



RESEARCH ARTICLE

Factors influencing nest survival and renesting by Piping Plovers in the Great Lakes region

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ABSTRACT

Renesting is an important breeding strategy used by birds to compensate for nest failure. If birds renest, clutch removal for captive rearing can be used to augment endangered populations; however, not all individuals renest following nest loss, and later nesting attempts may have lower survival rates and clutch sizes. We investigated variation in nest initiation date, clutch size, daily nest survival, renesting propensity, and renesting intervals of federally endangered Great Lakes Piping Plovers (*Charadrius melodus*) from 1993 to 2010. We also compared productivity under hypothetical clutch removal for captive rearing vs. non-removal scenarios. Nest initiation date was earlier for older adults and was more strongly affected by female than male age. Clutch size and nest survival decreased with later nest initiation, and nest survival increased with male age and nest age until close to hatching. Overall, Piping Plovers replaced 49% of failed nests. Renesting propensity decreased with later date, increased with each successive nesting attempt, and varied according to cause of failure; probability of renesting was highest following flooding and lowest for inviable clutches. Renesting intervals increased with age of the previous nest and averaged 4.2 days longer for birds that changed mates. Results also indicated that, compared to leaving eggs in situ, clutch removal for captive rearing would produce 43% fewer 1-year-old recruits, partly because renesting does not fully offset clutch removal; therefore, efforts to increase fledging success in this endangered population should focus on proactively protecting nests in situ rather than relying on collection of eggs for captive rearing.

Keywords: captive rearing, *Charadrius melodus*, clutch size, endangered species, nest success, Piping Plover, replacement clutch

Factores que influyen sobre la supervivencia de los nidos y la anidación repetida en *Charadrius melodus* en la región de los Grandes Lagos

RESUMEN

La anidación repetida es una importante estrategia reproductiva usada por las aves para compensar el fracaso de un nido. Si las aves vuelven a anidar, la remoción de las nidadas para su cría en cautiverio puede ser usada para aumentar las poblaciones amenazadas. Sin embargo, no todos los individuos vuelven a anidar luego de la pérdida de sus nidos y los intentos posteriores de anidación podrían tener menores tasas de supervivencia y tamaños de nidada. Investigamos la variación en la fecha de inicio de anidación, el tamaño de la nidada, la supervivencia diaria de los nidos, la predisposición a volver a anidar y los intervalos entre nidadas de un ave amenazada a nivel federal, *Charadrius melodus*, entre 1993 y 2010. También comparamos la productividad bajo la remoción hipotética de los nidos para su cría en cautiverio contra escenarios de no remoción. La fecha de inicio de la anidación fue más temprana para adultos mayores y se vio más fuertemente afectada por la edad de las hembras que por la edad de los machos. El tamaño y la supervivencia de la nidada disminuyeron cuando la anidación comenzó más tarde, y la supervivencia se incrementó con la edad de los machos y con la edad del nido hasta justo antes de la eclosión. En general, la población de *C. melodus* reemplazó el 49% de los nidos perdidos. La predisposición a volver a anidar disminuyó con fechas más tardías, se incrementó con cada intento sucesivo de anidación y varió de acuerdo a la causa de fracaso de los nidos; la probabilidad de volver a anidar fue mayor luego de inundaciones y menor en nidadas no viables. Los intervalos entre intentos de anidación se incrementaron con la edad del nido anterior y en promedio fueron 4.2 días más largos en aves que cambiaron de pareja. Los resultados también indican que, en comparación con dejar los huevos in situ, la remoción de la nidada para su cría en cautiverio produciría 43% menos aves reclutas de un año de edad, en parte debido a que la anidación repetida no sobrepasa totalmente la remoción de la nidada. Por ende, los esfuerzos para incrementar el éxito de emplumamiento en esta población amenazada deberían enfocarse en la protección proactiva de los nidos in situ en vez de basarse en la recolecta de los huevos para su cría en cautiverio.

Palabras clave: *Charadrius melodus*, cría en cautiverio, especie amenazada, éxito de anidación, nidada de reemplazo, tamaño de nidada



FIGURE 1. A male Piping Plover brooding 5-day-old chicks. Male and female Piping Plovers share incubation and chick-tending duties, but females may desert broods before they fledge. Photo credit: Roger Eriksson

INTRODUCTION

Renesting is an important reproductive strategy, especially among bird species with high rates of nest failure (Sandercock et al. 1999, Hipfner 2001, Arnold et al. 2010, Lishman et al. 2010); however, the relative value of renesting is tempered by the fact that renesting attempts may be less successful or produce poorer quality young than earlier nesting attempts. For many species, clutch size and nest survival decline as the breeding season progresses (Klett and Johnson 1982, Tjørve and Underhill 2008, Verhulst and Nilsson 2008), and replacement nests, which necessarily occur later in the year than initial nests, may have smaller clutches and lower survival rates than first nests (Storaas et al. 2000, Suarez et al. 2005, Gregg et al. 2006, Devries et al. 2008). Likewise, pre- and post-fledging survival may be lower for young hatched later in the season (Roche et al. 2008, Gruebler and Naef-Daenzer 2010, Brudney et al. 2013) and for young hatched from renesting attempts (Martin and Hannon 1987, De Neve et al. 2004, Becker and Zhang 2011).

Potential reasons for seasonal declines in reproductive success include decreases in food availability (Verhulst and Nilsson 2008), changes in predator dynamics or environmental conditions (Grant et al. 2005), variation in parental quality (Saunders et al. 2012), or time constraints on migration or other post-breeding activities (Verboven and Visser 1998). Also, lower survival of replacement nests may

occur if physical condition of breeding adults declines with subsequent nesting attempts (Wendeln et al. 2000, Gasparini et al. 2006).

Even among species capable of renesting, not all individuals will renest after nest failure. Renesting propensity, the likelihood of renesting following nest failure, may vary according to timing of the breeding season (Amat et al. 1999, Brinkhoff et al. 2002), number of previous nesting attempts (Arnold et al. 2010), age of the previous nest at the time of nest failure (Fondell et al. 2006, Antczak et al. 2009), or the age, experience, and physical condition of breeding adults (Wendeln et al. 2000, Arnold et al. 2010).

Timing of a renesting attempt is influenced by date of previous nest failure and the amount of time it takes for a bird to initiate a replacement nest (i.e. the renesting interval). The renesting interval may vary according to season (Wendeln et al. 2000, Becker and Zhang 2011), number of previous nesting attempts (Arnold et al. 2010), age of the previous nest (Fondell et al. 2006), or quality of breeding adults (Wendeln et al. 2000). Also, renesting intervals may vary depending on type of nest failure (e.g., predation vs. abandonment) or whether breeding birds change mates or locations between subsequent nesting attempts (Haig and Oring 1988, Amat et al. 1999, Lishman et al. 2010).

