et al., 1997). Captivity offers imperiled populations a respite from threats faced in the wild. In addition, captive-based recovery programs may breed animals for maximal genetic diversity or rear and release juveniles to supplement a wild population (Harvey et al., 2004; Powell et al., 1997; Galbraith et al., 2007). When the wild population is imperiled but remains viable a segment may be taken into captivity to reinforce wild-reproduction and confer protection from persisting threats (Crone et al., 2007).

Successful hand-rearing of killdeer (*Charadrius vociferus*) as a surrogate species suggested that captive-rearing of piping plovers was a potential management strategy (Powell et al., 1997); consequently, egg salvage and release of captive-reared piping plover chicks began in 1992 (Powell et al., 1997; USFWS, 2003). The program is currently a collaborative endeavor between the US Fish and Wildlife Service (USFWS), the University of Michigan Biological Station, Detroit Zoological Society, > 20 American Zoological Institutions and the University of Minnesota.

The goal of the Great Lakes captive-rearing program is to produce fledglings that can be released into the wild to augment the wild-breeding population. This effort has continued on a small scale from 1992-2008, thereby mitigating the impact of egg loss due to natural causes (e.g. predation of incubating adults, weather events). It has also coincided with a population-wide mark-recapture study that has allowed investigators to determine survival and reproductive success of individually-marked birds. Using banding and nesting data obtained 1993 – 2008 we estimated: 1) apparent annual survival, 2) mean number of eggs laid, 3) mean number of eggs hatched, and 4) mean number of chicks fledged. We compared these estimates to assess the relative fitness of captive versus wild-reared piping plovers and employed matrix-based reproductive values to project lifetime reproductive contribution for both groups.

2. Methods

2.1 Field methods

Historical, recent and potential nesting habitats were surveyed at the beginning of each breeding season to locate nesting pairs. Once located, pairs were monitored from nest initiation through chick fledging. All piping plovers were banded using U.S. Geological Survey (USGS) metal bands and Darvic color bands. Nesting adults and captive-reared chicks received unique color combinations, whereas wild-reared chicks received brood-specific color combinations. Nesting adults were trapped on the nest using a single-chambered Potter trap (Lincoln, 1947); chicks were caught by hand. As authorized under federal permit, eggs abandoned as a result of mate-loss, storm damage or other forms of disturbance were collected and transported to the salvage captive-rearing facility at the University of Michigan Biological Station, Pellston, MI. Procedures used to hand-rear piping plover chicks are detailed in Powell et al. (1997). Number of viable eggs collected, hatched, and successfully reared to release age (circa 27 – 35 days) were recorded annually beginning in 1992. For wild-nesting birds we recorded the number of nests, eggs laid, eggs hatched and chicks fledged per pair.

2.2 Survival

Annual estimates of apparent survival (ϕ) and detection probability (ρ) were calculated using program MARK (White and Burnham, 1999). We constructed a Cormack-Jolly-Seber (CJS) 'recaptures only' data set with 15 encounter occasions and two attribute groups (i.e. captive- or wild-reared). We included days-old at banding (DOB) and Julian hatch date (HATCH) as covariates. The covariate DOB accommodated differing ages at capture for wild-reared chicks and differing ages at release for captive-reared chicks as captive-reared plovers are banded a day prior to release. Model structure for both Φ and ρ was allowed to vary by plover age (1-4 annual age categories), year (constant or fully temporal), rearing-method (captive or wild), HATCH and DOB.

A bootstrap goodness-of-fit test of the most highly parameterized model was used to generate expected deviance (Cooch and White, 2004). This value was divided by observed model deviance to estimate the variance inflation factor ($\hat{c} = 1.07$). Inclusion of the adjusted $\hat{c}$ yielded corrected quasi-AIC ($QAIC_c$) values for each model (Burnham and

Anderson, 2002). $QAIC_c$ values account for overdispersion, effective sample size and number of estimable parameters in model ranking (Larson et al., 2000; Sandercock et al., 2006). Model ranking and selection was based on ΔQAIC and model weight (w_i), which is an estimate of each model's likelihood of being the best model, given the model set and the data (Burnham and Anderson, 2002).

