APPARENT SURVIVAL OF SNOWY PLOVERS VARIES SEASONALLY

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ABSTRACT

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Survival is an important vital rate that contributes to population viability, but is infrequently monitored and studied, especially compared to productivity. Furthermore, factors that limit survival and the relative effect on survival are often unknown. I used mark-resight observations of a small (~350) population of threatened Snowy Plovers (*Charadrius nivosus nivosus*) to quantify seasonal and annual variation in survival and movement between three coastal locations across ~70 km in Humboldt County, California. The return of individuals to non-breeding flocks at three locations was high between years (75-81%). Movement between three locations varied greatly, although most (n = 137) individuals resided at a single location throughout the 7-month study period (Sep-Mar). Apparent survival was lowest (0.88 ± 0.02) during late winter (Feb-Mar), and highest during the breeding season (0.97 ± 0.005). Annual survival was also higher in this study than previously reported for the population (0.85 ± 0.03). Given that apparent survival is predictably lowest during the winter (Dec-Mar), management directed at protecting non-breeding plover flocks from disturbance and other threats may make plovers less susceptible to mortality.

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INTRODUCTION

To effect population growth of declining species, managers require detailed knowledge of vital rates, particularly productivity and survival. Productivity (i.e., per capita fledging success) is most frequently monitored and managed because it can be easy to estimate and improve (Cohen and Gratto-Trevor 2011). However, population stability and growth in some species is mostly influenced by survival (i.e., the probability that individuals alive in one year survive to successive years; Sæther and Bakke 2000, Larson et al. 2002, Sandercock et al. 2005). This is especially true of long-lived species with slow reproduction, such as shorebirds (Sandercock 2003). Survival has been studied in many shorebird populations, but few projects have examined how sources of mortality affect survival.

Survival varies seasonally and annually due to factors such as predation (Lank et al. 2003, van der Hout et al. 2008), food availability (Kober and Barlein 2009, van Gils et al. 2013, Bowgen et al. 2015), and weather conditions (Stenzel et al. 2007, Clark 2009, Mullin et al. 2010, Ryan et al. 2015). Weather, in particular, can have a strong effect on survival at both short and long time scales, which can cause either acute (i.e., episodic) or cumulative effects on survival (Yalden and Pearce-Higgins 1997, Eberhart-Phillips and Colwell 2014).

For shorebirds, estimates of annual survival have been provided for many species based on the return of color-marked individuals to breeding or non-breeding sites (see Evans and Pienkowski 1984 for an early review). Adult survival is characterized as high

Table 1. Apparent survival estimates of selected shorebirds based on individually marked birds.

Species		Type	Adult	Juvenile	Source
Pacific Golden-Plover	*Pluvialis fulva*	Annual	0.80 ± 0.02	0.90 ± 0.04	Johnson et al. 2010
Kentish Plover	*Charadrius alexandrinus*	Annual	0.63 ± 0.01		Sandercock et al. 2005
Snowy Plover	*Charadrius nivosus*	Annual	0.69 ± 0.03	0.46 ± 0.02	Stenzel et al. 2007
		Male	0.73 ± 0.03		Stenzel et al. 2011
		Female	0.69 ± 0.03		Stenzel et al. 2011
		Male	0.61 ± 0.08		Mullin et al. 2010
		Female	0.50 ± 0.11		Mullin et al. 2010
		Annual		0.40 ± 0.06	Mullin et al. 2010
Piping Plover	*Charadrius melodus*	Annual	0.80 ± 0.03	0.57 ± 0.05	Cohen and Gratto-Trevor 2011
Red Knot	*Calidris canutus*	Annual	0.84 ± 0.06		Brochard et al. 2002
		May-Aug	0.99 ± 0.00		Leyrer et al. 2013
		Sep-Apr	0.94 ± 0.01	0.86 ± 0.02	Leyrer et al. 2013
Western Sandpiper	*Calidris mauri*	Male	0.72 ± 0.06		Johnson et al. 2010
		Female	0.57 ± 0.08		Johnson et al. 2010

while juvenile survival is lower and more variable (Table 1; Yalden and Pearce-Higgins 1997, Stenzel et al. 2007, Roche et al. 2010). For example, Stenzel et al. (2007) used 16 years of mark-resight data to estimate juvenile and adult Snowy Plover (*Charadrius nivosus nivosus*) survival: juvenile survival varied from 0.283 ± 0.03 to 0.575 ± 0.06, and adult apparent survival averaged 0.691 ± 0.03 (Stenzel et al. 2007) with similar temporal variation in survival in juveniles and adults.