The Piping Plover (*Charadrius melodus*) is a small migratory shorebird with breeding populations in the Atlantic Coast, Great Plains, and Great Lakes region; the Great Lakes breeding population is federally endangered (Figure 1; COSEWIC 2003, USFWS 2003). Great Lakes Piping Plover numbers declined dramatically from the 1950s to 1990, prompting intensive conservation efforts (USFWS 2003). Low reproductive success is thought to have contributed to the species' decline, and conservation efforts in the U.S. have focused primarily on protecting Piping Plover breeding sites in the Great Lakes region, including the use of predator exclosures to safeguard nests and beach closures to minimize human disturbance (USFWS 2003).

Because Piping Plovers nest on the ground, near water, and in exposed areas with little vegetative cover, their nests are especially vulnerable to predation, flooding, and disturbance (Haig and Oring 1988, Wemmer et al. 2001, Knetter et al. 2002, USFWS 2003). Piping Plovers are known to renest following the loss of earlier nests and may renest several times during the breeding season if their nests continue to fail (Cairns 1982, Haig and Oring 1988). A study of individually marked Piping Plovers in Manitoba found no difference in hatching success between first nests and renests (Haig and Oring 1988), but causes and consequences of individual variation in renesting propensity were not investigated. In a study of unmarked Piping Plovers in Saskatchewan, seasonal declines in hatching

success and clutch size were speculated to be an effect of renesting (Harris et al. 2005); however, first nests could not confidently be separated from renests. The Great Lakes population has a high proportion (>90%) of individually color-banded adults, presenting an opportunity to investigate sources of variation in renesting behavior by individual Piping Plovers.

From a conservation perspective, it is important to assess how renesting contributes to overall reproductive success of Great Lakes Piping Plovers and to ensure the effectiveness of management strategies employed to augment this federally endangered population. One current strategy is egg salvage from recently abandoned nests for captive rearing and release of fledged chicks back into the wild (Powell and Cuthbert 1993, Powell et al. 1997, Roche et al. 2008). Proactive population augmentation has also been considered (USFWS 2003), which would entail active collection of eggs from first nests for captive rearing, assuming that wild birds will renest with little impact to overall reproductive success. Captive-reared individuals, however, have lower survival and reproductive success than wild-reared birds (Roche et al. 2008). Furthermore, not all wild individuals will renest following clutch removal, and replacement clutches will be initiated later in the season and likely have lower reproductive success. Thus, any serious consideration of proactive clutch removal for captive rearing must properly measure the costs associated with renesting.

The objectives of our study were to investigate causes and consequences of variation in (1) timing of nest initiation, (2) clutch size, (3) daily nest survival, (4) renesting propensity, and (5) length of the renesting interval. Specifically, we sought to understand and quantify the contribution that renesting behavior makes to overall reproductive success while also measuring the cost of delay, which is an inevitable consequence of renesting. This information has important management implications for Great Lakes Piping Plovers and other shorebird populations whose nests are affected by incidental take (McGowan and Ryan 2009). Our results can also be used to assess the costs and benefits of proactive vs. salvage egg collection programs for Great Lakes Piping Plovers.

METHODS

Study Area

Since 1993, Piping Plovers have been banded with U.S. Geological Survey metal and Darvic colored bands and monitored annually in the Great Lakes region of North America. The study area included public and private sites on Lakes Michigan, Huron, and Superior used by breeding Piping Plovers during 1993–2010; the majority of sites were in Michigan, and a few were in eastern Wisconsin and southern Ontario, Canada (figure 1 in Brudney et al. 2013).

Sites consisted of wide, sparsely vegetated sand and gravel lakeshore beaches, the preferred breeding habitat of Piping Plovers (Wemmer et al. 2001, USFWS 2003).

Data Collection

We analyzed Piping Plover nest data collected from 1993 to 2010 by a network of contributing partners as part of an ongoing recovery effort for the Great Lakes population (USFWS 2003). Shoreline surveys were conducted each year from late April to early August to locate nesting sites of Piping Plovers. Once located, nests were monitored until termination (i.e. until all eggs either hatched or were determined to have failed). Nests were usually visited every 1–2 days, although a few sites (~7%) were visited less regularly with intervals between visits ranging from 3 to 9 days. For each nest, data were collected on clutch size, nesting attempt, nest fate (success or failure), date of hatch or failure, cause of nest failure, and adult identities. In cases of nest abandonment (i.e. nest unattended for ≥ 4 –5 hours), eggs were collected for captive rearing.

Predator exclosures consisting of wire fencing and plastic mesh were erected immediately upon location of a nest (USFWS 2003). Small, wire mesh box exclosures were used during egg laying and until full-sized exclosures could be erected (Melvin et al. 1992, USFWS 2003). Predator exclosures were used for nearly all nests; 100% of nests have been protected by this method since 2004 (Saunders et al. 2012). Additionally, rope fencing and signs were used to cordon off many of the nesting beaches to reduce human disturbance. Adult Piping Plovers were nest-trapped during mid-incubation and fitted with unique individual colored band combinations (USFWS 2003).

We investigated causes of variation in nest initiation date, clutch size, daily nest survival rate (DSR), renesting propensity, and length of the renesting interval. We examined only the nesting period (egg laying and incubation stages) up until hatching. For nest survival analyses, a nest was defined as successful if at least one egg hatched under natural conditions or if the nest was brought to full term (34 days) before eggs were salvaged for captive rearing. For renesting propensity analyses, a nest was considered to have failed if eggs only hatched in captivity and was only considered successful if at least one egg hatched under natural conditions.

We defined renesting propensity as the proportion of individuals that renested following a failed previous nesting attempt (Arnold 1993, Fondell et al. 2006). We calculated the renest interval as the number of days between failure of a previous nest and initiation of the replacement nest; for example, if a nest failed on June 3 and the first replacement egg was laid on June 10, then the renest interval was estimated as 7 days. Number of nesting attempts was tallied assuming that we found all initiated nests, but we likely missed some nests that were destroyed

during early laying (McPherson et al. 2003), so counts of previous nests represent minimum values.