Because of sparse data, especially for captive-reared chicks, we could not consider fully parameterized models, so we adopted a sequential approach to model construction (Lebreton et al., 1992; Chouinard and Arnold, 2007). We first considered models of age-dependent survival and resighting, while holding rates constant across years. For survival, we began with a model considering 4 separate age-classes (hatch year [1], second year [2], third year [3], and after third year [4+]), and then we sequentially pooled the oldest age class with the second-oldest age class (i.e., 4+ with 3 in round 1) until further pooling was not supported by lower $QAIC_c$ values. The same procedure was then repeated for estimates of age-dependent resighting rates (second year [2], third year [3], fourth year [4], and after fourth year [5+]). The model allowing the greatest number of meaningful age-dependent estimates was used to model effects of year and rearing-method. Models incorporating temporal variation in survival or resighting probabilities for captive-reared individuals were constrained to have parallel structure between wild- and captive-reared individuals (Lebreton et al., 1992). This presumes that wild- and captive-reared plovers will have similar patterns of year-specific variation in survival or resighting rates (i.e., certain years were bad for survival among both groups, or certain years were good for resighting among both groups), but did not presume that these rates were the same across groups, only that they fluctuated in parallel. This constraint resulted in large parameter savings and was necessary to even consider models of time-dependent survival and recapture probabilities in captive-reared chicks. We modeled influences of rearing method (wild vs. captive) last, because we were most interested in this variable and so we wanted to have the most appropriate age- and time-specific model with which to test for rearing effects (Lebreton et al., 1992). We reasoned that effects of captive rearing might be negligible, persist for only a short term (i.e., the first year after release), or persist for longer terms, so we considered models with no captive effect, captive effects for the first year only, or captive effects persisting throughout all age classes. After we fit rearing group effects, we added days old at banding (DOB) and Julian hatch-date (HATCH) as individualized covariates to all top-fitting models. We considered permutations where the relationship between stage 1 survival and each covariate was described by a common logistic regression (i.e., one pooled intercept and slope), parallel regressions (i.e., separate intercepts but common slope), or independent regressions (i.e., separate intercepts and slopes) for captive- and wild-reared chicks (Cooch and White, 2004). All well supported models incorporated DOB and HATCH as covariates in life stage 1 $\phi$for both rearing groups. When estimating stage 1 ϕ we entered user-specified covariate values of DOB for the two rearing-groups to minimize differences between the two groups (DOB: wild-reared = 15 days, captive-reared = 25 days), but we did not set them equal because there was essentially no overlap in covariate values between groups (wild-reared: 9 ± 4 days; captive-reared: 27 ± 3 days) and we would have had to extrapolate outside the typical range of our covariates in order to set them equal.

We used the best-supported MARK model to generate mean estimates of Φ and ρ for each recognized age class for both captive- and wild-reared plovers. Mean values for time-specific parameters were generated by taking the geometric mean of annual estimates from the best-supported model. We excluded estimates for the final year (ϕ: 2007 – 2008, ρ: 2008) because they were not fully resolvable (i.e., the final ϕ and ρ can only be estimated as their product; Cooch and White 2004).

2.3. Reproduction

We compared the mean number of eggs laid, chicks hatched (all nests), chicks hatched (successful nests) and chicks fledged by captive-reared parents to wild-reared male parents. A ‘successful nest’ was a nest from which at least one chick fledged. All breeding captive-reared individuals nested with a wild-reared mate. If an individual nested more than once, the arithmetic mean was taken for eggs laid, chicks hatched and chicks fledged. We limited the number of nesting wild-reared individuals used in our analyses due to the small number of breeding captive-reared individuals (n = 10). We used wild-reared male plovers in our analyses because conditioning on one sex insured that all individual-based breeding histories were independent. We further restricted the wild sample to male plovers that bred during 1998-2008 (time-period with breeding captive-reared individuals) and were 1-5 years of age (age distribution of breeding captive-reared individuals). An upper-tailed random permutation test was coded using R version 2.6.2 (CRANS, 2006) and used to compare hatching and fledging success of wild-reared male parents versus captive-reared parents (Araki et al., 2007). The mean hatching and fledging success was estimated for wild-reared (n = 57) and captive-reared (n = 10) parents and a difference taken (e.g. T.obs = $\bar{x}_{\text{wild}} - \bar{x}_{\text{captive}}$). The two groups were then pooled (*n* = 67) and a sample of 10 individuals was randomly drawn from the pooled group without replacement; the mean of this sample was taken. The mean of the random sample was then subtracted from the mean of the group without these sampled individuals. This process was repeated over 9999 iterations. P-values were generated by summing the number of differences ≤ T.obs and dividing by 10,000.

To compare the reproductive contribution of captive versus wild-reared plovers, we constructed simple matrix-based life-cycle models (Beissinger et al., 2006) and estimated age-specific reproductive value and finite population growth rate using PopTools version 3.0.2 (Hood, 2008). We estimated breeding propensity of second year captive and wild-reared plovers as the number of plovers known to have nested divided by the estimated number of second year plovers (no. banded× stage 1 ϕ). For plovers in their third year and greater we estimated breeding propensity as age-specific ρ because virtually all breeders were identified each year so non-breeding was the most likely explanation for resighting failures (Arnold et al., 2002). We did not use this same approach for second year breeding propensity because wild-reared plovers received brood-specific band combinations in their first year while captive-reared plovers received individual-specific combinations, thus rendering second year captive-reared plovers more visible than wild-reared. We assumed fledging success was constant from stages 2 – 5+. We estimated fecundity by taking the product of breeding propensity, fledging rate, and stage 1 survival. These values were generated for one sex only.

