APPARENT SURVIVAL OF SNOWY PLOVERS (*CHARADRIUS NIVOSUS*) VARIES WITH REPRODUCTIVE EFFORT AND YEAR AND BETWEEN SEXES

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ABSTRACT.—Life history theory predicts a tradeoff between reproductive effort and survival, which suggests that some management practices aimed at increasing productivity may compromise population growth. We analyzed a 10-year data set of 225 individually marked Snowy Plovers (*Charadrius nivosus*), a threatened shorebird, to determine whether individual reproductive effort was correlated with low apparent survival. Most adults resided in the population an average of 2 years (range: 1–10 years), during which females laid 3–60 eggs, and both males and females invested considerable time in incubation and brooding. Apparent survival varied annually and was higher for males than for females. Contrary to theory, we found no evidence that increased reproductive effort, either current or cumulative, compromised survival. Instead, apparent survival was correlated positively with incubation time, which may be related to either high-quality individuals having high reproductive rates and high survival or permanent emigration of failed breeders (who incubated for shorter intervals). Although our results suggest that some predator management practices (e.g., nest exclosures) aimed at increasing productivity will not compromise survival in a subsequent year, we caution that these same practices may have serious negative consequences for population growth if (1) reproductive effort does not translate into higher per capita fledging success and (2) direct mortality of adults results from the practice. *Received 4 October 2012, accepted 27 August 2013.*

Key words: apparent survival, *Charadrius nivosus*, incubation, reproductive effort, Snowy Plover, threatened.

La Supervivencia Aparente de *Charadrius nivosus* Varía con el Esfuerzo Reproductivo y entre Años y Sexos

RESUMEN.—La teoría de historias de vida predice un compromiso entre el esfuerzo reproductivo y la supervivencia, lo que sugiere que algunas prácticas de manejo que se enfocan en incrementar la productividad podrían comprometer el crecimiento de las poblaciones. Analizamos un conjunto de datos de 10 años de 225 individuos de *Charadrius nivosus*, un ave playera amenazada, para determinar si el esfuerzo reproductivo individual se correlaciona con una baja supervivencia aparente. Muchos adultos permanecieron en la población un promedio de 2 años (rango: 1–10 años), tiempo durante el cual las hembras pusieron 3 a 60 huevos, y tanto hembras como machos invirtieron tiempo considerable en la incubación y el cuidado de la nidada. La supervivencia aparente varió anualmente y fue mayor en machos que en hembras. Contrario a la teoría, no encontramos evidencia de que un incremento en el esfuerzo reproductivo, ya sea actual o acumulado, compromete la supervivencia. Por el contrario, la supervivencia aparente se correlacionó positivamente con el tiempo de incubación, lo que podría relacionarse con individuos de alta calidad que tienen altas tasas reproductivas y alta supervivencia, o con la emigración permanente de los individuos que fracasan en reproducirse (y que incubaron por intervalos de tiempo más cortos). Aunque nuestros resultados sugieren que algunas prácticas de manejo de depredadores (e.g. cercar los nidos) que se enfocan en incrementar la productividad podrían no comprometer la supervivencia en el siguiente año, advertimos que estas mismas prácticas podrían tener consecuencias negativas serias para el crecimiento poblacional si (1) el esfuerzo reproductivo no se traduce en mayor éxito de emplumamiento per cápita y (2) tales prácticas resultan en la mortalidad directa de los adultos.

LIFE HISTORY THEORY predicts a tradeoff between reproductive effort and survival (Stearns 1976), with individuals that invest more in reproduction suffering higher mortality. A rich body of experimental (e.g., Daan et al. 1990, Verhulst 1998, Murphy 2000) and observational (Rotella et al. 2003, VanderWerf and Young 2011) evidence offers wide support for this tradeoff, although exceptions exist (Waser and Jones 1991; see review in Murphy 2000). Roff (1992) suggested that observational studies may provide limited insight into tradeoffs for several reasons. First, high-quality individuals may both reproduce and survive well (Moyes et al. 2006). Second, individuals

may adjust their reproductive effort to match varying environmental conditions and, thus, minimize subsequent survival costs (Waser and Jones 1991). Third, apparent survival does not account for individuals that fail early in reproduction and permanently emigrate (Sandercock 2003). Despite these shortcomings, observational studies continue to provide valuable insights into tradeoffs.