Nest initiation dates were estimated by backdating, assuming a 2-day laying interval between eggs (Elliott-Smith and Haig 2004; E. A. Roche personal observation) plus a 28-day incubation period after the last egg was laid (see Results). For nests found after the last egg was laid, but failed prior to hatching and thus had unknown initiation dates (6% of nests), we assumed the nests were the average age of discovery (7 days old) and backdated accordingly. Birds of unknown age were assigned a minimum age of 1 the first time they were captured (Roche et al. 2010, Saunders et al. 2012). We considered a nest to be abandoned if adults were observed again during the breeding season or in a subsequent year, and we considered an adult to have died if it disappeared early in the breeding season during incubation and was not seen again during that breeding season or any subsequent years (Neuman et al. 2004, Roche et al. 2010).

For renesting analyses, we excluded birds presumed to have died (Neuman et al. 2004, Roche et al. 2010) and therefore incapable of renesting, but the surviving mate was included in the analyses. For renesting propensity analyses, we only included breeding attempts that failed during the nesting stage; we excluded 8 pairs that renested after complete or partial brood mortality, and we also excluded one female that renested after successfully fledging a first brood. For clutch size analyses, we excluded all nests that failed prior to clutch completion, and one-egg clutches that had likely experienced partial predation before they were discovered.

Nesting attempts were divided into 3 categories: first attempts, second attempts, and \geq third attempts. Because birds did not always reunite with their former mate for renesting, we analyzed male and female renesting attempts separately for renesting propensity and renesting interval analyses. We assumed that a renesting attempt was a continuation nest (i.e. replacement nests of birds that lost a nest during egg laying and renested soon after, with no interruption in laying) if nest loss occurred during egg laying and the replacement nest was initiated within 5 days of nest loss. In the nest survival analyses, inviable nests that were continuously tended by adults were treated as successful on the 34th day after they were initiated (i.e. average laying and incubation periods for a 4-egg clutch), at which point they were censored from further analysis; however, inviable nests were treated as failures for purposes of investigating renesting propensity.

Statistical Analyses

Nest survival analyses were conducted using the NLMIXED procedure with SAS software (Rotella et al. 2004; SAS Institute, Cary, NC), which provides maximum likelihood estimates of DSR and allows interval censoring,

daily covariate values, and a single random effect. We used a logit link function to constrain DSR to be between zero and one. Because penultimate visits to nests were not routinely recorded during nest monitoring efforts, we estimated dates of penultimate visits based on the nest monitoring frequency for each site. For ease of interpretation, we converted estimates of DSR into cumulative nest survival (the probability of a nest surviving the entire nesting period) by taking the product of predicted DSR for each day of an average 34-day exposure period, using appropriate covariate values for each day (Shaffer and Thompson 2007); most important, this involved incrementing nest age by 1 day for each successive day.

We investigated sources of variation in renesting propensity, renesting interval, clutch size, and nest initiation date using general linear models (Glm function) and generalized linear mixed models (package Lme4; Bates and Sarkar 2006) using R statistical software (version 2.15.1; R Development Core Team 2012). For renesting propensity analyses, we used the binomial family (logit link). For nest initiation date, renesting interval, and clutch size analyses, we compared models using Gaussian and Poisson distributions and determined that Gaussian models fit better.

For each of the 5 response variables (DSR, nest initiation date, clutch size, renesting propensity, and renesting interval), we investigated variation in response to relevant covariates such as date of nest initiation, date of nest failure, nest age, nesting attempt, year, cause of nest failure, male age, female age, sex of adult, clutch size, whether an adult changed location between consecutive nesting attempts, and whether an adult changed mates between consecutive nesting attempts. For each analysis we included only covariates for which we had formulated a priori hypotheses regarding how each covariate might explain variation in the specific breeding parameter of interest (Table 1). For date, we considered day 1 = April 20. We considered nest age = 1 to be the day the first egg was laid and then incremented daily. We treated cause of nest failure as a categorical factor with 5 levels: predation, flooding, abandonment, adult mortality, or all eggs inviable.

To avoid overfitting models, and because some covariates were correlated (e.g., nest initiation date and nesting attempt), we used a forward selection approach to model building, starting with the simplest model containing an intercept-only term and sequentially adding variables to each model. At each stage of the model selection process, we moved forward with the best-supported model. We evaluated models using an information-theoretic approach, ranking models according to their Akaike's Information Criteria values adjusted for small sample sizes (AIC_c ; Burnham and Anderson 2002). If a model under consideration included a main effect (linear term) for a

TABLE 1. A priori hypotheses about variables affecting daily nest survival rate (DSR), nest initiation date, renesting propensity, renesting interval, and clutch size of Great Lakes Piping Plovers during 1993–2010.

Explanatory variable	Abbreviation	A priori hypotheses
Nest initiation date	INITDATE	Later nests will have lower DSR and smaller clutches.
Nest failure date	FAILDATE	Later nest failure date will result in lower adult renesting propensity and longer renesting intervals.
Nesting attempt	ATTEMPT	Later nesting attempts will have lower DSR, lower renesting propensity, longer renesting intervals, and smaller clutches.
Nest age	NESTAGE	Older nests will have higher DSR, lower renesting propensity, and longer renesting intervals.
Cause of nest failure	CAUSE	Renesting propensity will be lower and renest intervals will be longer for birds that need to find a new mate if their previous mate died (or was infertile).
Age of adult	M_AGE, F_AGE	Older males (M_AGE) and females (F_AGE) will have higher DSR, earlier nesting, higher renesting propensity, shorter renesting intervals, and larger clutches.
Sex of parent	SEX	Females may have lower renesting propensities and longer renesting intervals due to greater investment in clutch production.
Clutch size	CLUTCH	Because small clutches are likely indicative of poorer quality adults, small clutches will be less likely to be replaced and will have longer renesting intervals.
Location change	LOCATION	Changing location between consecutive nesting attempts will increase the renesting interval.
Mate change	MATE	Changing mates between consecutive nesting attempts will increase the renesting interval.

covariate, we also considered the quadratic term for that covariate. We identified the best-supported model in each candidate set based on minimal AIC_c and the largest Akaike weight (w_i), which is the probability that each model is best, conditional on the data and model set (Burnham and Anderson 2002). We considered a model to be competitive if it was ≤ 2 AIC_c units of the best model, as long as it was not merely the best model plus one uninformative parameter (Burnham and Anderson 2002, Arnold 2010).