3. Results

The Great Lakes salvage captive-rearing program released 142 piping plover chicks between 1992 and 2008 (Table 1); 22 of these captive-reared plovers survived their first year and 10 subsequently nested in the Great Lakes (Table 1). As of 2008, captive-reared plovers have fledged 26 chicks in the wild. An additional 10 chicks were captive-reared from eggs salvaged from the nest of a captive-reared plover. Captive-reared plovers have raised 5 offspring that returned and nested in the Great Lakes.

The best-supported CJS models had 2 life stages for apparent annual survival (1 ϕ, 2+ ϕ) and 4 life stages for detection probability (2 ρ, 3 ρ, 4 ρ, and 5+ p) (Table 2, Fig. 1). Temporal variability in 1 ϕ and 2+ ϕ was constrained to reflect parallel variation between rearing groups and age classes, but evidence for temporal variation in adult survival was weak and the second best model treated 2+ ϕ as constant. All top models included DOB and HATCH as 1 ϕ covariates for both captive- and wild-reared plovers (Table 2). The best supported model assumed captive- and wild-reared plovers had separate intercepts and slopes (Table 2, Fig. 3). Temporal variability in ρ was incorporated for 2ρ, 3 ρ, 4 ρ, and 5+ p individuals in both rearing groups, with ρ constrained to reflect parallel variability across all 8 age-by-rearing-group combinations. Intercepts were nearly identical in 6 of the 8 groups (3 ρ C ~ 3 ρ W, 4 ρ C ~ 4 ρ W, and5+ ρ C ~ 5+ ρ W), and so we made a post-hoc decision to pool these groups for purposes of estimating ρ, leaving only 5 intercepts estimated for ρ (2 ρ C, 2 ρ W, 3 ρ, 4 ρ, and5+ ρ). This model supported differences between captive- and wild-reared plovers in 1 ϕ and 2+ ϕ, yielding higher estimates of Φ for wild-reared plovers than for captive-reared plovers (Table 3). This model also supported differences in ρ between captive- and wild-reared birds in their second year (Table 3).

There was no difference in the number of eggs laid by wild- and captive-reared plovers. However, wild-reared plovers hatched significantly more eggs and fledged slightly more chicks per breeding season than did captive-reared plovers (Table 4). The expected future reproductive contribution of newly released captive-reared plovers was only about a third that of newly fledged wild-reared plovers; however, if captive-reared plovers survived their first year, their future reproductive contributions were almost identical to those of wild-reared plovers (Fig. 2). The survival and reproductive values ascribed to captive-reared plovers did not project positive rates of population growth (Fig. 2).

4. Discussion

The Great Lakes piping plover salvage and captive-rearing program was initiated to bolster productivity by preventing complete clutch loss in situations of nest flooding and parental nest abandonment (Powell et al., 1997). As a percentage of the total number of clutches initiated the annual number of clutches lost has remained at approximately 15% since 1993. In recent years, flooding during severe weather events (18 of 69 lost clutches) and predation of nesting adults (30 of 69 lost clutches) has accounted for most clutch loss outside egg predation. The captive-rearing program has released at least 12 plovers that survived their first year but were not observed breeding despite being observed in appropriate nesting habitat (Table 1). In addition, the program has released individuals that have returned to nest and produced young that have also returned to nest (Table 1). Given the small size of the Great Lakes piping plover population this contribution should be considered a success for the program. However, when compared to wild-reared plovers, captive-reared plovers showed clear evidence of diminished survival and were less likely to hatch eggs and raise chicks that fledged. To encourage the long-term survival of captive-reared individuals, factors causing these differences should be identified and redressed.

4.1. Survival

Most published hatch year survival estimates of captive-reared birds have occurred over short study periods (e.g. < 3 years) for non-migratory or island species. In general, captive-reared birds appear to survive as well as wild-reared birds in most studies. Captive-reared snowy plovers (*Charadrius alexandrinus*) and puaiohi (*Myadestes palmeri*) had return-rates that were comparable to wild-reared individuals (Quinn, 1989; Tweed et al., 2003), whereas hand-reared Mississippi sandhill cranes (*Grus canadensis pulla*) had higher survival rates than parent-reared birds (Ellis et al., 2000). Mauritius kestrels (*Falco punctatus*) hacked over a 14 year period had comparable apparent survival to wild birds; however, the wild population used for comparison was itself originally composed of reintroduced captive stock which may have resulted in lower than ‘natural’ survival rates (Nicoll et al., 2004). Captive or hand-reared chicks may also disperse differently than wild-reared individuals; an important consideration in studies that measure apparent (i.e. local) survival (Sandercock, 2006). Movements and habitat selection of captive-reared takahē (*Porphyrio mantelli*) differed significantly but not detrimentally from wild-reared birds (Maxwell and Jamieson, 1997); however, hacked aplomado falcons (*Falco femoralis septentrionalis*) had higher juvenile dispersal and lower apparent survival than wild-reared falcons, suggesting an intrinsic difference in fitness (Brown et al., 2006). Analysis of captive-reared female mallards (*Anas platyrhynchos*) suggests that low return-rates are indicative of compromised pre-fledging or pre-migratory survival (Yerkes et al., 1998).