In 1998, Snowy Plover survival estimates were significantly lower along the Pacific Coast (Stenzel et al. 2007). This suggests that the strong El Niño conditions of 1997-98 played a role in the decline in Snowy Plover survival (Stenzel et al. 2007). However, the once annual sampling was too infrequent to determine the effect of weather on survival. This may be because the Southern Oscillation Index (SOI) and corresponding El Niño/La Niña events are large-scale processes that effect local coastal conditions. Therefore, El Niño/La Niña could drive local weather conditions which may affect apparent survival rates, and researchers could test for the significance and size of these effects by sampling at shorter intervals.

Sampling during the non-breeding season is also essential to uncover the factors driving survival rates. For example, Roche et al. (2010) found that the differences in wintering areas had the single strongest effect on apparent survival for Piping Plovers (*Charadrius melodus*), rather than breeding locations. Piping Plovers share non-breeding grounds along the Gulf of Mexico and Atlantic Coast, and breed in distinct populations in the Great Plains, Great Lakes, and Atlantic Coast (Gratto-Trevor et al. 2012, Gratto-Trevor et al. 2016). Distinct breeding populations (e.g., Great Lakes and New York) experienced similar changes in apparent survival despite differing conditions on breeding grounds, which suggests that factors during the non-breeding season drove the observed changes in apparent survival (Roche et al. 2010). Monitoring during the non-breeding season has also identified hurricanes and Merlin (*Falco columbarius*) abundance as factors that have a strong cumulative effect on apparent survival of Piping Plovers (Noel and Chandler 2008, Saunders et al. 2014).

Survival rates are known to also vary within the annual cycle (Stenzel et al. 2007, Roche et al. 2010, Leyrer et al. 2013). Migratory Red Knot (*Calidris canutus canutus*) experienced exceptionally high apparent survival (0.99 SE 0.4×10^{-4}) during the breeding season and migration (i.e., May through August) compared with significantly lower apparent survival during the non-breeding season (0.94 SE 0.01; Leyrer et al. 2013). Predation (van der Hout et al. 2008) and food availability (van Gils et al. 2013) contributed to the increased mortality rate for Red Knots (Leyrer et al. 2013), though the relative effect of those factors on survival is unknown. Sampling at short intervals within the annual cycle can identify the timing of mortality, and can distinguish between acute, short term changes in survival compared with cumulative effects over long periods of time.

Episodic mortality has been detected in several long-term studies of shorebirds, and it is thought that cold temperatures contribute to the observed mortality rates (Yalden and Pearce-Higgins 1997, Stenzel et al. 2007, Mullin et al. 2010). For example, Mullin et al. (2010) observed that 50% of marked Snowy Plovers permanently disappeared during a period of cold temperatures in coastal northern California. Sustained cold temperatures can significantly increase adult mortality (Eberhart-Phillips and Colwell 2014). It may be possible to detect episodic mortality in a marked population if these episodic events are related to weather and occur predictably, and if a population is studied at short intervals.

The Western Snowy Plover (hereafter, plover) is a threatened population segment that occurs on the Pacific Coast from central Washington, USA south to Baja California, Mexico. US Fish and Wildlife Service listed the population as threatened in 1993 due to the small and declining population (USFWS 2007). The population decline was caused by loss of suitable breeding habitat, expanding predator populations, and human disturbance (USFWS 2007). USFWS divided the plovers' range into six recovery units (i.e., geographic regions, Figure 1), each with unique recovery goals defined by population size and productivity (USFWS 2007). Recovery Unit 2 (RU2) in Northern California encompasses Del Norte, Humboldt and Mendocino counties; the recovery goal for RU2 is 150 breeding adults maintained for 5 years and an average reproductive success of 1 fledged chick per male for 10 years (USFWS 2007).