Because we assumed there was variation between years, and we wanted to account for this source of heterogeneity, we included year as an a priori random effect. Thus, for each response variable, our base model contained an intercept term and a random year effect. If random year effects were not supported ($\sigma^2_{\text{year}} = 0$; Zuur et al. 2009) in the best model from the resulting candidate set, we removed random year effects and repeated the entire model-selection procedure using fixed effects only. Unless otherwise indicated, means are reported ± 1 standard deviation (SD).

Removal vs. Non-removal of Clutches

We compared Piping Plover productivity (number of 1-year-old recruits into the Great Lakes population) under 2 different management scenarios: (1) removal of eggs from first nests for captive rearing and (2) leaving eggs in situ. We assumed a sample size of 20 nesting pairs under each scenario. Under the captive rearing scenario, we assumed

eggs were removed at nest age = 10; we considered clutch removal to be nest loss.

Total productivity (number of 1-year-old recruits from first nests and renests) was compared between the captive rearing and in situ management scenarios. We estimated productivity of first nests as: productivity = sample size of clutches * clutch size (this study) * nest success (hatching success of captive-incubated eggs [Roche et al. 2008] or cumulative nest survival of wild clutches [this study]) * fledging success (captive-reared fledging success [Roche et al. 2008] or wild fledging success [Brudney et al. 2013]) * hatch year (HY) survival (Saunders et al. 2014) * reproductive value of 1-year-old recruits (0.75 for captive-reared, or 1 for wild 1-year-old recruits, Roche et al. 2008). We estimated productivity of renests as: productivity = sample size of nesting pairs that lost first nests * renesting propensity (this study) * clutch size of renests (this study) * nest success of renests (this study) * fledging success from renests (Cuthbert and Roche 2010) * HY survival (Saunders et al. 2014). Estimates of renesting propensity, renest interval (and hence initiation date for replacement nests), clutch size, and renest survival were made using best-supported models from this study, based on predicted timing of renests.

RESULTS

We obtained data from 772 nests over 18 years (1993–2010). The average age of nests at discovery was 7.0 (SD

TABLE 2. Model selection results of the top 5 models of nest initiation date, clutch size, nest survival, renesting propensity, and renesting interval of Piping Plovers in the Great Lakes region during 1993–2010. Intercept models are also listed for reference.

Model ^a	ΔAIC_c^b	w_i^c	K^d	Dev ^e
Nest Initiation Date^f				
AGE_F ² + AGE_M ²	0	0.573	6	5117.8
AGE_F ² + AGE_M	0.6	0.427	5	5128.1
AGE_F ²	13.9	0.001	4	5151.0
AGE_F	41.5	0	3	5188.2
AGE_M ²	75.1	0	4	5211.8
Intercept	170.4	0	2	5326.3
Clutch Size				
INITDATE ²	0	0.9997	3	520.4
INITDATE	16.2	0.0003	2	539.3
ATTEMPT_F	36.3	0	2	559.3
ATTEMPT_M	42.4	0	2	565.3
Intercept	45.1	0	1	570.9
Daily Nest Survival (DSR)				
INITDATE ² + NESTAGE ² + AGE_M	0	0.519	6	1846.7
INITDATE ² + NESTAGE ²	0.1	0.470	5	1848.8
INITDATE ² + NESTAGE	3.9	0.011	4	1854.7
INITDATE ² + AGE_M	7.7	0.0002	4	1858.5
INITDATE ²	10.0	0	3	1862.8
Intercept	19.7	0	1	1876.5
Renesting Propensity^f				
FAILDATE ² + CAUSE + ATTEMPT	0	0.847	8	237.5
FAILDATE ² + CAUSE + NESTAGE	4.8	0.077	8	242.2
FAILDATE ² + CAUSE	4.9	0.073	7	245.3
FAILDATE ² + ATTEMPT	12.8	0.001	5	259.1
FAILDATE ² + NESTAGE	14.0	0.0008	5	260.2
Intercept	105.0	0	2	359.4
Renesting Interval^f				
NESTAGE ² + MATE	0	0.831	5	652.8
NESTAGE ²	3.2	0.169	4	663.3
CLUTCH	19.9	0	3	687.0
MATE	22.4	0	3	689.4
NESTAGE	29.9	0	3	696.6
Intercept	38.0	0	2	712.3

^a Lowest Akaike's Information Criterion values adjusted for small sample sizes (AIC_c) were: 5185.68 (Nest Initiation Date), 805.94 (Clutch Size), 1876.80 (DSR), 262.54 (Renesting Propensity), and 852.75 (Renesting Interval). ² Indicates a quadratic effect plus lower-order term. + Indicates an additive effect.

^b The difference in AIC_c value between the model and the best-supported model.

^c Akaike weight.

^d Number of model parameters.

^e Model deviance.

^f All models (including intercept models) contain year as a random effect.

6.7) days old. For 328 nests monitored from egg laying until hatching, the mean exposure period was 33.7 (SD 2.3) days from the day the first egg was laid, and 27.7 (SD 2.3) days from the day the last egg was laid.

Nest Initiation Date

The mean initiation date for first nests was May 17 (SD 13 days; 90% range: April 30 to June 10; $n = 674$). The best-supported model of nest initiation date included a random effect of year and quadratic effects of both female and male age (Tables 2 and 3). Older adults initiated nests earlier in

the season than did younger adults, with the greatest advancements occurring between ages 1 and 3 (Figure 2). The effect of age was stronger for females than males; a 9-year-old female nested ~ 14 days earlier than a 1-year-old female, but a 9-year-old male only nested ~ 9 days earlier than a 1-year-old male (Figure 2).

Clutch Size

Observed size of completed clutches was 3.9 (SD 0.4) eggs (range: 2–6 eggs; $n = 739$), excluding 4 one-egg nests that likely experienced partial predation. The best-supported

TABLE 3. Parameter estimates, standard errors, and 95% confidence intervals from the best-supported models of nest initiation date, clutch size, nest survival, nest initiation date, renesting propensity, and renesting interval of Piping Plovers in the Great Lakes region during 1993–2010.