The mechanism by which high reproductive effort compromises survival is less well understood, and it probably varies among taxa that differ in life history traits (Sæther and Bakke 2000). Individuals with increased workload may experience higher mortality owing to greater vulnerability to predation (Collier et al. 2009), increased parasitemia (Stjernman et al. 2004), or inability to recoup energy reserves sufficient to withstand overwinter conditions (Verhulst 1998). Regardless of the mechanism, these observations pose a dilemma for conservationists because management practices aimed at increasing population size often emphasize enhancing productivity of individuals, with less concern for negative consequences to adult survival. This is especially problematic because adult survival has been identified as the vital rate that most strongly affects population growth (Hitchcock and Gratto-Trevor 1997, Sæther and Bakke 2000, Sandercock 2003; but see Sim et al. 2011).

In avian conservation, the potential for a tradeoff in vital rates (i.e., productivity and adult survival) is exemplified by the practice of enhancing reproductive success using certain nonlethal methods of predator control. For example, predator exclosures are protective cages that exclude egg predators from nests; they are commonly used to boost hatching success of ground-nesting birds (shorebirds: Suborder Charadrii). Although exclosures have been shown to increase hatching success (Isaksson et al. 2007, Pauliny et al. 2008; but see Mabee and Estelle 2000), they also have been linked to higher adult mortality because incubating birds are more susceptible to predation (Isaksson et al. 2007, Hardy and Colwell 2008, Catlin et al. 2011). Moreover, exclosures may have subtle effects on demography if individuals invest energy and time in eggs, only to have low reproductive success because nidifugous chicks exit exclosures and become prey of the same predators that consume eggs. In this case, the tradeoff between individual reproductive success and survivorship may be exacerbated if individuals both fail to reproduce and suffer higher mortality owing to greater reproductive investment.

The Pacific Coast population of the Snowy Plover (*Charadrius nivosus*; hereafter "plover") was listed as threatened in 1993 under the U.S. Endangered Species Act (U.S. Department of Interior 1993). The species' recovery plan (U.S. Fish and Wildlife Service [USFWS] 2007) identified three factors that are thought to limit recovery of the population by compromising productivity: (1) predation of eggs and chicks by native Striped Skunks (*Mephitis mephitis*) and Common Ravens (*Corvus corax*) and introduced Red Foxes (*Vulpes vulpes*); (2) habitat loss and degradation owing to the spread of invasive European Beachgrass (*Ammophila arenaria*) in breeding areas; and (3) reproductive failure owing to human disturbance. Predation is widely thought to be the most important of these three limiting factors. Accordingly, various nonlethal and lethal methods of predator control have been used to increase plover productivity, often with mixed results. In northern California, exclosures increased hatching success, but per capita fledging success remained low at some sites where activity of Common Ravens was associated with low chick survival (Colwell et al. 2007a, Hardy and Colwell 2008, Burrell and Colwell 2012). Similarly, in central California, there was little evidence to suggest that a combination of lethal and nonlethal

predator management positively affected plover productivity (Neuman et al. 2004). Importantly, the recovery plan does not directly address adult survival and management practices that may either enhance or compromise this vital rate.

Here, we examine relationships between apparent survival and various measures of individual reproductive effort in a small population of plovers breeding in coastal northern California. Our objectives are to analyze the individual histories of color-marked birds to (1) characterize variation in breeding effort and reproductive success for male and female plovers and (2) examine relationships between individual breeding effort and apparent survival. Our primary goal is to use these findings to inform and refine management aimed at recovering the listed population segment of the plover.

