Apparent Nest Abandonment as Evidence of Breeding-Season Mortality in Great Lakes Piping Plovers (*Charadrius melodus*) - Abandono Aparente de Nidos como Evidencia de Mortalidad Durante la Estación Reproductiva en *Charadrius melodus*

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APPARENT NEST ABANDONMENT AS EVIDENCE OF BREEDING-SEASON MORTALITY IN GREAT LAKES PIPING PLOVERS (*CHARADRIUS MELODUS*)

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Abstract.—Abandonment was the most frequent cause of nesting failure in Great Lakes Piping Plovers (*Charadrius melodus*) during 1993–2007, and observations of color-banded adults suggested that most abandonments involved disappearance of attendant adults rather than behavioral decisions by adults to desert their nests. The purpose of our study was to integrate nest-monitoring histories with mark–resighting analyses to determine whether nest abandonment indicated adult mortality or nest desertion. Nesting Piping Plovers had extremely high within-year resighting probabilities (10-day mean $p = 0.908 \pm 0.025$ [SE]), and cumulative probabilities of being detected approached 1 for individuals that were present on the breeding grounds for ≥20 days post-abandonment. These observations suggested that desertion would be readily identified unless Piping Plovers left the monitoring areas immediately after deserting their nests. None of the 31 that disappeared (as indicated by nest-monitoring histories) was ever observed again, and an among-year mark–resighting analysis suggested that all had died. From 2002 to 2007, annual mortality associated with disappearances averaged 5.7% of the marked population. Disappearances occurred primarily from 16 May to 19 June, were more common among females, involved individuals that were older than average, and were most frequently attributed to predation by Merlins (*Falco columbarius*). Our results reveal that most early-season nest abandonment in Piping Plovers was attributable to the death of attendant adults. We believe that this phenomenon may be widespread among other species of birds in which adults are vulnerable to mortality during nesting. *Received 4 December 2008, accepted 17 September 2009.*

Key words: *Charadrius melodus*, endangered species, nest abandonment, Piping Plover, Program MARK, survival.

Abandono Aparente de Nidos como Evidencia de Mortalidad Durante la Estación Reproductiva en *Charadrius melodus*

Resumen.—El abandono fue la causa más frecuente de fracaso de los nidos en *Charadrius melodus* entre 1993 y 2007, y las observaciones de adultos marcados con anillos de colores sugirieron que la mayoría de los abandonos involucró la desaparición de adultos que cuidaban los nidos en lugar de decisiones de comportamiento de desertar los nidos por parte de los adultos. El propósito de nuestro estudio fue integrar las historias de monitoreo de los nidos con análisis de marcado y avistamiento repetido para determinar si el abandono de los nidos indicaba la mortalidad de los adultos o la deserción de nidos. Las probabilidades de avistar repetidamente en el mismo año a individuos de *C. melodus* que estaban anidando fueron extremadamente altas (media de 10 días $p = 0.908 \pm 0.025$ [EE]) y las probabilidades acumulativas de ser detectados se aproximaron a 1 para los individuos que estuvieron presentes en las áreas de anidación por ≥20 días luego del abandono. Estas observaciones sugirieron que la deserción sería identificada fácilmente a menos que los individuos dejaran las áreas de monitoreo inmediatamente después de abandonar sus nidos. Ninguno de los 31 individuos que desaparecieron (de acuerdo a las historias de monitoreo de los nidos) fueron observados de nuevo y un análisis interanual de marcado y avistamiento repetido sugirió que todos habían muerto. Desde 2002 hasta 2007, la mortalidad anual asociada con las desapariciones fue, en promedio, del 5.7% de la población marcada. Las desapariciones ocurrieron principalmente desde el 16 de mayo hasta el 19 de junio, fueron más comunes entre las hembras, involucraron individuos más viejos que el promedio y fueron atribuidas más frecuentemente a depredación por *Falco columbarius*. Nuestros resultados mostraron que la mayoría de los abandonos de los nidos al inicio de la estación fueron atribuibles a la muerte de los adultos de *C. melodus* que atendían los nidos. Creemos que este fenómeno puede estar ampliamente difundido entre otras especies de aves en las que los adultos son vulnerables a la mortalidad durante la anidación.