The plover population in Humboldt County has been studied since 2001 (Colwell et al. 2017), including productivity (Herman and Colwell 2015), survival (Mullin et al. 2010), and population viability analyses (Eberhart-Phillips and Colwell 2014). In January 2007, about 50% of the plovers in RU2 permanently disappeared from non-breeding flocks (Mullin et al. 2010) coincident with a period of cold weather (Eberhart-Phillips and Colwell 2014). It is unknown whether the assumed mortality of half of the northern California population was a direct result of inclement weather, and, if so, whether environmental conditions had an episodic or cumulative effect on apparent survival.

Therefore, my objectives were to: 1) describe the non-breeding plover flocks in northern California, including the number of plovers, distribution in flocks, return rates and movements; 2) estimate the variation in apparent survival during the non-breeding season and in comparison with the breeding season; and 3) evaluate whether and to what extent variation in survival is explained by cold and inclement weather.

METHODS

Study Area

Observers surveyed for non-breeding plovers along 2.5 km transects of ocean-fronting beach at three locations (Figure 1; Brindock 2009, Brindock and Colwell 2011). At each location, researchers established transects where winter flocks of plovers predictably occurred during the day (Brindock 2009, DeJoannis 2016). Little River State Beach is the northernmost transect location (124º6’51”W 41º0’56”N), the South Spit transect lies west of Humboldt Bay (124º14’29”W 40º45’1”N), and Centerville Beach is the southernmost transect (124º20’37”W 40º35’12”N). Plovers typically roosted during the day amidst open, sparsely vegetated habitat of the wrack and foredune. Native plants (e.g., *Abronia*, *Leymus*) occurred along the foredune, which was backed by dense stands of European beach grass (*Ammophila arenaria*). Beach slope was steepest at Centerville, compared with South Spit and, especially, Little River State Beach (Brindock 2009). Mean monthly invertebrate abundance (mean ± SD) from core samples during the 2015 non-breeding season was highest at South Spit (115.3 ± 7.9) compared with Little River (63.8 ± 8.0) and Centerville (26.0 ± 4.4; D. Orluck pers. comm.), and was predominantly talitrid amphipods which are a principal prey item of plovers (Page et al. 2009).