Methods

Study area

We studied a color-marked population of plovers in coastal northern California from 2001 through 2010. During this interval, nearly all plovers bred in Humboldt County (Colwell et al. 2010, Mullin et al. 2010), one of three (including Del Norte and Mendocino) counties that comprise Recovery Unit 2 (RU2), as designated in the recovery plan (USFWS 2007). We monitored plovers on ocean-fronting beaches and riverine gravel bars, which differed greatly in habitat quality (Colwell et al. 2010). On ocean beaches, plovers bred amid homogeneous sandy substrates that were sparsely vegetated (Muir and Colwell 2010) and littered with natural and anthropogenic debris. On gravel bars, plovers frequented habitats with coarser, heterogeneous substrates that were sparsely vegetated with willow (*Salix* spp.) and White Sweet Clover (*Melilotus alba*), occasionally sparsely cluttered by driftwood. Colwell et al. (2010) provide a detailed contrast of these two habitat types.

Field Methods

We started monitoring plovers in 2000 by marking as many breeding adults and chicks as possible. Each subsequent year, we continued to mark all adults and newly hatched chicks. As a result, we are confident that we marked nearly all breeding adults in the population (Colwell et al. 2010, Mullin et al. 2010). Observers monitored reproductive effort and survival by surveying suitable breeding habitats at approximately weekly intervals from mid-March until the last chick fledged in late August or early September; frequency of surveys increased to every 1–4 days when we observed plovers at a site. During surveys, observers walked slowly along beaches and gravel bars and scanned for plovers using binoculars and spotting scopes. When observers detected a plover, they recorded the bird's identity (i.e., color bands), behaviors (e.g., feeding, incubating, tending chicks), and associations with other plovers to determine pairing status. Observers also searched for nests and monitored broods. On beaches, plover tracks often led us to nests and locations of broods, but this approach did not work amid the coarse substrates of gravel bars. After we detected a nest or brood, we assigned ownership to a pair on the basis of repeated observations of plovers in the vicinity of the nest, incubating eggs, or tending chicks. In most cases, low population density facilitated these determinations (at any one time, only one or a few pairs occurred in an area). Additional details on field methods are provided elsewhere (Colwell et al. 2007a, 2010; Mullin et al. 2010).

Data Summary and Analysis

Initial marking and resightings.—Our data set consisted of the life histories of 123 females and 102 males marked with a unique combination of a single, numbered metal band wrapped with colored tape and three plastic color bands. Each of these plovers bred (i.e., had a nest with 1–3 eggs) at least once in our study area. The 225 individuals consisted of (1) yearlings first marked as chicks in the study area and recruited into the population (29.8%), (2) immigrant adults color-marked elsewhere along the Pacific coast (23.1%), and (3) unmarked immigrants of unknown age and origin that we first banded with a unique color-band combination (47.1%). Capture histories of individuals began with the first year an individual bred locally, and for encounter histories were coded as "1" and "0" for present or absent, respectively, in the local breeding population each year (15 March–20 July). A small percentage of plovers left the study area each year but returned in a subsequent breeding season (Pearson and Colwell 2013). We recorded these individuals as absent (0) if they did not initiate a clutch in the study area (RU2). We determined the sex of individuals using differences in plumage (Page et al. 1995), confirmed by repeated observations of behaviors (e.g., copulation, incubation, and brooding). We aged birds as yearlings or adults on the basis of when they were marked and subsequently entered the local population (i.e., yearlings marked locally or elsewhere along the Pacific coast). A small proportion of adults were marked immigrants. We assumed that all unmarked birds that we captured and banded were 1 year old. Mullin et al. (2010) have provided a detailed breakdown of these categories.

Breeding and reproductive effort.—The plover population was a mix of year-round residents and migrants that returned to breed after wintering elsewhere along the Pacific coast (Colwell 2007b). Some resident pairs associate in winter flocks, with courtship beginning in February; migrants may enter the population from April into July. Plovers typically initiated their first clutches (modal clutch size = 3) in March, especially during warm weather. The plover's serially polygamous breeding system is driven by a pattern of unequal investment by the sexes in parental care (Page et al. 1995). Females lay eggs at a minimum interval of 2 days, such that a clutch typically requires 4 or 5 days to complete (Colwell 2006). Incubation begins with the laying of the third egg. Parents share incubation for 28 days, with females tending to incubate during the day and males at night (Page et al. 1995). The nidifugous young hatch synchronously (i.e., generally within 24 h), after which they are tended mostly by males for ~28 days. Females sometimes assist the male in caring for newly hatched chicks by brooding or remaining alert nearby, but most search for a new mate, especially if time remains in the breeding season. The long breeding season and pattern of parental care allow males and females to reproduce successfully up to 2 and 3 times year^{-1}, respectively.