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Nesting studies typically recognize three principal nest fates: successful, depredated, and 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 the death of an attendant adult. However, this explanation has been acknowledged only anecdotally (e.g., Yorio and Boersma 1994, Wiktander et al. 2001, Cohen et al. 2006). A notable exception, Neuman et al.'s (2004) study, used nest-monitoring histories from a color-banded population of Snowy Plovers (*Charadrius alexandrinus*) to infer that ~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 (*C. 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 individuals, identify nesting distributions, facilitate nest-site protection, and collect data on annual reproduction (U.S. Fish and Wildlife Service [USFWS] 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 because the adults had died, the true costs associated with abandonment were much higher than the loss of a single clutch. Because most adults were uniquely banded and conspicuously visible in open beach habitats, monitors were able to distinguish between nest abandonments in which both adults were still known to be alive (i.e., nest desertion) and cases in which one or both of the attendant adults were no longer present at the breeding site (i.e., potential disappearance). However, the disappearance of a nesting adult does not necessarily imply mortality; these events could represent detection failure or temporary emigration rather than mortality (Dinsmore 2008). Distinguishing among these possibilities is important for understanding the demographic consequences of nest abandonment.

To determine whether disappearances were caused by detection failure, we conducted a detailed analysis of within-season detection probabilities for uniquely banded Piping Plovers during the 2008 breeding season to determine whether they remained at local nesting sites but managed to avoid detection. We conducted an among-year (1993–2008) mark–resighting study to determine whether adults that disappeared had died or temporarily emigrated 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 nest failure on subsequent apparent survival of the affected adults. Finally, we characterized the sex and age distributions of nesting versus disappearing individuals and identified the timing and potential causes of 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, on Long Island, Wisconsin, and on the Bruce Peninsula of Ontario, Canada (USFWS 2003). For our among-year mark–recapture analysis, we used Piping Plovers banded throughout this entire region from 1993 to 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 Piping Plovers were conducted by local volunteers beginning in late April at contemporary nesting locations throughout Michigan. By mid-May, monitors working for participating governmental, nonprofit, and educational institutions began daily surveys of contemporary and historical Piping Plover 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" (≥1 egg hatched), "depredated" (eggs missing or destroyed), "abandoned" (intact eggs no longer tended by adults), or "flooded." Since 1993, nesting Piping Plovers have been captured during incubation using single-chambered Potter traps (Lincoln 1947) and banded with unique combinations of U.S. Geological Survey (USGS) aluminum bands and Darvic (Avinet, Dryden, New York) color bands, which facilitated future identification of banded individuals without recapture. At most sites with nesting pairs, monitors made regular visits through mid-July to check on the status of nests and chicks and to confirm the identity of Piping 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 five color bands upon first recapture. Adults that were not recaptured retained chick bands, which allowed for limited identification of individuals on the basis of 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 concurrently 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 in which both members of the breeding pair were subsequently observed alive (desertion). We used the following criteria to categorize nesting adults as "disappeared": (1) the discovery of dead individuals 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 other ($n = 17$). If both members of a pair were not