Parameter ^a	Estimate	SE	95% Confidence Interval	
			Lower	Upper
Nest Initiation Date				
INTERCEPT	38.891	1.346	36.254	41.529
AGE_F	−4.778	0.606	−5.966	−3.591
AGE_F ²	0.304	0.06	0.185	0.423
AGE_M	−3.011	0.638	−4.262	−1.76
AGE_M ²	0.213	0.065	0.085	0.341
Clutch Size				
INTERCEPT	3.886	0.044	3.799	3.973
INITDATE	0.009	0.003	0.002	0.015
INITDATE ²	−0.0002	−0.00005	−0.0001	−0.0003
Daily Nest Survival (DSR)				
INTERCEPT	3.142	0.551	2.061	4.22
INITDATE	0.033	0.022	−0.01	0.076
INITDATE ²	−0.0005	0.0002	−0.0009	−0.0001
NESTAGE	0.101	0.033	0.037	0.165
NESTAGE ²	−0.002	0.0008	−0.0037	−0.0004
AGE_M	0.06	0.043	−0.023	0.143
Renesting Propensity				
INTERCEPT	0.746	1.597	−2.385	3.877
FAILDATE	0.044	0.068	−0.089	0.178
FAILDATE ²	−0.0017	0.0008	−0.0032	−0.0002
CAUSE2 (mate loss)	−1.482	0.454	−2.372	−0.592
CAUSE3 (abandonment)	−0.378	0.497	−1.352	0.596
CAUSE4 (flooding)	0.672	0.458	−0.226	1.571
ATTEMPT	1.139	0.422	0.311	1.966
Renesting Interval				
INTERCEPT	−0.678	0.993	−2.625	1.269
NESTAGE	0.776	0.136	0.509	1.043
NESTAGE ²	−0.018	0.004	−0.026	−0.011
MATE	3.27	0.812	1.679	4.861

^a CAUSE was a categorical factor with 4 levels: CAUSE1 (predation), CAUSE2 (mate loss), CAUSE3 (abandonment), and CAUSE4 (flooding). ² Denotes a quadratic term.

model of clutch size included a quadratic effect of nest initiation date (Tables 2 and 3); this model received nearly all of the support among models in the candidate set (Table 2). Clutch size increased slightly from 3.8 (SE 0.04) for nests initiated early (April 20) to 3.9 (SE 0.02) for nests initiated mid-season (May 25), but then declined to 3.4 (SE 0.07) for nests initiated late in the season (June 25; Table 3).

For female plovers that lost nests during laying, 21 of 75 renesters (28%) produced continuation nests. On average, continuous layers produced 6.4 (SD 1.4) consecutive eggs (range: 4–8 eggs); only 9% of continuous layers stopped laying after 4 consecutive eggs. Because the occurrence of supranormal continuation clutches may have influenced model results regarding effects of female nesting attempt on variation in clutch size, we conducted a post hoc

analysis with continuation nests removed from the dataset, but results were unchanged.

Nest Survival

Our sample included 772 nests (680 first nesting attempts and 92 nests that were second or later nesting attempts for at least one parent). Apparent nest success was 76% (recall that nearly all nests were protected by predator exclosures). Initiation date had the most influence on DSR, and all top models included the quadratic term of this covariate. The best-supported model of DSR also included a quadratic effect of nest age and a linear effect of male age (Table 2). Parameter estimates from the best-supported model showed that DSR increased with nest age from nest initiation until late in incubation but declined as nests approached hatching age (Table 3; Figure 3). DSR

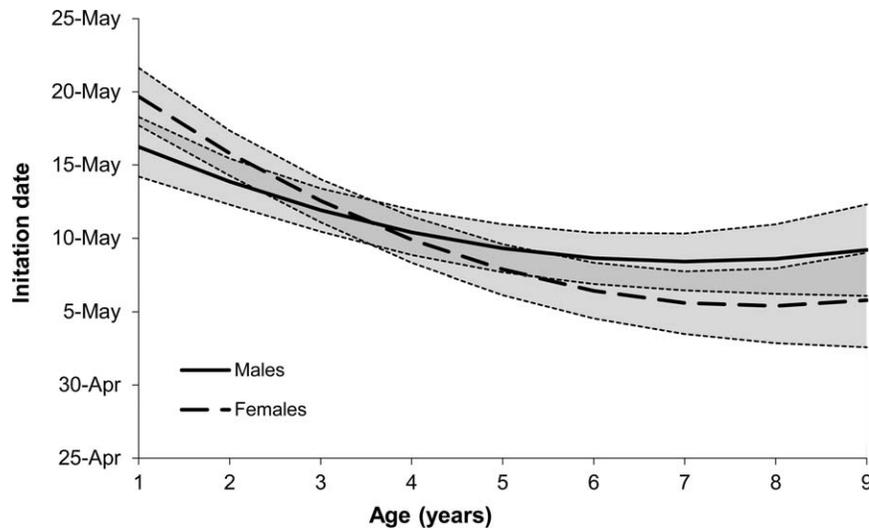


FIGURE 2. Effects of male and female age on initiation date of first nests of Great Lakes Piping Plovers during 1993–2010. Dotted lines indicate 95% confidence intervals.

increased with nest initiation date until mid-season (~May 20) but then declined among late season nests (Figure 4; DSR was converted to cumulative nest survival for ease of interpretation). Also, DSR increased with age of the male parent (Table 3). Cumulative nest survival averaged 0.70 (SE 0.04) for a 1-year-old male, 0.74 (SE 0.02) for a 4-year-old male (mean age), and 0.81 (SE 0.05) for a 10-year-old male for nests initiated on May 15.

Renesting Propensity

Piping Plovers replaced 138 of 280 failed nests, a 49% apparent renesting propensity; there was no difference in apparent renesting propensity between males and females.

The greatest number of nesting attempts in a single season was 5; the same pair renested 4 times, laying a total of 15 eggs. Estimates of renesting propensity represent minimum values because some nests likely failed prior to detection.

Nest losses were due to predation (34%), flooding (25%), death of a breeding adult (20%; surviving adult was included in the analysis), abandonment (17%; both adults still alive), and clutch inviability (4%). In 12 cases of inviable clutches, eggs were removed 7–16 days after the predicted hatching date, but none of these birds renested; however, models that included inviable nests as a separate cause of nest failure did not converge, so we removed