We found the majority of nests prior to clutch completion (Colwell et al. 2010), used egg flotation methods (Liebezeit et al. 2007) to determine clutch initiation dates for nests found with complete clutches, and monitored nests (Hardy and Colwell 2008) and broods (Colwell et al. 2007a) frequently to determine fates. These efforts provided detailed information on numbers of eggs, chicks, and fledglings produced annually with encounter histories, and gauged reproductive effort in two ways. First, we summarized the total number of eggs, chicks, and juveniles produced (females) or tended (males) by an individual each year. In nine cases (4%; 5 females and 4 males), we did not detect an individual breeding in the study areas during a given year, but they bred in a subsequent year (i.e., we missed the individual's breeding attempt). In these instances, we substituted an individual's average numbers of eggs, chicks, and fledglings (per year) for those of the missing year because we knew that these birds bred outside our study area. Second, we indexed effort as the proportional amount of time invested in incubation and brooding, based on the time required to successfully hatch chicks (28 days) and rear young to independence (28 days) (Page et al. 1995). For example, if an individual successfully hatched chicks, they received a value of 1.0 for that breeding attempt; by contrast, an individual whose nest failed 14 days into incubation received a value of 0.5. We applied the same method to index time invested in rearing a brood. As a result, the typical male that shared incubation with his mate and successfully reared chicks alone received a score of 2.0 for that breeding attempt. If the same male successfully bred again that season (i.e., fledged a second brood), his total score for the year would be 4.0. We applied the same method to female breeding records. We used this method to index time (and energy) invested in parental care, recognizing that successful breeders may have indices similar to those of plovers that renested frequently after experiencing reproductive failure owing to predation of eggs or chicks.

Survival analyses.—We used the Cormack-Jolly-Seber model implemented in Program MARK (White and Burnham 1999) to model annual survival (ϕ) and conditional capture probability (*p*) based on individual encounter histories from 2001–2010. We modeled survival using individual time-varying covariates for sex, status (migrant or year-round resident), and origin (local recruit or immigrant), as well as indices of reproductive effort (i.e., number of eggs, number of chicks hatched, number of chicks fledged, and summed indices of investment in incubation and brooding). For each of these five measures, we included a year-specific covariate (e.g., number of eggs laid each year) and a cumulative covariate (e.g., total number of eggs across years that an individual bred locally).

We used MARK to construct competing models to explain the possible influence of annual and cumulative reproductive effort on annual survival. Our model set included a global model with full sex and time variation in both parameters. We used Program RELEASE (Burnham et al. 1987) to assess model fit by pooling the results of tests 2 and 3, a common goodness-of-fit approach for Cormack-Jolly-Seber data. We used the median $\hat{c}$ procedure in MARK to check for overdispersion in the data (Burnham and Anderson 2002). Estimates of median $\hat{c}$ were slightly less than 1, so we did not adjust $\hat{c}$ in MARK (Cooch and White 2011).

Our model set began by incorporating information from a previous analysis of adult apparent survival in this population (Mullin et al. 2010), which reported evidence of annual variation in adult survival and conditional capture probability. Consequently, we started with models that included those sources of variation. Holding apparent survival constant, we fit four structures to conditional capture probability (constant [.], linear across years [T], quadratic across years [TT], and varying by sex [sex]) and evaluated their support using Akaike's information criterion (AIC). Once we had determined an appropriate structure for *p*, we constructed models to investigate variation in annual apparent survival as a function of sex, status, origin, and the individual time-varying reproductive effort covariates representing time invested in incubation and brooding. Because of a lack of independence, our analyses were limited to models that included only single measures of reproductive effort (i.e., no interactions).