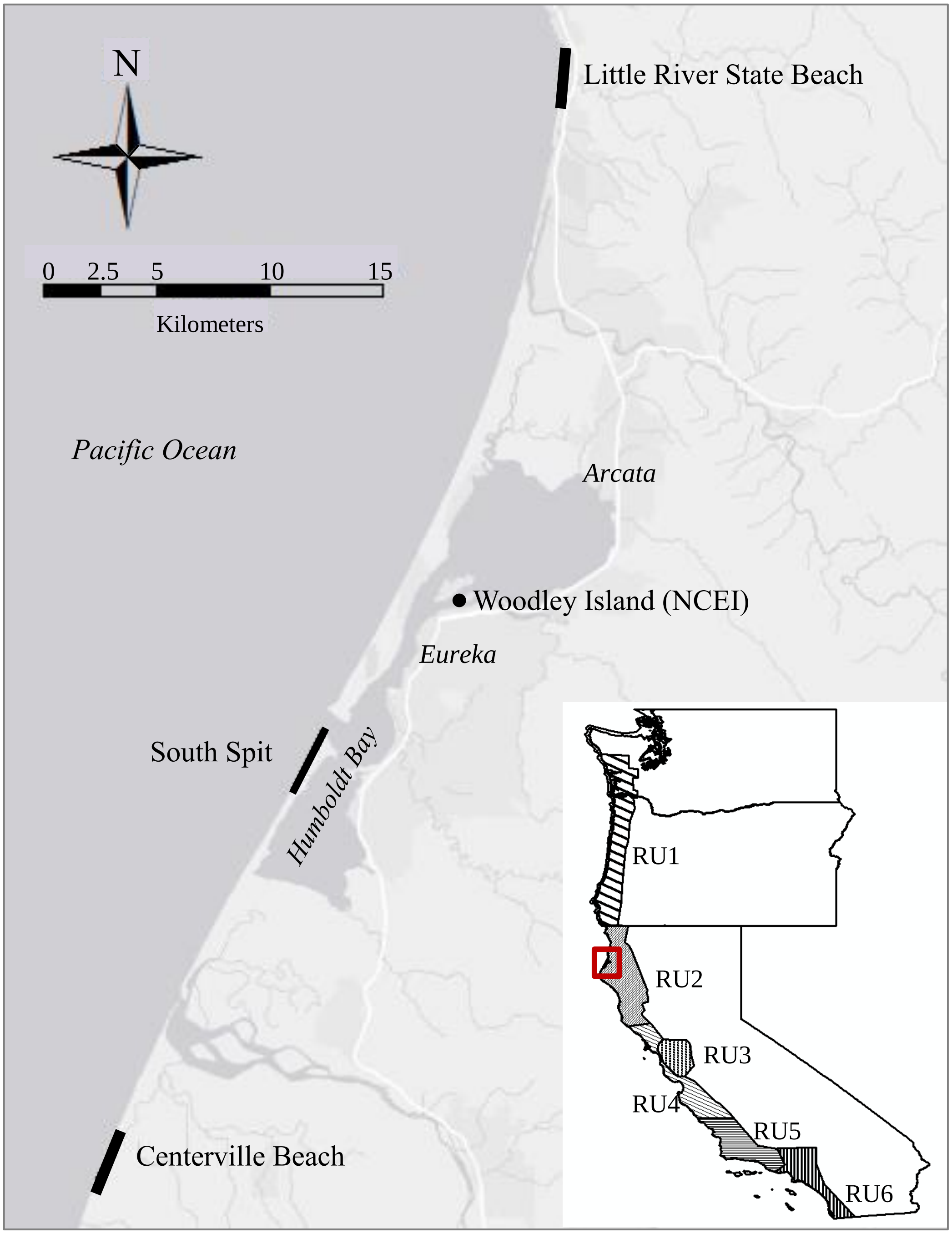

Figure 1. Snowy Plovers occurred at three locations in Humboldt County, California where observers surveyed flocks bimonthly from September through March to resight color-marked individuals for use in survival analyses.

Data Collection

Most plovers (n=149) wore unique combinations of colored leg bands applied during the breeding season locally (n=53) or in other recovery units (n=96). Early in each non-breeding season (August–December), we captured and banded plovers using mist-nets and noose mats placed amidst the wrack and foredune at the Little River and Centerville transects. Upon capture, we applied unique color-band combinations to the tarsometatarsus of unbanded and group-banded plovers. These unique color-band combinations consisted of a USFWS metal band wrapped in colored tape on the lower right leg, and three plastic color bands to create a four-color combination. We determined age by known hatch date or the presence of juvenile plumage (Pyle 2008), and sexed birds by plumage characteristics and breeding behavior (e.g., copulation position) when possible.

Beginning in September, observers conducted bimonthly surveys of each transect starting 30 minutes after sunrise by walking the most recent high tide (i.e., wrack) line while scanning for plovers using binoculars (8-10x) and spotting scopes (20-60x). When researchers encountered plovers, one observer remained with the initial flock to record band combinations, flock size, behavior, and locations with a hand held geographic positioning system (GPS); the other observer continued to survey the transect, recording band combinations of additional plovers. Observers collected data under federal (USFWS #TE-73361A-1; banding permits #23844 and #10457), state (Department of Fish and

Wildlife #SC0496; Department of Parks and Recreation #17-635-005), and university (Humboldt State University IACUC #14/15.W.07-A) permits and protocols.

Data Summary and Analysis

I combined the number of plovers observed per survey and the identity of all plovers encountered to show changes in flock size, the distribution of plovers in the study area, and the movement of plovers. Observers recorded the minimum number of unbanded plovers encountered and all brood-specific band combinations encountered in addition to individually marked plovers. I estimated the total number of unbanded plovers for a non-breeding season from the maximum number encountered during a single survey throughout the non-breeding season. I determined where plovers were banded as a proxy for origin, as band combinations are specific to each recovery unit.

I created an encounter history record for each individually marked plover based on the bimonthly records of their presence on the transects (Table 2). I included where a plover was observed – L (Little River), S (South Spit), or V (Centerville) – to estimate movement between transects in the study area. If we observed a plover at two sites during a survey occasion, I kept only the first location in the data. I included all three non-breeding seasons in each encounter history record to examine overall effects on apparent survival and to compare the non-breeding seasons. Because survival intervals must be of equal length (Cooch and White 2015), I added ten bimonthly occasions without data between each non-breeding season to account for the breeding season when transect surveys were not completed. This resulted in 62 occasions in each encounter history

Table 2. Examples of encounter histories for two Snowy Plovers.