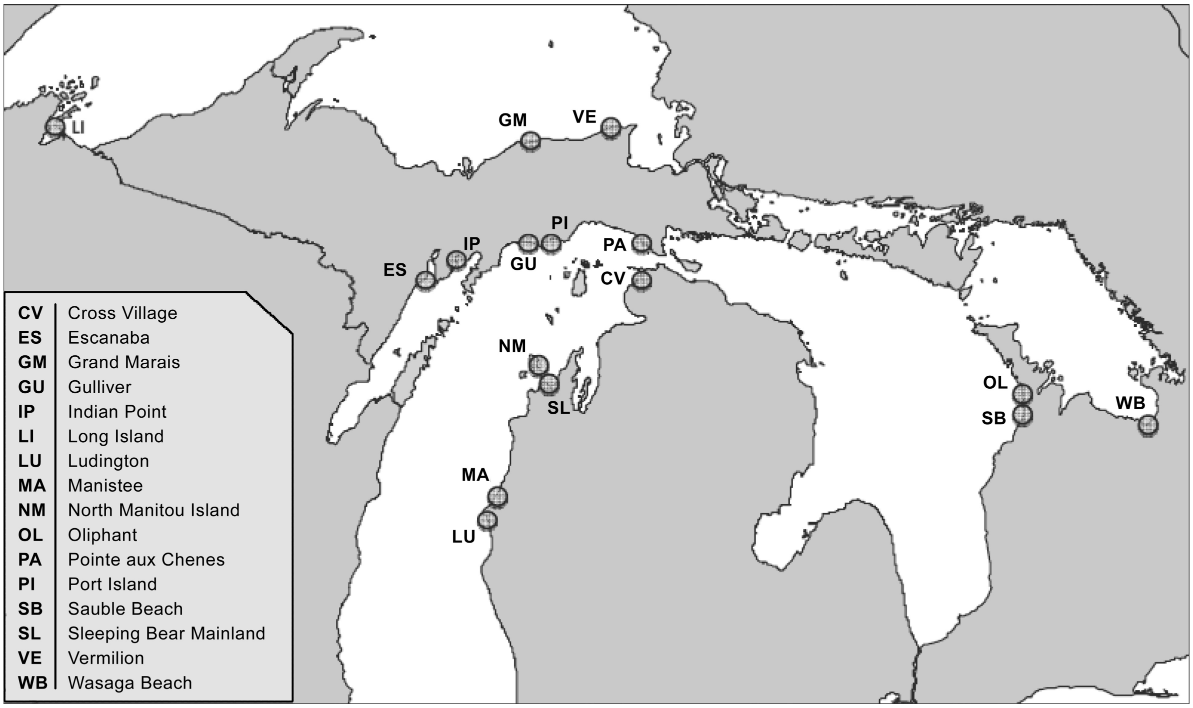

Fig. 1. Distribution of Great Lakes nesting sites that participated in Piping Plover detection surveys during April–July 2008. Circles represent sites with monitors that reported band combinations observed throughout the 2008 breeding season. Observations occurred on a near daily basis at CV, ES, GM,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

observed on the beach during a site visit, Great Lakes monitors were given the task of remaining at a nest site to observe the nest until an incubation switch occurred. Monitors also recorded 3 suspicious disappearances that occurred during the pre-nesting period (after the pair had been observed copulating, scraping, and involved in other courtship activities) and 5 apparent brood abandonments that occurred during the first week after hatching (well before Piping Plovers typically abandon their broods), and we also coded these 8 individuals 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 whether individuals that disappeared remained alive on the breeding grounds but simply went undetected, we used a Cormack-Jolly-Seber recaptures-only model in Program MARK (White and Burnham 1999) to estimate the probability of detecting Piping Plovers during sub-intervals of the breeding season. Because 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 where band combinations were recorded on a near daily basis during 2008 (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 an individual 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 individuals, and individual differences in band type. We measured monitoring effort as the number of days (n) on which monitoring occurred at each site during each 10-day detection period, which we standardized to a value between –1 and 1. The breeding status of each individual during each detection period was coded as 1 if the bird was tending eggs or chicks at any time during this period and 0 if not. Individuals that initiated more than one nesting attempt were also considered to be breeding during their renesting intervals. Birds that carried non-individualized combinations of chick bands were coded with band type = 0, whereas those with individual-specific adult combinations were coded as band type = 1. This distinction allowed us to test for decreased detection probability (p') of individuals marked with ambiguous band combinations and for differences in apparent survival (φ') caused by limited fidelity of non-nesting Piping 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 ($1 - \varphi'$) 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 [$\varphi'(t), p'(t)$] and obtained an estimate of overdispersion of $\hat{c} = 1.96$, which we used to rank models according to Akaike's information criterion corrected for sample size and overdispersion ($QAIC_c$; Burnham and Anderson 2002, Cooch and White 2009). 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 began with the simplest possible model [φ′(.),p′(.)] (Lebreton et al. 1992) and built from there. We modeled all after-hatch-year (AHY) individuals as a single age-class and introduced increasing complexity by allowing either φ′ or *p*′ to vary among periods [e.g., φ′(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 individuals. For this analysis, each annual breeding season represented a single occasion, and individuals were coded as "detected" if they were observed at any time during the breeding season. We conducted 1,000 bootstrap simulations using the model [φ(t),p(t)] and estimated $\hat{c} = 0.96$, which we left as 1 (Burnham and Anderson 2002, Cooch and White 2009). We assigned year-specific covariates to indicate forms of nest loss experienced by each individual during each of the breeding seasons from 1993 to 2007. These included the apparent disappearance of a nesting or brood-rearing individual (disappeared), mate of an individual that apparently disappeared (widowed), nest abandonment where both mates were subsequently observed (deserted), nest loss due to flooding (flooded), and nest loss due to clutch predation (depredated). Individuals 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 [φ(.),p(.)]. We modeled all AHY individuals as a single age-class and introduced increasing complexity by allowing φ and *p* to vary annually [i.e., φ(t) and p(t)]. We also considered models that allowed φ or *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 to describe 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).