We used program R to conduct our analyses (R Development Core Team 2010) and used univariate statistics ($\bar{x} \pm$ SD) to compare various measures of reproductive effort between the sexes and across years.

Results

Longevity.—Males and females were resident in the local population for similar durations, as evidenced by average longevity (males: 2.3 ± 1.6 years; females: 1.9 ± 1.2 years). Overall, most plovers (males: 46%; females: 69%) bred locally for only 1 year; a few (10 males and 7 females) were present for ≥5 years (Table 1).

Reproductive success.—Most males and females produced just one or two clutches (Table 1). With each added year ($n = 10$), cumulative reproductive effort increased significantly (Kendall's tau; all $P < 0.05$) as indexed by the number of eggs laid or tended (females: 0.77; males: 0.75). However, relationships grew progressively weaker when we examined the numbers of chicks hatched (males: 0.63; females: 0.62), young fledged (males: 0.53; females: 0.43), and, finally, yearlings recruited into the local population as breeders (males: 0.45; females: 0.22).

Reproductive effort.—Plovers varied greatly in reproductive effort, as gauged by time invested in incubation and brooding (Fig. 1). Males and females overlapped widely in incubation effort, but males expended greater effort in brooding than females. There was no evidence that reproductive effort varied with an individual's age.

Apparent survival.—The global model fit the data well ($\chi^2 = 28.71$, df = 52, $P = 0.99$), with no evidence of a lack of model fit. The best model included the effects of year, sex, and a year-specific index of time spent incubating on annual survival and a quadratic time trend in conditional capture probability across years (Table 2). This model was >18 AIC units better than the next best model, which had zero weight; hence, all results presented here are from the best model. Although no other model was competitive, the top nine models all included year and sex effects on apparent survival and a quadratic time trend on recapture probability. The top model included strong evidence for annual variation in apparent survival, with 2005–2006 and 2006–2007 having lower survival than the other years (Fig. 2). Females had lower apparent survival than males ($\hat{\beta}_{female} = -0.54$; 95% CI: –1.13 to 0.05), although the confidence interval barely included zero. Finally, apparent survival was positively associated with a yearly measure of the amount of time invested in incubation ($\hat{\beta}_{time} = 2.69$; 95% CI: 1.40 to 3.97). Conditional capture probabilities varied during the 10-year period and ranged from 0.63 to 0.96.

Discussion

Contrary to theory, we found no evidence that reproductive effort, whether measured on an annual basis or cumulatively across years, compromised survival. In fact, the only competitive model indicated that apparent survival increased with reproductive effort the previous year, as gauged by incubation time. Studies of costs of reproduction in birds have produced mixed results. Murphy (2000) reviewed the literature and found conflicting evidence that reproductive effort compromised adult survival. Most of the studies he examined were conducted on altricial species in which provisioning of young (i.e., effort) was increased by supplementing clutch size, and in most studies (68%), increased effort did not result in greater adult mortality. Other studies, however, have demonstrated a survival cost of reproduction. Daan et al. (1990) manipulated clutch size in European Kestrels (*Falco tinnunculus*) and found that adults tending larger-than-normal broods suffered higher mortality than individuals caring for smaller broods. Collier et al. (2009) showed that survival of Wild Turkey (*Meleagris gallopavo*) hens was correlated negatively with duration of incubation. In this case, high mortality of females tending eggs and chicks seemed to be related to predation, rather than being a carryover cost of poor condition that translated into lower survival the subsequent winter. The tradeoff between reproduction and survival is also evident in long-lived species. VanderWerf and Young (2011) showed that male Laysan Albatrosses (*Phoebastria immutabilis*) that successfully reared young suffered higher mortality than those that failed. By contrast, female albatrosses were more likely to skip a year after successfully breeding. Plovers are precocial, nidifugous breeders with a comparatively short life span (Page et al. 1995). Consequently, one would predict greater effort in egg laying and incubation owing to the low probability of surviving another year to breed.