Plover	Interval Length	2014 Non-breeding							2015 Breeding					2015 Non-breeding							2016 Breeding					2016 Non-breeding						
		S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M
AG:AB	14 Days	L	0	L	0	L	0	0	.	.	.	.	.	0	L	L	L	L	L	0	.	.	.	.	.	L	L	L	L	L	L	0
		L	L	L	L	L	0	L	.	.	.	.	.	L	L	L	L	L	L	L	.	.	.	.	.	L	L	L	L	L	0	0
	30 Days	L	L	L	L	L	0	L	.	.	.	.	.	L	L	L	L	L	L	L	.	.	.	.	.	L	L	L	L	L	L	0
RY:GW	14 Days	0	0	0	0	0	0	0	.	.	.	.	.	0	0	0	0	S	0	0	.	.	.	.	.	L	L	0	V	S	S	S
		0	0	0	0	0	0	0	.	.	.	.	.	0	V	0	0	0	0	0	.	.	.	.	.	L	L	L	L	V	0	S
	30 Days	0	0	0	0	0	0	0	.	.	.	.	.	0	V	0	0	S	0	0	.	.	.	.	.	L	L	L	V	S	S	S

Plover	Interval Length	2015 Non-Breeding														2016 Breeding									
		Sep		Oct		Nov		Dec		Jan		Feb		Mar		Apr		May		Jun		Jul		Aug	
AG:AB	14 Days	0	L	L	L	L	L	L	L	L	L	L	L	0	L	.[4]	.	.	.	.	.	.	.	.	.
	30 Days	L[1]		L		L		L		L		L		L		.		.		.		.		.	
RY:GW	14 Days	0	0	0	V	0	0	0	0	S[3]	0	0	0	0	0	.	.	.	.	.	.	.	.	.	.
	30 Days	0		V[2]		0		0		S		0		0		.		.		.		.		.	

[1]L = Little River State Beach flock; [2]V=Centerville Beach flock; [3]S=South Spit flock; [4] "."=Missing sampling occasion, survey not completed for that interval.

record for the study (September 2014 through March 2017). I pooled the data from bimonthly (~14 day intervals) to monthly (30 days) intervals; if we observed a plover at different locations during the bimonthly occasions, I kept only the first transect location. Each encounter history record consisted of 31 month-long occasions: 21 survey occasions for the three non-breeding seasons, and two sets of five occasions without data corresponding to the two breeding seasons (Apr–Aug 2015 and 2016; Table 2).

I used the Multi-State Mark-Recapture (MSMR) model framework in Program MARK to estimate survival and movement probabilities (MARK Version 8.1; Burnham and White 1999). The MSMR framework is a generalized Cormack-Jolly-Seber (CJS) model that relies on capture histories of individually marked animals to estimate three parameters: survival (S), detection (p), and transition between states (ψ; Cooch and White 2015). Survival measures the probability of surviving a month interval between survey occasions. Detection measures the probability of observing an individual during a survey occasion if it is present in the study area. Transition measures the movement of individuals between states (i.e., transects) during a month interval (Cooch and White 2015). I used the simulated annealing optimization algorithm to improve model convergence (Cooch and White 2015). Multi-state data with more than two states may have multiple local likelihood maxima; simulated annealing is recommended in this case as it increases the ability of the maximization algorithm to find the global maximum likelihood (Peterson et al. 2014).

I used a two-stage model selection approach in which I first determined the best model structure for detection and transition while holding the survival model constant, then evaluated alternative survival models using the most supported models for detection and transition. I compared the relative support of competing models using an information-theoretic approach (Burnham and Anderson 2000). I evaluated the relative support of physical (i.e., transects) and temporal effects in detection and transition models. Temporal effects included year (Sep-Aug), non-breeding season (Sep-Mar and Apr-Aug), and season. I defined seasons as follows: fall (Sep-Nov), winter (Dec-Jan), spring (Feb-Mar), and breeding (Apr-Aug). I then compared the relative support for survival models that included physical (i.e., location), temporal and weather effects. I used the same temporal effects from the detection and transition models for survival models. included additive and interactive effects in the temporal and weather covariates.