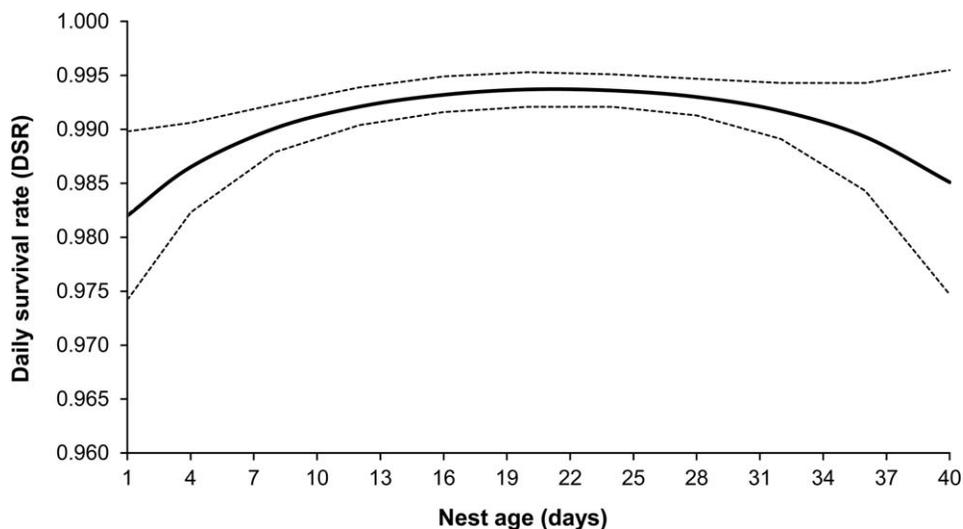


FIGURE 3. Effect of nest age on daily survival rate (DSR) of Great Lakes Piping Plover nests. Dotted lines indicate 95% prediction intervals. Note that all nests were protected by predator enclosures.

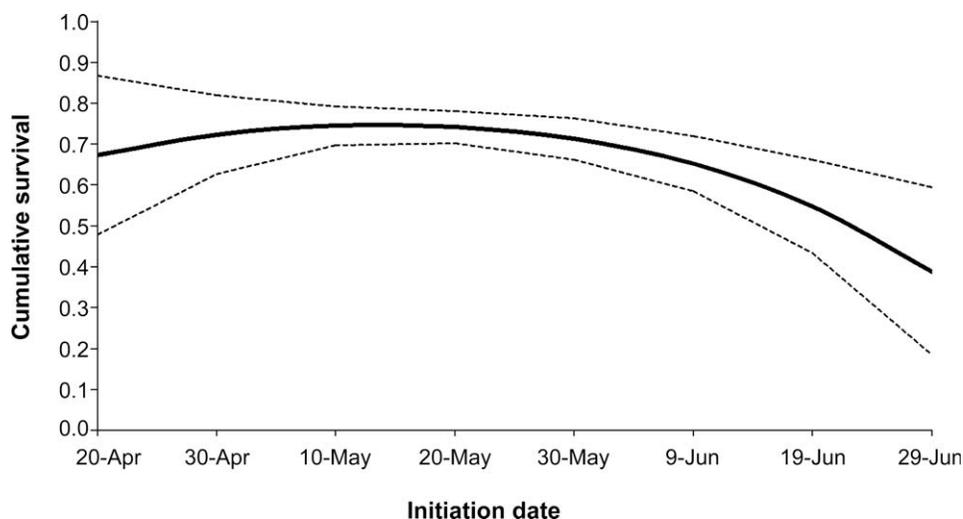


FIGURE 4. Effect of nest initiation date on cumulative survival of Great Lakes Piping Plover nests for an average 34-day exposure period. Dotted lines indicate 95% prediction intervals. Note that all nests were protected by predator exclosures.

inviability from the dataset and reanalyzed data for the remaining 268 nest failures with 4 rather than 5 causes of nest failure.

Renesting propensity was most strongly affected by date; the inclusion of date covariates resulted in models with the lowest AIC_c values. Nest failure date explained variation in renesting propensity better than nest initiation date and therefore was retained in subsequent models. The best-supported model of renesting propensity included a random effect of year, a quadratic effect of nest failure date, cause of nest failure, and nesting attempt (Table 2). Parameter estimates from the best-supported model showed that renesting propensity decreased according to the date of nest failure (Table 3; Figure 5A, 5B). Renesting propensity was also related to cause of failure, with flooding losses being most likely to be replaced, followed by predation, abandonment, and death of a mate (Figure 5A). Additionally, renesting propensity increased for birds with a greater number of prior nesting attempts (Figure 5B).

Renesting Interval

The mean observed renesting interval was 5.9 (SD 4.5) days ($n = 138$). The best-supported model of renesting interval included a random effect of year, a quadratic effect of nest age, and an effect of changing mates. This model received nearly all of the support among models in the candidate set (Table 2). Estimated renesting intervals were ~ 4 days when nest failure occurred shortly after initiation but increased to ~ 8 days when nest failure occurred during mid-incubation. Also, renesting intervals were ~ 3 days longer for birds that renested with a new mate than for individuals that renested with the same mate; 80% of mate changes ($n = 25$) were due to death of a previous mate.

Removal vs. Non-removal of Clutches

We compared potential productivity (number of 1-year-olds recruited into the population) between 2 management scenarios: (1) removal of initial clutches for captive rearing, and (2) leaving clutches in situ. Under the captive rearing scenario, removal of 20 first nests at age 10 days resulted in the equivalent of 3.7 one-year-old recruits from captive-reared first nests and 4.0 one-year-old recruits from wild renests of those 20 pairs, totaling 7.6 one-year-old recruits (Table 4). Under the non-removal scenario, leaving all 20 first nests in situ resulted in 12.3 one-year-old recruits from first nests, and 1.0 one-year-old recruits from natural renests, totaling 13.3 one-year-old recruits. Thus, clutch removal resulted in 5.7 fewer one-year-old recruits into the population and only 57% productivity compared to leaving clutches in situ.

DISCUSSION

Renesting is an important component of Piping Plover reproduction; nearly half of all individuals renested after failure of an earlier nest. In a natural scenario, nests would not be protected by individual predator exclosures and renesting would undoubtedly play an even more important role; however, we found that renests were less productive than initial nests, not because renests are less productive per se, but because they were initiated later in the season and consequently had lower average clutch size and nest survival (Table 2; Figure 4) as well as lower chick survival (Brudney et al. 2013) and post-fledging survival (Saunders et al. 2014).