It is possible that apparent survival was not affected negatively by reproductive effort because individuals adjusted their effort to environmental conditions (e.g., food availability) in order to minimize future costs of reduced survival (Murphy 2000). This explanation was proposed by Waser and Jones (1991) to explain the absence of a relationship between reproductive effort, survival, and future fecundity in Banner-tailed Kangaroo Rats (*Dipodomys spectabilis*). By contrast, Eastern Kingbirds (*Tyrannus*

TABLE 1. Summary of tenure and reproductive success of male and female Snowy Plovers breeding in coastal northern California, 2001–2010. Values are the percentage of the total number of individually marked males and females. Integer increments for eggs, chicks, and fledglings correspond to 1, 2, 3, 4, or 5+ 3-egg clutches.

	Males ($n = 102$)						Females ($n = 123$)						t-test	P
Tenure (year)	$\bar{x} \pm$ SD	1	2	3	4	5+	$\bar{x} \pm$ SD	1	2	3	4	5+		
	2.3 ± 1.7	46	23	14	9	10	1.9 ± 1.2	69	19	22	6	7	1.88	0.06
Eggs	$\bar{x} \pm$ SD	1–3	4–6	7–9	10–12	>12	$\bar{x} \pm$ SD	1–3	4–6	7–9	10–12	>12	t-test	P
	12.5 ± 14.4	27	20	14	6	35	10.9 ± 11.2	41	28	11	5	36	0.92	0.36
Chicks	$\bar{x} \pm$ SD	0	1–3	4–6	7–9	>10	$\bar{x} \pm$ SD	0	1–3	4–6	7–9	>10	t-test	P
	5.0 ± 5.0	19	38	17	13	15	4.1 ± 4.1	32	48	15	12	16	1.58	0.12
Fledglings	$\bar{x} \pm$ SD	0	1–3	4–6	7–9	>10	$\bar{x} \pm$ SD	0	1–3	4–6	7–9	>10	t-test	P
	2.3 ± 3.1	35	47	11	5	4	1.8 ± 2.4	53	50	13	5	2	1.20	0.23

FIG. 2. Annual variation in average (± SE) apparent survival of male and female Snowy Plovers in Humboldt County, northern California, 2001–2010.
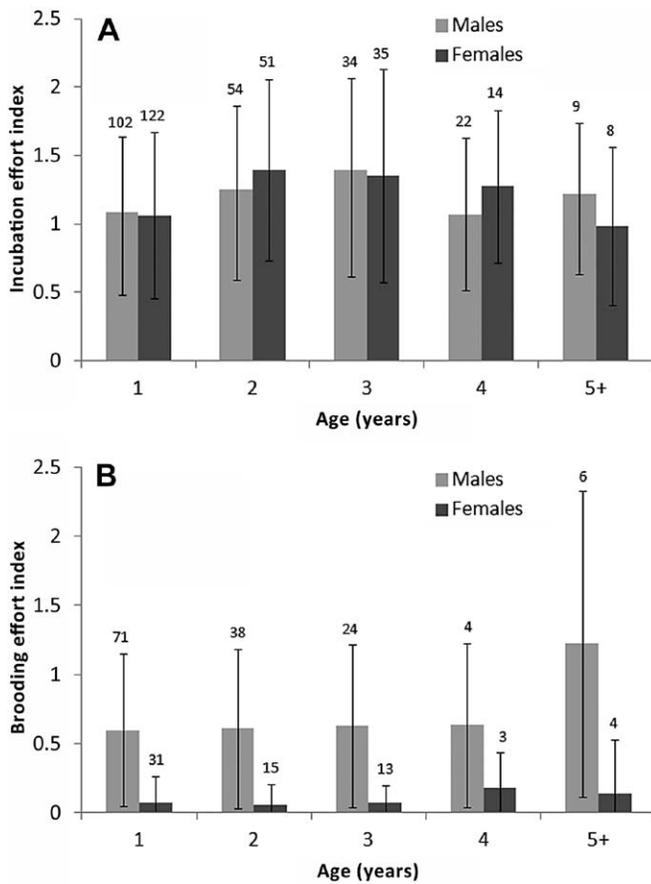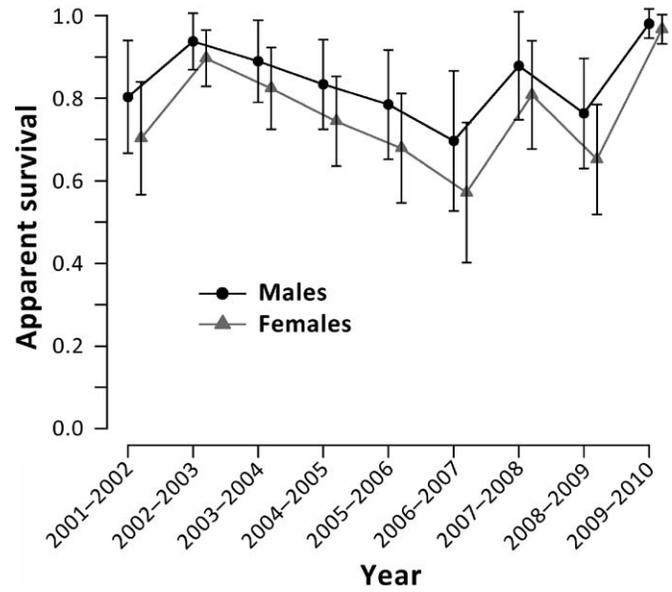
FIG. 1. Average (± SE) variation in time invested in (A) incubation and (B) brooding by male and female Snowy Plovers of different ages in Humboldt County, northern California, 2001–2010. Time invested is scaled to the 28-day intervals required to both successfully incubate eggs and brood chicks (total = 56 days).