To evaluate the effect of weather conditions on apparent survival, I accessed daily minimum temperature and precipitation records from the Woodley Island National Weather Service (NWS)-National Centers for Environmental Information (NCEI) Station in Eureka, California, which is located about halfway between the Little River and Centerville transects. I calculated the mean minimum (average) temperature, lowest minimum (minimum) temperature, and total precipitation for each month-long interval during the study. In a previous analysis, Eberhart-Phillips (2012) found that the number of cold days during the winter (i.e., Dec-Feb) had a strong effect on apparent survival in the northern California plover population. A cold day was defined as at or below 2.29ºC, which is one standard deviation below the mean minimum temperature for winter from 1941 to 2011 (5.53 ± 3.24ºC). I used a similar threshold of 2.3ºC for a cold day for consistency between projects. I summed the number of days below 2.3ºC for each interval to use as an additional weather covariate.

I derived annual, non-breeding season, and seasonal (e.g., winter and spring) survival estimates by taking the product of the appropriate monthly apparent survival estimates. I calculated the variance of these estimates using the delta method (Cooch and White 2015). The derived annual survival estimates are not directly comparable with previous survival analyses. Therefore, I also completed an annual survival analysis using a CJS model framework in Program MARK (MARK Version 8.1; Burnham and White 1999). For this analysis I included plovers observed at any time from October through December. I incorporated five groups into the analysis: juvenile male, juvenile female, adult male, adult female, and unknown. I used group, age, the age at entry to the population (first age), and time to evaluate the variation in survival (φ) and detection (p). I utilized simulated annealing in the analysis to improve optimization (Cooch and White 2015). I tested for over-dispersion with the median-$\hat{c}$ test in Program MARK (Cooch and White 2015).

RESULTS

Flock Composition

Flocks of post-breeding plovers began to form as early as July and reached maximum size in October and November (Figure 2). Observers detected at least 350 plovers during the three years of study, during which the population grew from a minimum of 169 (2014) to at least 234 (2016). The non-breeding flock at Little River State Beach was consistently the largest, with 73% of the population each year (Figure 3). The number of plovers wintering at Centerville Beach remained steady throughout the study, although the proportion of plovers occurring there decreased from 27% (2014) to 22% (2016). The South Spit flock was absent in 2014, but increased to 5% of the population by 2016.

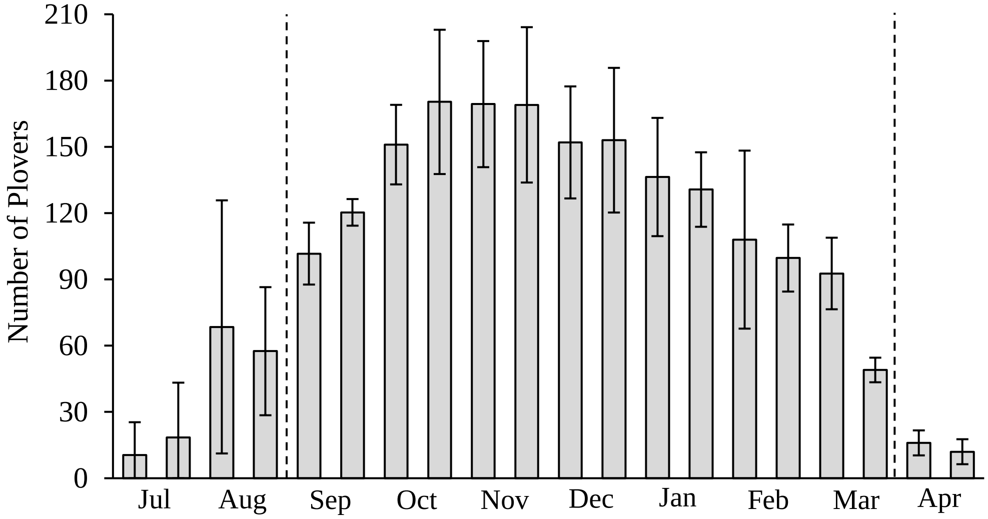

Figure 2. Mean (± SD) number of plovers encountered across the three transects during the non-breeding season. Dashed lines bound the period when observers surveyed the transects.