The age distribution of 297 nesting Piping Plovers with individual-specific band combinations was determined for each year from 1993 to 2007. If an individual was AHY when first banded ($n = 99$), we assumed that it was 1 year old and incremented the age by 1 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 Piping Plovers aged 1 to 13 years nested in the Great Lakes. The age distribution of the 31 individuals that disappeared were estimated similarly (19 were of known age) but were not partitioned by year. Age distributions of nesting and disappeared individuals were compared in aggregate and for each sex separately, using a Kolmogorov-Smirnov test in program R, version 2.6.2 (see Acknowledgments). We compared the sex ratio of disappeared Piping Plovers against a 50:50 distribution using a likelihood-ratio chi-square test.

Results

Approximately 16% of monitored clutches laid by Great Lakes Piping Plovers from 1993 to 2007 were lost before hatching (recall that virtually all nests were protected by predator exclosures). Abandonment was the most common cause of nest loss (50% of all nest losses), but predation (31%) and flooding (19%) were also important (Table 1).

Table 1. Annual numbers of Great Lakes Piping Plover nests lost because the attendant adults disappeared or deserted the nest or because of egg predation or flooding, versus the 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 males or females that were not uniquely banded.

		Abandonment											
		Disappearance[a]			Desertion			Egg predation			Flooding		
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

[a] There were three instances (one each in 2002, 2004, and 2007) in which both pair members disappeared; the remaining pair members were categorized as "widowed."

Table 2. Top-ranking models describing the effects of monitoring period (c denotes constant and t denotes interval-specific temporal variation), band type (band), site*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 that have 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.

Table 3. Models describing the effects of year (c denotes constant, t denotes fully temporal annual variation, and T denotes linear trend) and of two types of nest abandonment (disappeared or deserted) on apparent annual survival (φ) and annual detection probabilities (p) of Great Lakes Piping Plovers during 1993–2008. Parameters that have 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	1,018.43
T + disappeared	T	1.69	0.30	5	1,022.15
T + deserted	T	72.51	0.00	5	1,092.97
T	T	73.11	0.00	4	1,095.60
t	T	80.48	0.00	17	1,076.21
T	t	82.99	0.00	17	1,078.73
t	t	89.12	0.00	30	1,057.17
c	c	90.78	0.00	2	1,117.30

[a] AIC_c of top-ranking model = 1,030.53; $\hat{c}$ = 0.96
[b] Model weight.
[c] Number of parameters.

Among abandoned nests, 70% were abandoned concurrently with the disappearance of one or both members of the nesting pair, whereas 30% of abandonments appeared to be desertions, given that both pair members were subsequently resighted. Predation and desertion occurred at consistently low levels each year, losses due to flooding tended 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 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 Piping Plovers during 27 April to 15 July was $p´ = 0.908 \pm 0.025$ (SE), and for non-nesting individuals it was $p´ = 0.791 \pm 0.045$. There was ≥0.97 probability of resighting a nesting individual at least once if it was still alive and remained on the nesting grounds for ≥20 days after 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 individuals but exceeded 0.95 for those that remained 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 individuals that disappeared or deserted their nests (Table 3). Detection probability averaged 0.939 and increased over time, ranging from 0.851 ± 0.047 in 1994 to