tyrannus) adjusted reproductive effort in association with enlarged clutches to successfully rear young under varying environmental conditions (Murphy 2000). Similar reasoning applied to plovers posits that individuals increased effort during the breeding season in anticipation of favorable conditions during the nonbreeding season. We find this argument untenable because two facets of plover breeding biology make it difficult for individuals to adjust

TABLE 2. Model selection results examining apparent survival of Snowy Plovers in Humboldt County, northern California, 2001–2010, as a function of reproductive effort, year, and sex. K = number of parameters.

Model	K	ΔAIC_c [a]	w_i	Deviance
ϕ Year + sex + time	14	0.00	1.00	594.94
ϕ Year + sex + eggs	14	18.70	0.00	613.64
ϕ Year + sex + chicks	14	19.66	0.00	614.60
ϕ Year + sex + fledge	14	33.72	0.00	628.66
ϕ Year + sex + brood	14	37.26	0.00	632.20

[a] Akaike's information criterion (AIC) value of best model was 623.94.

their reproductive effort to match environmental conditions. First, shorebirds are "income breeders" (Morrison and Hobson 2004, Morrison et al. 2005), relying on the immediate availability of energy (e.g., food) and nutrients (e.g., calcium) to form eggs and maintain their body condition during incubation and brooding. As such, they rely on resources in an unpredictable environment to fuel reproduction. Moreover, precocial chicks are not fed by parents, and so the care required by young (e.g., frequent brooding; Colwell et al. 2007a) is different from that in altricial species. Finally, we detected no obvious differences in reproductive effort among years or across individuals of different age classes (Fig. 1). Hence, it is unlikely that individuals adjusted their reproductive effort (1) as they gained experience or (2) to match vagaries of the environment.

Others have reported positive relationships between survival and reproductive effort. For example, Moyes et al. (2006) showed that survival of older female Red Deer (*Cervus elaphus*) increased with lifetime reproductive effort. They suggested that one possible explanation for this pattern was that effort could be linked to the quality of the individual, with individuals of good quality reproducing more frequently and having a higher survival rate. Although this explanation is plausible, we find it inconsistent with our data because there was no evidence to link any measure of cumulative effort with survival.