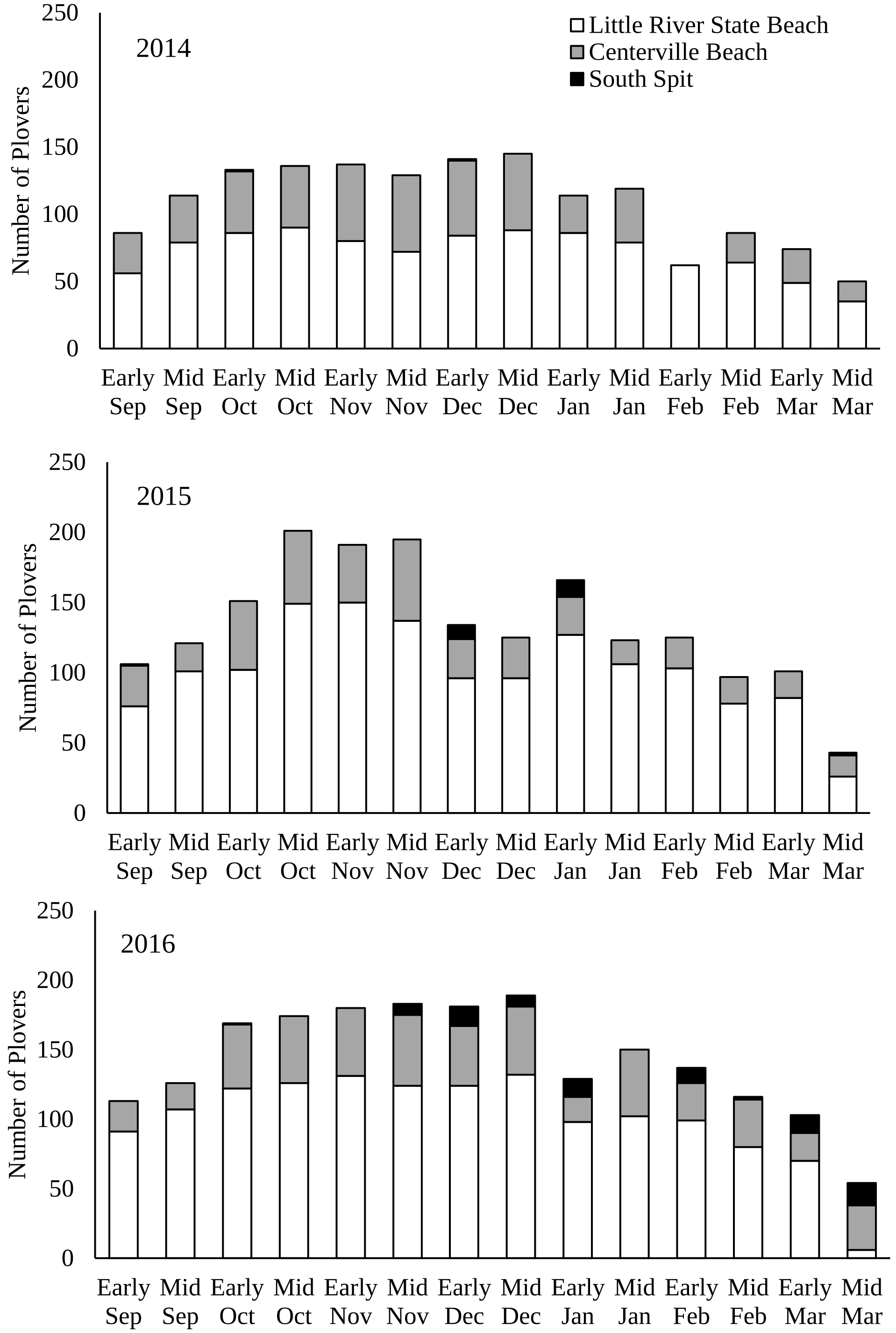

Figure 3. Maximum number of plovers observed during one survey on each transect during the study.

Observers recorded a minimum of 293 marked plovers, including 154 uniquely marked individuals and 139 plovers marked with brood-specific bands; the 154 individually marked plovers comprise the study population. The origins of marked plovers varied: 49% of the marked plovers wore band combinations from Recovery Unit 1 (RU1, Oregon and Washington), 43% originated from coastal northern California (RU2), and 8% came from southern recovery units. For the 154 uniquely marked plovers (i.e., included in the survival analysis), 25% wore bands from RU1, whereas 62% had RU2 band combinations. Most (62%) of the individually marked plovers occurred only during the non-breeding season (i.e., they did not breed in RU2); 38% occurred year-round in RU2 (i.e., they bred and wintered locally).