Approximately 90% of all chicks hatched in the captive rearing facility are banded and released (~27 days of age); in contrast, only about 40% of all chicks hatched in the wild survive long enough to be banded (~ 9 days of age). By incorporating days-old-at-banding (DOB) as a covariate when estimating apparent stage 1 survival for captive- and wild-reared plovers we attempted to correct for age-dependent variation in stage 1 ϕ associated with differential ages at banding/release. While we expected to see an effect of DOB on survival in wild-reared plovers (pre-fledged birds are subject to higher mortality risks), we were surprised to see that this effect was also apparent in captive-raised chicks. According to our best-fitting MARK model, the apparent survival of captive-reared chicks did not approach rates observed among wild-reared plovers until age at release exceeded 30 days (Fig. 3). Since 2005, all captive-reared plovers have been released at >30 days of age, but given the projections of this model we recommend releasing captive plovers at even greater ages (ca. 35 days of age).

Stage 1 apparent survival of captive- and wild-reared plovers was negatively impacted by later hatch dates. Although the distributions of hatch dates for both groups were similar, this negative association was more pronounced in captive-reared chicks (Fig. 3). These results suggest captive-reared plovers hatched after the beginning of July are significantly less likely to survive to their second year than wild-reared plovers. Relatively few plovers have hatched in the captive-rearing facility past the beginning of July as generally the frequency of clutch losses decreases as the season progresses. Captive-reared plovers hatched and released later in the breeding season will likely suffer the same compromising factors as their wild-reared counterparts, but of additional concern is the increased likelihood that there will be no wild-reared plovers for these captive-reared plovers to associate with upon release.

There are several possible explanations for why captive-reared plovers have lower apparent survival rates than wild-reared plovers. Salvaged eggs may be inherently compromised if they are the result of a genetically unfit pairing of adults (Keller and Waller, 2002; Briskie and Mackintosh, 2004). They may be developmentally compromised if exposed to fluctuating temperatures or microbial infection between abandonment and collection (Batt and Cornwall, 1972; Cook et al., 2005; Godard et al., 2007). Finally, captive-reared chicks may develop abnormal behavior as a result of the captive-rearing process. Piping plovers are precocial, show no signs of imprinting and migrate separately from adults at the end of the summer (Powell et al., 1993). However, young spend extensive time with parents prior to fledging (Cairns, 1982; Elliott-Smith and Haig, 2004). The exact behaviors these chicks may learn during this period remain unknown, but it is likely chicks benefit from parental recognition and response to potential threats. Captive-reared chicks demonstrate an innate crouch-response to recorded parental alarm calls played when zookeepers enter the captive-rearing facility (Powell et al., 1993). However, we have not encouraged captive-reared young to associate parental alarm calls with other potential threats such as predators. Although there is evidence altricial and precocial avian species may have innate predator and alarm-call responses (Veen et al., 2000; Galbraith et al., 2007), captive-reared individuals across species have been observed to be typically less wary than wild individuals (Hellstedt and Kallio, 2005; Hess et al., 2005; Kelley et al. 2005). Predator-avoidance training has been used to encourage the development of fear response prior to reintroduction or release in other species (van Heezik et al., 1999; Griffin et al., 2000). Given the documented benefits of predator-avoidance training in other captive-reared species, it may benefit the Great Lakes captive-rearing program to adopt this technique in the future.

4.2. Reproduction

The goal of most captive-rearing programs is the addition of successfully breeding individuals into the wild population. Ideally, introduced captive-reared birds will be recruited into the breeding population, hatch eggs and fledge young with the same frequency as individuals hatched in the wild. However, assessments of reproductive success are few and mixed across studies of captive-reared and released avian species. Captive-reared aplomado falcons were less likely to survive and recruit into the breeding population (Brown et al., 2006). However, female captive-reared takahē recruited at an unexpectedly high frequency, a result of a skewed sex ratio in the wild breeding population; first-time breeding captive takahē had similar success to that expected for first-time breeders in this species (Maxwell and Jamieson, 1997). Although low sample sizes precluded statistical assessment, captive-reared puaiohi had comparable nest success to the wild-reared population, but built significantly more nests in trees than the cliff faces used by the wild population (Tweed et al., 2006). Hand-reared snowy plovers were as successful at fledging chicks as wild-reared plovers, but were slightly more likely to nest in low quality habitat (Page et al., 1989). Captive-rearing operations often occur on a small scale, over a short-duration, and suffer budget limitations that make follow-up observations of reproductive success challenging. These factors may account for the lack of consensus regarding reproductive success assessments of captive-reared birds.