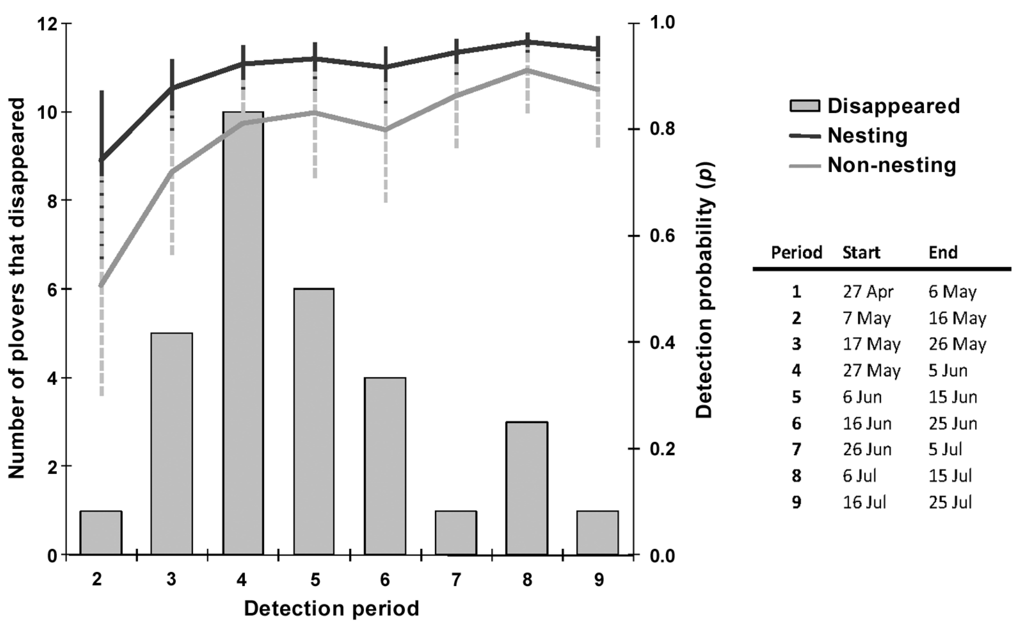

Fig. 2. Model-based detection probabilities of breeding (black line) and nonbreeding (gray line) Piping Plovers during 10-day detection periods in the 2008 breeding season in relation to the frequency with which Piping Plovers disappeared during those periods in 1997–2007 (gray bars, left axis). Error bars on detection probabilities represent 95% confidence intervals.

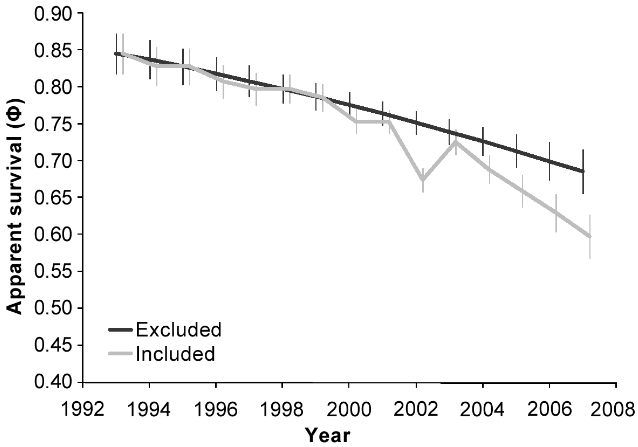

Fig. 3. Model-based estimates and 95% confidence intervals of annual survival of Great Lakes Piping Plovers when average annual losses due to disappearance and desertion are included (gray lines) versus excluded (black lines) from calculations, based on the best-supported model from Table 3.

0.986 ± 0.006 in 2008. Apparent survival exhibited a negative trend over time ($\beta_T = -0.066 \pm 0.021$; Fig. 3). None of the 31 AHY individuals coded as disappeared was ever observed again, and model-based estimates of their survival were <0.001. Estimated annual survival of individuals that deserted their nests was 0.570 $\pm$ 0.019, whereas individuals that did not desert or disappear during nesting had apparent annual survival of 0.771 ± 0.013. There was no evidence that individuals whose mates disappeared or that 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 Piping 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 individuals that disappeared differed significantly from that of Piping Plovers nesting in the Great Lakes from 1993 to 2007 (two-sided Kolmogorov-Smirnov test, $P < 0.01$). The median age of nesting males and females was 3.0 years (Fig. 4A), whereas the median ages of males and females that disappeared were 5.0 years (one-sided Kolmogorov-Smirnov test, $P = 0.01$) and 3.5 years (one-sided Kolmogorov-Smirnov test, $P = 0.02$), 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 demonstrates 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. Disappearances of adults that were attending nests occurred during a period of ~1 month characterized by high