Alternatively, the positive relationship between reproductive effort and survival may stem from field and analytical methods that occasionally failed to detect plovers. For example, some individuals may have gone undetected during the 4 months over which plovers initiated nests. However, our regular surveys of known breeding sites, coupled with increased effort when we detected plovers at previously unoccupied sites, minimized the chance of missing breeding birds. More importantly, apparent survival cannot distinguish between mortality and permanent emigration (Sandercock 2003), and the

latter is more likely among failed breeders (e.g., Haas 1998). In our study area, plovers breeding for the first time that fail to hatch eggs also incubate for short durations; these failed breeders are likely to disperse greater distances than successful breeders, although few actually leave the study area (Pearson and Colwell 2013). We suspect that this plays only a minor role in our results, because we are aware of only a few permanent emigrants.

Sex differences.—Males had higher apparent survival than females (Fig. 2; Mullin et al. 2010), a finding consistent with other reports of survival of Snowy Plovers (Paton 1994; Stenzel et al. 2007, 2011) and Kentish Plovers (Sandercock et al. 2005, Foppen et al. 2006). The most thorough analyses of Snowy Plover survival have been based on the population breeding around Monterey Bay, California (Stenzel et al. 2007, 2011), several hundred kilometers south of our study area. Stenzel et al. (2011) determined that true survival was higher for males (0.73) than for females (0.69). Our survival estimates (Fig. 2) were slightly higher than Stenzel et al.'s (2011) estimates, perhaps as a result of differences in analytical approaches (i.e., covariates included in the model and quadratic relationship for conditional capture probability), the long (120-day) interval over which we resighted individuals, and environmental variation associated with study areas and years included in analyses. Our apparent survival estimates are higher than those reported earlier in our study (Mullin et al. 2010), probably because we (1) used a longer resight interval (see above), (2) increased sample size associated with additional years, and (3) encountered a series of mild winters in later years during which individuals survived well (as indicated by high return rates; M. A. Colwell unpubl. data).

Annual variation in survival.—Apparent survival varied annually (Fig. 2), with lowest survival in 2006–2007. We reported this result in an earlier paper (Mullin et al. 2010) and argued that it stemmed from the combined effects of mortality associated with the use of nest exclosures at one site in June 2006 (Hardy and Colwell 2008) and a prolonged period of cold temperatures during January 2007 (Eberhart-Phillips and Colwell 2013). That finding was compromised by the fact that low survival occurred in the final year in the data set, which confounded the survival estimate with recapture probabilities. The present analysis confirms the low survival of plovers in that year. Our finding has an interesting parallel in true survival for plovers breeding in central California. Stenzel et al. (2011) analyzed a 10-year data set spanning 1993–2003 and showed a pronounced mortality event associated with one winter (1998–1999). In both studies, the pattern of annual variation in plover survival was driven by a single year in which survival was especially low. Anecdotally, weather data show that both of these years had intervals (December 1998, January 2007) during which subfreezing temperatures persisted across coastal California for 1–2 weeks. While suggestive, these data require formal testing using climate data standardized for the entire winter range of the listed population segment of the plover, and independent data sets.

Conservation implications.—In birds, population growth is most influenced by variation in adult survival (Sæther and Bakke 2000), although exceptions exist (Sim et al. 2011). Consequently, understanding factors that influence variation in survival is critical to effective population management. Our finding that survival of adult plovers was not compromised by reproductive effort is encouraging, given that management has emphasized increasing the productivity of this population by using nest exclosures (USFWS 2007). However,

we caution managers to carefully consider direct mortality associated with specific nonlethal measures, specifically predator exclosures, taken to lessen the negative effects of predation on productivity. The marked increase in mortality in one year (2006–2007) was associated with an episode during which an unknown avian predator killed as many as 8 breeding adults at one location in our study area over a 3-week period (Hardy and Colwell 2008, Mullin et al. 2010). In this case, we stopped using exclosures at this site in recognition of the dependence of population stability on adult survival. We urge others to carefully consider the immediate survival costs of exclosures (see Isaksson et al. 2007) in day-to-day management actions to boost the productivity of ground-nesting birds. Finally, it is imperative that conservationists understand the relative importance of poor weather-related annual variation in survivorship, especially in the context of the recovery (i.e., population growth) of threatened and endangered taxa at the limits of their range (Newton 1998). These events pose especially challenging management scenarios involving adult survivorship, the most important vital rate affecting population growth of most bird species.

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