Other studies of Piping Plovers have also found strong seasonal effects on reproductive success (Harris et al. 2005, Saunders et al. 2012, Brudney et al. 2013), and any factors

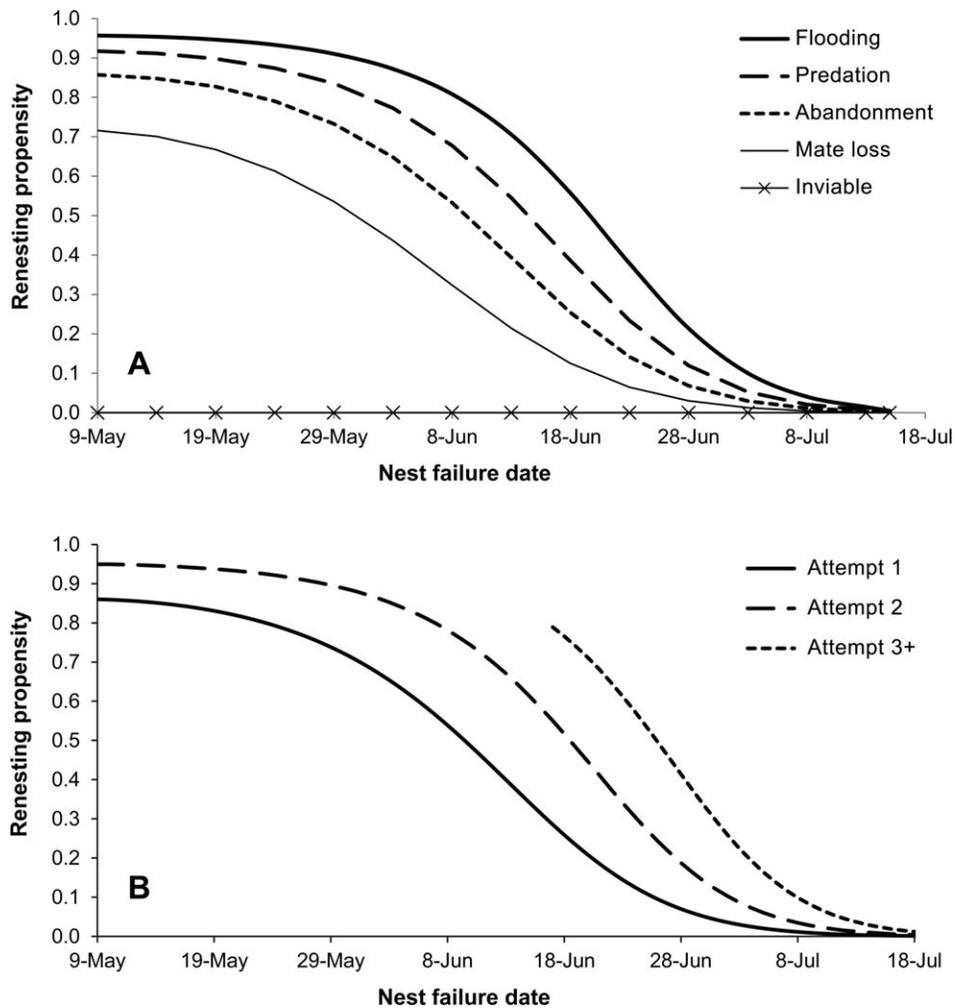


FIGURE 5. Effects of nest failure date on renesting propensity according to (A) cause of nest failure and (B) nesting attempt. In plot A, nesting attempt was held to the mean covariate value (1.22), and in plot B, cause of failure was held to the mean covariate value (0.25).

that cause plovers to nest later, including renesting, are likely to lead to lower breeding productivity. Studies of other precocial species have found that after controlling for later nest initiation date, renests were as productive as initial nests (Amat et al. 1999, Arnold et al. 2010). In this study, nest survival was influenced by nest initiation date but not by later nesting attempt (Table 2), suggesting that Piping Plover reproductive success is better explained by seasonal effects rather than prior investments in clutch formation and incubation. We speculate that seasonal declines in reproductive success may have been a result of diminishing food resources for adults or chicks, changes in predator abundance or behavior, or increased frequency or intensity of late summer storm surges. Alternatively, seasonally declining reproductive success may have indicated lower parental investment in late season nests given reduced survival rates for late-hatched chicks and fledglings (Roche et al. 2008, Brudney et al. 2013).

Nesting attempt was an important factor in explaining renesting propensity of adults, although less so than seasonal effects related to date of failure of the previous nesting attempt (Tables 2 and 3). Even though renesting propensity declined to zero toward the end of the breeding season, renesting propensity was higher for individuals that had a greater number of previous nesting attempts than for individuals with fewer previous nesting attempts (after controlling for nest failure date; Figure 5B). This result was contrary to our a priori hypothesis that renesting propensity would decline with later nesting attempt due to costs of reproduction. Instead it suggests that individual quality is an important determinant of renesting propensity; proven renesters are more likely to reneest repeatedly, owing to some unmeasured aspect of individual quality.

We used age of breeding adults as an indication of adult breeding quality. A number of studies of other species have

TABLE 4. Comparison of removing first nests for captive rearing vs. leaving first nests in situ, in terms of number of 1-year-old recruits into the Great Lakes Piping Plover population.

	Captive Component	Wild Component
First nests		
Number of clutches ^a	20	20
Clutch size ^b	4	4
Nest success	0.85 ^c	0.74 ^b
Fledging success	0.90 ^c	0.56 ^d
HY survival ^e	0.08 ^c	0.37 ^e
Reproductive value of 1-year-old recruits ^c	0.75	1
Number of 1-year-old recruits (first nests) ^f	3.67	12.27
Renames		
Number of pairs that lost first nests	20	5.2 ^b
Renesting propensity ^b	0.76	0.76
Clutch size ^b	3.81	3.81
Nest success ^b	0.65	0.65
Fledging success ^g	0.5	0.5
HY survival ^e	0.21	0.21
Number of 1-year-old recruits (renests) ^f	3.95	1.03
Total number of 1-year-old recruits ^h	7.62	13.29

found that older birds nest earlier (Wendeln et al. 2000, Becker and Zhang 2011), have higher nest survival rates (Devries et al. 2008), and have a greater likelihood of renesting after nest loss (Wendeln et al. 2000, Fondell et al. 2006, Arnold et al. 2010). In our study, nest survival increased with age of the breeding male (Tables 2 and 3). Renesting propensity was not affected by male or female age; however, both nest survival and renesting propensity were strongly influenced by initiation date, and older males and females initiated nests earlier than younger individuals (Figure 2). Saunders et al. (2012) had similar results with respect to the influence of adult age on hatching date.

We found that nest survival was more strongly influenced by male than female age (Table 2). Male Piping Plovers arrive on the breeding grounds before females, and older birds generally arrive before younger individuals (Stucker et al. 2010). Males also have the primary role in territory establishment and defense (Cairns 1982) and

exhibit higher breeding site fidelity than females (Haig and Oring 1988). Higher nest survival of older males in this study may have been due to earlier arrival times and greater ability to establish and maintain high-quality breeding territories. Roche et al. (2010) found that breeding females had higher mortality rates than males, and older females had higher mortality rates than younger females. In this study, perhaps the benefits of female age and experience on nest survival were counteracted by a higher probability of death for older females. Saunders et al. (2012) found that fledging success was more strongly influenced by age and experience of females than males. Females generally depart breeding grounds before males (Cairns 1982), and because older females nested earlier, they may have been less likely to abandon their broods before they fledged.