Piping plover hatching and fledging success is heavily influenced by parental behavior; one or both parents stay with a brood of chicks from hatching until the chicks are capable of flight (Cairns, 1982; Elliott-Smith and Haig, 2004). Chicks are capable of independent foraging shortly after hatch but are dependent on the parent for thermoregulation, threat identification and defense of a suitable foraging territory (Cairns, 1982; Elliott-Smith and Haig, 2004). The significant difference in the number of chicks hatched from nests tended by captive-reared plovers suggests that captive-reared parents may differ from wild-reared parents in terms of their ability to identify potential threats or possibly select adequate nesting habitat (e.g. too close to water or parking lots). Because captive-reared chicks are hand-reared in an artificial environment, they have little exposure to adult piping plover behavior. Failure to learn predator associations as chicks may translate to an inability to recognize potential threats as an adult. Captive-reared plovers do not seem to differ from wild-reared birds in terms of their likelihood to nest in their second year or the habitat in which they are observed. However, it is disconcerting that only one of the 12 non-breeding captive-reared plovers observed during a breeding season was observed in two consecutive years. For the captive-reared plovers that did nest and raise young, there was not a statistically significant difference in the ability of captive-reared plovers to fledge chicks relative to wild-reared plovers. However, given the average number of chicks fledged for pairs with one captive-bred bird was 30% less than that of pairs with two wild-bred parents, captive-reared nesting adults should continue to be monitored to assess their reproductive potential. Without increased sample sizes, no definitive conclusions regarding this potential difference can be made.

5. Conclusion

If released at less than 30 days of age and after mid-June, captive-reared piping plovers had apparent survival rates far lower than wild-reared plovers. However, captive-reared piping plovers recruited into the breeding population and had comparable reproductive success to wild plovers. The relative rarity of breeding by captive-reared individuals indicates that, although salvage captive-rearing has coincided with population growth, it has not caused it. Instead, the captive-rearing effort provides a second-chance to pedigrees that might otherwise reach dead-ends. Ultimately, the small size of the Great Lakes population makes the contribution of each reproducing individual significant.

American zoological institutions have participated in the Great Lakes piping plover salvage captive rearing program by providing an experienced volunteer captive-rearing staff that has furthered knowledge of precocial avian husbandry, behavior and biology. Many participants have expanded their volunteer role to assist with monitoring and census efforts on the wintering grounds, thus playing a role in recovery outside the bounds of egg-salvage and captive-rearing. Therefore, aside from fulfillment of its original mission, the Great Lakes salvage and captive-rearing program has become increasingly important to building stakeholder involvement and strengthening volunteer support in the range wide recovery of the piping plover.

Table 1 – Summary of captive-rearing activities for Great Lakes Piping Plovers, 1992 – 2008. Non-breeding (NB) and breeding (B) captive-reared plovers resighted in life stage 2+ are listed according to the year they were released.

	Viable Eggs Salvaged	Eggs Hatched	Chicks Released	Resighted (AHY) NB	Resighted (AHY) B
1992	2	2	2	0	0
1993	4	3	3	0	0
1996	3	3	2	0	0
1997	4	4	4	1	2
1998	8	8	8	0	0
1999	4	2	2	0	0
2000	10	10	9	2	1
2001	4	3	3	0	0
2002	19	19	19	1	1
2003	12	12	8	1	1
2004	9	9	10	0	0
2005	18	18	15	3	0
2006	27	27	17	4	3
2007	27	16	12	0	2
2008	41	28	28	na	na
Total	192	164	142	12	10

Table 2 – Top supported Cormack-Jolly-Seber models used to estimate apparent annual survival (Φ) and detection probability (p) for Great Lakes Piping Plovers, 1993-2008. Akaike's information criterion (AIC) values were corrected for small sample size and overdispersion ($\hat{c} = 1.07$), yielding quasi-AIC ($QAIC_c$) values. $\Delta QAIC_c$ values and model weights (w_i) were used to rank best-fitting models according to variation in rearing method (CW means captive- and wild-reared groups different), age (Φ: 1 vs. 2+; ρ: 4 age specifies separate estimates for life stages 2, 3, and 4 and 5+), temporal variation (t specifies year-specific variation), Julian hatch date (HATCH) and days-old at banding (DOB). Parameters having independent (i.e. factorial relationships) are joined by *, whereas parameters having parallel (additive) relationships are joined by +.