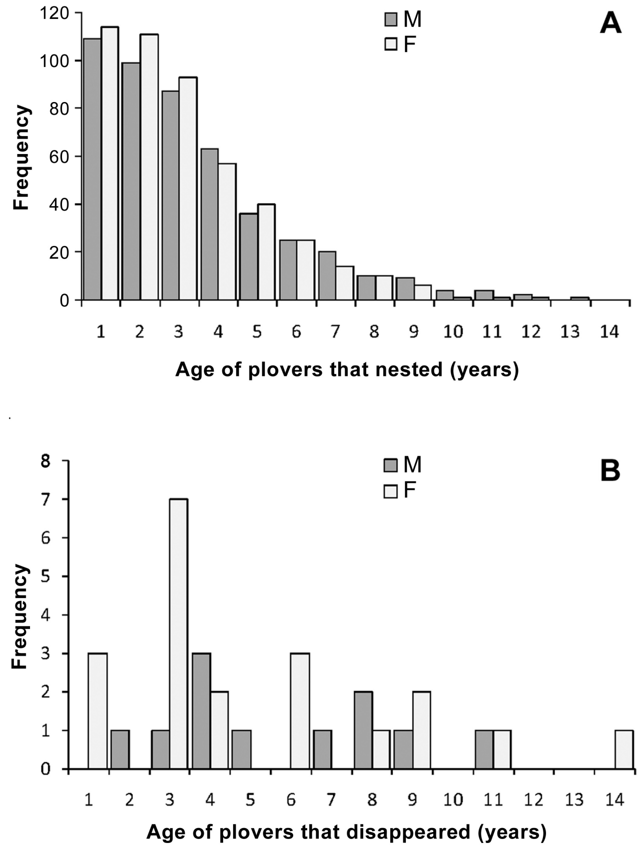

Fig. 4. (A) Age distribution of the male (M) and female (F) Piping Plover population nesting in the Great Lakes during 1993–2007 ($n_M = 151$, $n_F = 146$). (B) Age distribution of male and female Piping Plovers suspected to have disappeared during 1997–2007 ($n_M = 11$, $n_F = 20$). Because many individuals were first banded as adults of unknown age, these represent minimum age distributions.

resighting rates; thus, disappearances were not attributable to detection failure. Individuals 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 might even have 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 attributable to the death 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 3 cases in which 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 Piping Plovers had a very high probability of being seen, both within and between breeding seasons. In 2008, the detection probability for breeding individuals 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 individuals that spent at least 20 days at breeding sites approached 100%. Individuals with nests and young are generally tied to a particular stretch of beach for the duration of the incubation and rearing periods (Haffner et al. 2009). Thus, the likelihood of observing a nesting Piping Plover during a detection period in May through early June, but never again, was essentially zero, assuming that the individual was still alive and available for detection. Detection probabilities were somewhat lower for nonbreeding individuals (Fig. 2), but cumulative detection probabilities for individuals that remained at breeding sites for ≥30 days also approached 100%. This indicates that breeding Piping Plovers that disappeared from nesting beaches during the early or middle nesting season almost certainly died or emigrated from the monitoring areas.

Detection probabilities were also extremely high in our among-year analysis, averaging 0.94 over the entire study period. Detectability approached 100% during each of the past 5 years, when most disappearances were recorded. Thus, disappearances were not likely the result of 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 Piping Plovers noted as having "disappeared" during the breeding season were ever observed again, and mark–resighting analysis suggests that these were deaths. Cormack-Jolly-Seber analysis cannot formally distinguish death from permanent emigration (Cooch and White 2009), and the adjective "apparent" usually denotes 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), we obtain frequent resightings of our color-banded Great Lakes Piping Plovers from the wintering grounds (LeDee 2008), and none of the individuals that disappeared during the breeding season were seen again during winter or at other Great Lakes nesting sites. Individuals that deserted their nests also had lower survival prospects, and our analysis suggests that they suffered ~20% additional mortality (apparent annual survival averaged 0.77 for individuals that did not disappear or desert, versus 0.57 for those that deserted their nests). We suspect that some of the abandonments that were coded as desertions because of insufficient evidence were actually disappearances. Alternatively, Piping Plovers that desert their nests may be of lower quality or in poorer nutritional condition than nondeserting individuals (Arnold et al. 1995), and the same factors that predispose individuals to desert their nests also place them at greater risk of mortality during the coming year. By contrast, individuals that lost nests because of other factors did not show evidence of decreased survival; nor did widow(er)s of disappeared Piper 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 period spanning ~34 days (2 June ± 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 of 8 cases where death was confirmed, avian predators were implicated in 6. 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 that Merlins have been implicated in plover mortality; Neuman et al. (2004) also attributed the loss of 9 breeding Snowy Plovers to Merlin predation. Piping 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 females as males disappeared during breeding, which suggests that costs associated with egg laying may predispose females to higher rates of desertion and mortality (Yorio and Boersma 1994).

We encourage other investigators to consider parental mortality as a potentially important cause of nest abandonment. Failure to recognize that a nest abandonment is attributable to adult mortality can result in misinterpretation of the abandonment as a behavioral decision of the parents. Although radiotelemetry is probably the easiest way to document such mortality (Devries et al. 2003), we have demonstrated 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, in which 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.

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