Daily nest survival increased from nest initiation until mid-incubation but then followed a quadratic pattern of decline among older nests (Figure 4). The apparent decline in survival of older nests may be an artifact of fitting a quadratic model to data exhibiting a strong pattern during early nesting; however, other investigators have found similar patterns among waterfowl and speculated that lower survival of older nests may be related to changes in adult behavior close to hatching (Grand et al. 2006, Grant and Shaffer 2012). Circumstantial evidence suggests that adult Piping Plovers also change their behavior, becoming increasingly attentive and restless close to hatching (S.P. Saunders personal observation).

We initially considered whether increased activity by attendant parents and/or increased noise associated with hatching might have increased the probability of nest loss to predators near hatching. During the last week of incubation prior to hatching, however, the proportion of clutch loss from predation decreased from 39% (average during first 4 weeks of the nesting period) to 26%, but death of a breeding adult increased from 18% (average during first 4 weeks of the nesting period) to 30%. We speculate that increased activity close to hatching may have increased the probability of predation on attending adults, thus indirectly causing nest failure.

Although age of the previous nest at the time of nest failure did not influence renesting propensity, it did influence length of the renesting interval (Table 2). Renesting intervals increased with age of the previous nest at the time of failure and were shortest for nests that failed during egg laying. Adults with nests that failed early in the incubation period had invested less time and energy in the previous nest, and females that lost clutches during egg laying potentially still had enlarged oviducts and developing follicles allowing prompt initiation of a continuation nest.

Renesting intervals were also ~3 days longer for adults that needed to find a new mate (Table 2). Divorce (i.e.

intra-year mate switching when both members of a pair were alive; Choudhury 1995) among Piping Plovers was rare, and 80% of intra-year mate changes were the result of the death of a previous mate.

After controlling for date of failure and nesting attempt, death of a mate resulted in the second lowest renesting propensity after egg inviability (Figure 5A). Birds did not renest if their clutches were inviable, even in cases where it was still early enough in the season for them to potentially do so; however, with the exception of one infertile male (inviability clutches in several different years) and one female who only survived a single breeding season, all birds with inviable clutches nested successfully in subsequent years. Renesting propensity was highest among birds with nests that failed due to flooding or clutch predation (Figure 5A). As with other shorebirds (Sandercock et al. 1999, Lishman et al. 2010), renesting by Piping Plovers is likely an evolutionary adaptation to compensate for high rates of egg loss to predators and weather-related events rather than other causes of nest failure such as clutch inviability or mate loss. We speculate that the failure to renest following death of a mate may be due to constraints imposed by lack of available mates late in the season or may reflect individual restraint when faced with longer renesting intervals and subsequent seasonal limitations resulting from delayed renesting.

Nearly all nests were protected by predator exclosures, which likely affected renesting propensity. Renesting rates in this study may have been lower than would have occurred naturally because nests likely survived longer before failing, and thus timing of nest losses occurred later in the season and after greater energy investments by incubating adults. Also, other studies have shown that use of exclosures may increase mortality risks for adult plovers (Johnson and Oring 2002, Murphy et al. 2003, Neuman et al. 2004). In this study, the likelihood of renesting was lower following death of a mate than for other types of nest loss (Figure 5A). Although there was no direct evidence of mortality due to exclosure use in this study, if exclosures contributed to adult disappearances, they may have thus indirectly affected renesting propensity of the surviving adult.

Clutch size exhibited a quadratic pattern of decline; model-estimated clutch size increased from 3.8 to 3.9 from early to mid-season before declining to 3.4 at the end of the breeding season (Tables 2 and 3). The slightly lower clutch size earlier in the season compared to mid-season may have been a result of low spring temperatures, a variable reported to affect clutch size in a closely related shorebird species (Nol et al. 1997). In general, clutch size of Great Lakes Piping Plovers declined with later nest initiation date, which is consistent with findings from studies of Piping Plovers elsewhere (Cairns 1982, Harris et al. 2005). Although Piping Plovers have a modal clutch size

of 4 eggs, we found that the frequency of 2- and 3-egg clutches increased toward the end of the breeding season. Continuation nesters were able to lay 5–8 eggs in normal succession, and the greatest number of eggs laid by a female in a single season was 15, suggesting that egg production capability of females was likely not the limiting factor for clutch size toward the end of the breeding season.

Although our results indicate that nest survival and renesting by Great Lakes Piping Plovers are strongly influenced by seasonal variation, parental quality was somewhat important as well. Older males had higher nest survival (Tables 2 and 3), and older males and females initiated nests earlier in the breeding season (Figure 2). A few Piping Plovers were able to produce replacement nests throughout the breeding season if their nests continued to fail; 5 nesting attempts was the maximum number recorded for a single bird in a single season. Although we did not find an effect of parent age per se on renesting propensity, perhaps other indicators of individual quality, such as foraging efficiency (Lescroël et al. 2010) or establishment of high-quality territories as a result of early arrival or competitive ability (Marra 2000) may better explain variation in renesting propensity among individuals.

Implications for Conservation

We compared 2 potential management strategies for Great Lakes Piping Plovers: (1) removing initial clutches for captive rearing and (2) leaving clutches in situ. Our results suggest that removal of clutches for captive rearing led to fewer 1-year-old Piping Plovers recruited into the Great Lakes population than leaving clutches in situ (Table 4). Lower productivity under the clutch removal scenario was primarily a result of reduced survival of captive-reared chicks compared to wild chicks (Roche et al. 2008), and renesting could only partially compensate for the removal of earlier nests.

Overall, about half the Piping Plovers in the Great Lakes renested after failure of an earlier nest. Renesting propensity varied according to date and cause of previous nest failure however, and renesting was more likely to occur following early-season predation rather than a late-season weather event (Figure 5A). Replacement nests are necessarily initiated later in the season and thus produce smaller clutches (Tables 2 and 3) and have lower chances of nest survival (Figure 4) and fledgling survival (Brudney et al. 2013). Based on our results, proactive removal of first nests for captive rearing is not recommended for this endangered population, although egg collection may be warranted in cases of probable nest failure (e.g., nest located within a flood zone). Our results suggest that as the breeding season progresses, conservation managers should be increasingly proactive with in situ nest protection

efforts (e.g., enhanced predator control efforts) rather than relying on collection of eggs for captive rearing.

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