1 Φ	**2+ Φ**	**ρ[1]**	**$QAIC_c$**	**$\Delta QAIC_c$**	**wi**	**No. parms.**	**Deviance**
(CW+t)*(DOB+HATCH)	+t	(CW*4-age)+t	1962.66	0.00	0.25	52	1854.94
(CW+t)*(DOB+HATCH)	Constant	(CW*4-age)+t	1962.87	0.21	0.23	41	1878.57
(CW+t)*HATCH	+t	(CW*4-age)+t	1970.63	7.97	0.01	50	1867.20
(CW+t)*DOB	+t	(CW*4-age)+t	1971.41	8.75	0.00	50	1867.97

[1]: The fully factorial CW*4-age model would have added 8 intercept parameters, but we combined life stages C-3 with W-3, C-4 with W-4, and C-5+ with W-5+ because they had virtually identical intercepts, so there were only 5 parameters.

Table 3 – Mean parameter estimates from the best-fitting MARK model comparing apparent annual survival and detection rates for captive-reared (C) and wild-reared (W) piping plovers. Stage 1 survival estimates are based on W plovers banded at 15 days of age and C plovers released at 25 days of age.

	Apparent Survival (Φ)				**Detection (ρ)**							
	1		**2+**		**2**		**3**		**4**		**5+**	
	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE
C	**0.081**	0.050	**0.682**	0.052	**0.808**	0.153	**0.580**	0.105	**0.834**	0.062	**0.962**	0.019
W	**0.293**	0.087	**0.780**	0.030	**0.293**	0.093	**0.580**	0.105	**0.834**	0.062	**0.959**	0.021

Table 4 – Comparative reproductive success of nesting captive-reared (C) and wild-reared male (WM) piping plovers.Successful nests were nests with a pair that fledged at least one chick.

		Eggs Laid			**Chicks Hatched** (all nests)			**Chicks Hatched** (succesful nests)			**Chicks Fledged**		
	n	Mean	SD	p-value	Mean	SD	p-value	Mean	SD	p-value	Mean	SD	p-value
C	10	**3.82**	0.38	0.15	**2.28**	1.31	0.03	**2.96**	1.03	0.04	**1.15**	1.39	0.08
WM	57	**3.91**	0.25		**3.10**	1.17		**3.56**	0.68		**1.80**	1.28	

Fig. 1– Annual apparent survival estimates from the best-fitting MARK model for stage 1 captive-reared (C) and wild-reared (W) piping plovers at 25 and 15 days of age respectively.

Fig. 1.

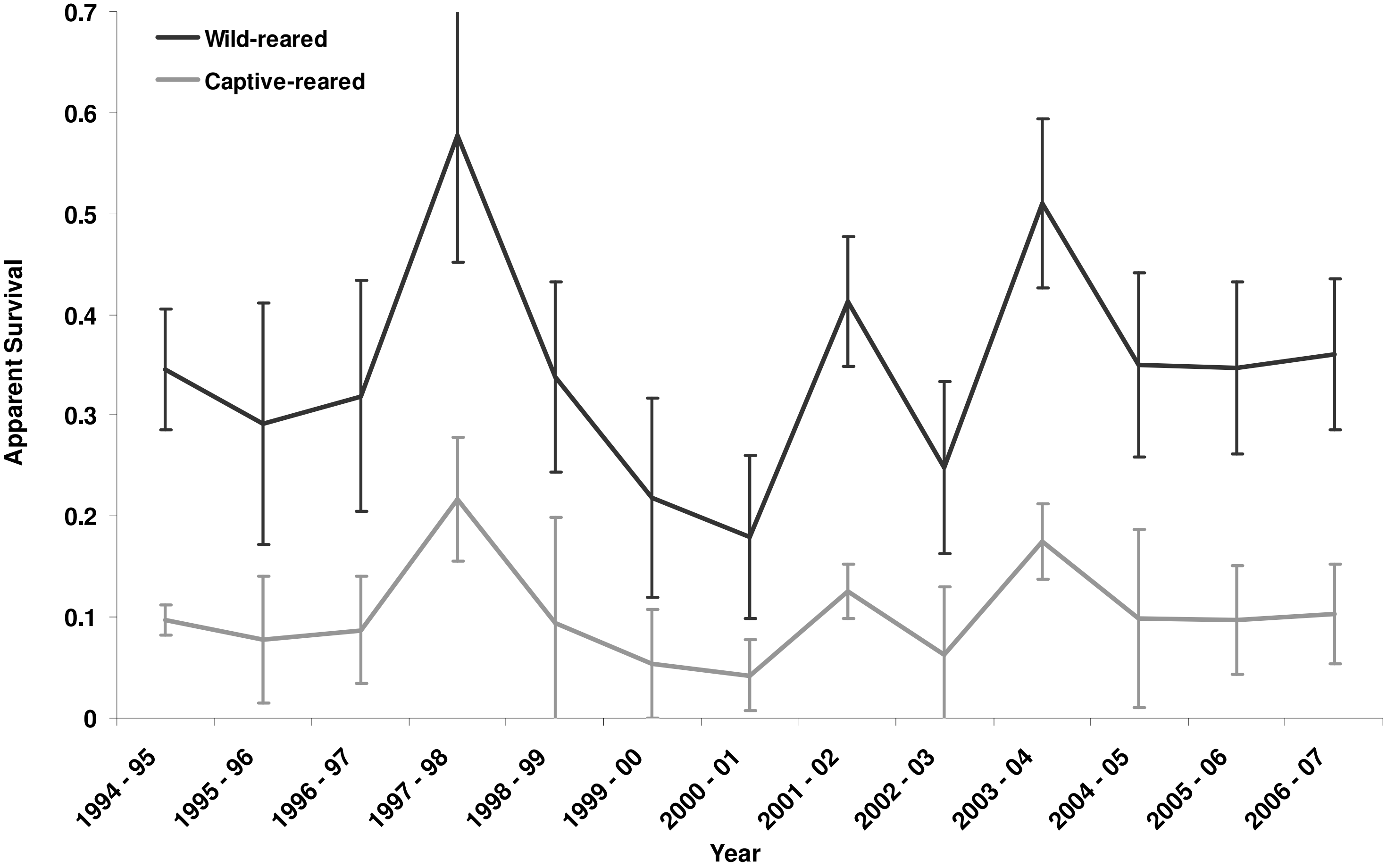

0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Apparent Survival
Wild-reared
Captive-reared
1994 - 95
1995 - 96
1996 - 97
1997 - 98
1998 - 99
1999 - 00
2000 - 01
2001 - 02
2002 - 03
2003 - 04
2004 - 05
2005 - 06
2006 - 07
Year

Fig. 2 – Reproductive contribution of captive-reared (C) and wild-reared (W) nesting Piping Plovers in the second year (2) to after fourth year (5+) following hatch year (1).Valuesare depicted as a proportion of total lambda for both groups.

Fig. 2.

	C				W			
	1	2	3	4+	1	2	3	4+
Breeding Propensity	0.78	0.58	0.83	0.96	0.63	0.58	0.83	0.96
Fledging Rate	0.58	0.58	0.58	0.58	0.91	0.91	0.91	0.91
Stage 1 Survival	0.08	0.08	0.08	0.08	0.29	0.29	0.29	0.29
Stage 2+ Survival	0.68	0.68	0.68	0.68	0.78	0.78	0.78	0.78
Fecundity	0.04	0.23	0.33	0.38	0.17	0.41	0.59	0.68
Lambda				0.71				1.00

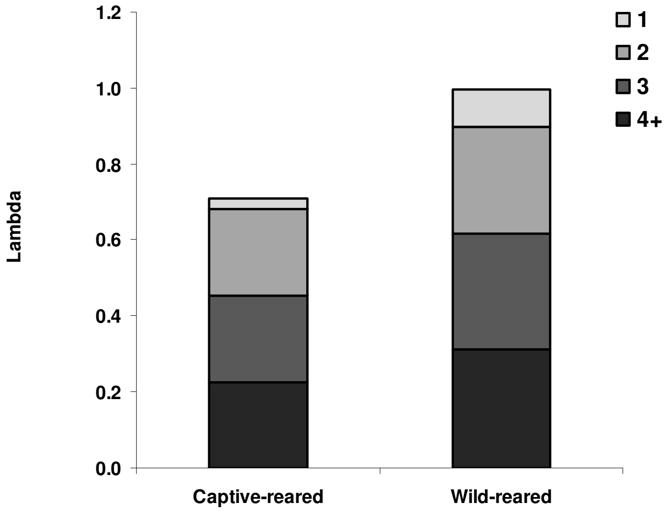
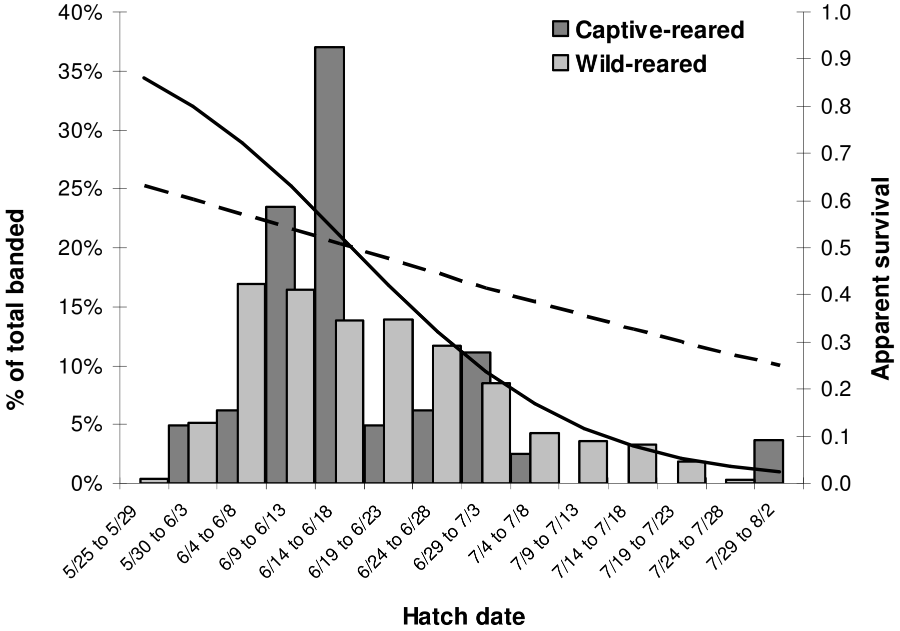


Fig. 3 – Influence of Julian hatch date (HATCH) and days old at banding (DOB) on apparent first-year survival (1φ) for captive-reared (C) and wild-reared (W) plovers. Percent of total plovers in a given group are represented by histograms with values on the left y-axis. Model-based survival estimates for captive-reared plovers are plotted as solid black lines on the appropriate distribution with values on the right y-axis; survival estimates for wild-reared plovers are plotted as dashed black lines.

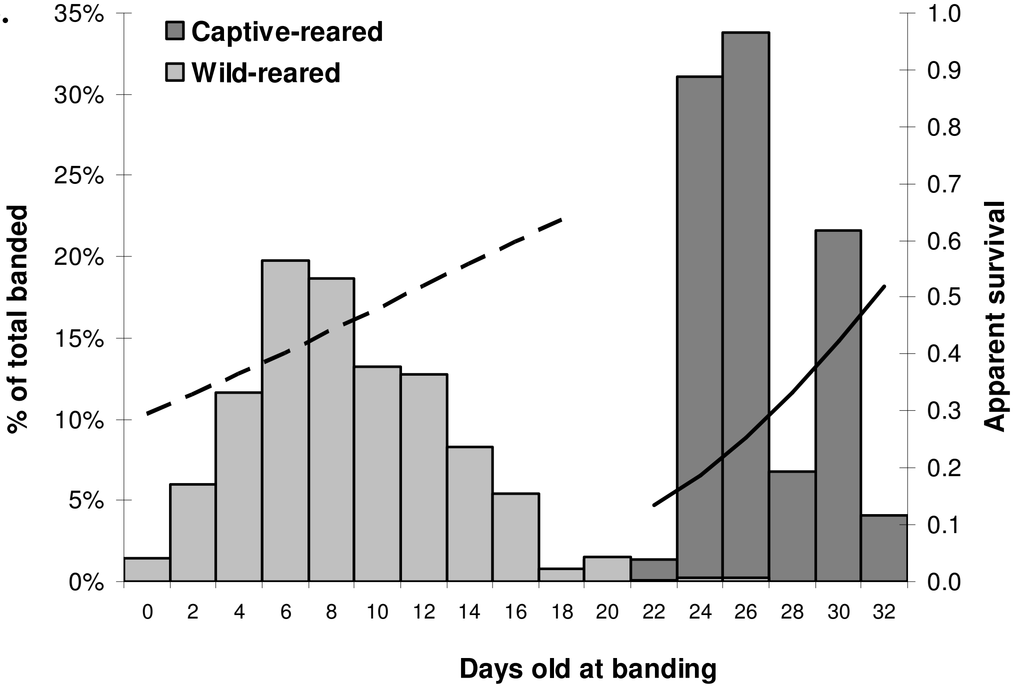
Fig. 3.

a



40%
35%
30%
25%
20%
15%
10%
5%
0%
% of total banded
Captive-reared
Wild-reared
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Apparent survival
5/25 to 5/29
5/30 to 6/3
6/4 to 6/8
6/9 to 6/13
6/14 to 6/18
6/19 to 6/23
6/24 to 6/28
6/29 to 7/3
7/4 to 7/8
7/9 to 7/13
7/14 to 7/18
7/19 to 7/23
7/24 to 7/28
7/29 to 8/2
Hatch date

b.



35%
30%
25%
20%
15%
10%
5%
0%
% of total banded
Captive-reared
Wild-reared
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Apparent survival
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
Days old at banding

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