Return Rates and Individual Movements

Return rates (i.e., the percentage of uniquely marked birds present in one field season that observers detected the next season) varied between 75 and 95% (Table 4). During the non-breeding season, most plovers (84%) occurred at a single location (i.e., transect), and I considered these individuals to be residents at a site. The Little River flock had the highest proportion of residents at 86%, whereas the Centerville flock included 58% residents; 14% of the South Spit flock was resident.

Table 3. Number of returned (return rate, %) individually marked plovers in the study population.

Non-breeding Season	Female	Male	Juvenile	Adult	Overall
2014 to 2015	25 (73.5)	36 (78.2)	20 (87.0)	48 (77.4)	65 (75.6)
2015 to 2016	39 (95.1)	48 (81.4)	23 (88.5)	63 (82.9)	90 (81.8)

Survival

I included 154 individually marked plovers in the seasonal survival analysis. We aged (90%) and sexed (83%) most of the individually marked plovers. Most plovers entered the population as adults (60%) and the majority (55%) were male, although only 77% (n=119) were of known age and sex. Therefore, I excluded age and sex groups from the seasonal analysis.

I modeled detection and transition in the first stage of the analysis. The model with the most relative support incorporated variation by transect for both detection and transition. Plovers had the highest detection probabilities at Little River State Beach ($\hat{p}$ = 0.91; 95% CI 0.88-0.94) and Centerville Beach ($\hat{p}$ = 0.88; 0.81-0.93), and significantly lower detection probability at South Spit ($\hat{p}$ = 0.15; 0.10-0.21). Transition (i.e., movement) varied by transect as well: estimated movement away from Little River was lowest, whereas movement between Centerville and South Spit was higher (Figure 4).

I used the best model structure for detection and transition, which was variation by transect, to evaluate the relative support for different survival models (Table 4). The top survival model included interactive seasonal (e.g., fall and winter) and annual effects on survival. The seasonal effect on survival was included in the top seven models, which accounted for 99% of the AIC_c weight.

Table 4. Model selection table.

Survival (S)	Detection (p)	Transition (ψ)	ΔAICc	AICc Weights	Model Likelihood	K[a]	Deviance
Season[b] * Year	Location	Location	0.00	0.57	1.00	20	1694.53
Season + Year + Cold + Precip.	Location	Location	3.25	0.11	0.20	17	1697.78
Season + Year + Precipitation	Location	Location	3.45	0.10	0.18	16	1697.97
Season + Year + Cold	Location	Location	4.24	0.07	0.12	16	1698.77
Season + Year + Minimum	Location	Location	4.43	0.06	0.11	16	1698.96
Season	Location	Location	4.95	0.05	0.08	13	1713.80
Season + Year	Location	Location	5.61	0.03	0.06	15	1700.14
Non-breeding Season	Location	Location	11.12	0.00	0.00	11	1724.03
Year	Location	Location	11.69	0.00	0.00	12	1722.57
Year + Cold	Location	Location	15.74	0.00	0.00	11	1726.62
Year + Precipitation	Location	Location	18.27	0.00	0.00	11	1729.15
Constant	Location	Location	19.98	0.00	0.00	10	1734.92
Seasonal Average	Location	Location	23.69	0.00	0.00	11	1718.22
Seasonal Minimum	Location	Location	29.91	0.00	0.00	11	1724.44
Seasonal Precipitation	Location	Location	30.69	0.00	0.00	11	1725.22
Seasonal Cold	Location	Location	30.93	0.00	0.00	11	1725.46
Month Minimum	Location	Location	65.05	0.00	0.00	11	1720.03
Month Average	Location	Location	65.42	0.00	0.00	11	1720.40
Month Precipitation	Location	Location	69.18	0.00	0.00	11	1724.16
Month Cold	Location	Location	71.55	0.00	0.00	11	1726.54
Constant	Constant	Constant	192.36	0.00	0.00	3	1921.43

a: K = number of parameter

b: Season defines survival as constant during the following months: Sep-Mar (fall), Dec-Jan (winter), Feb-Mar (spring), and Apr-Aug (breeding).

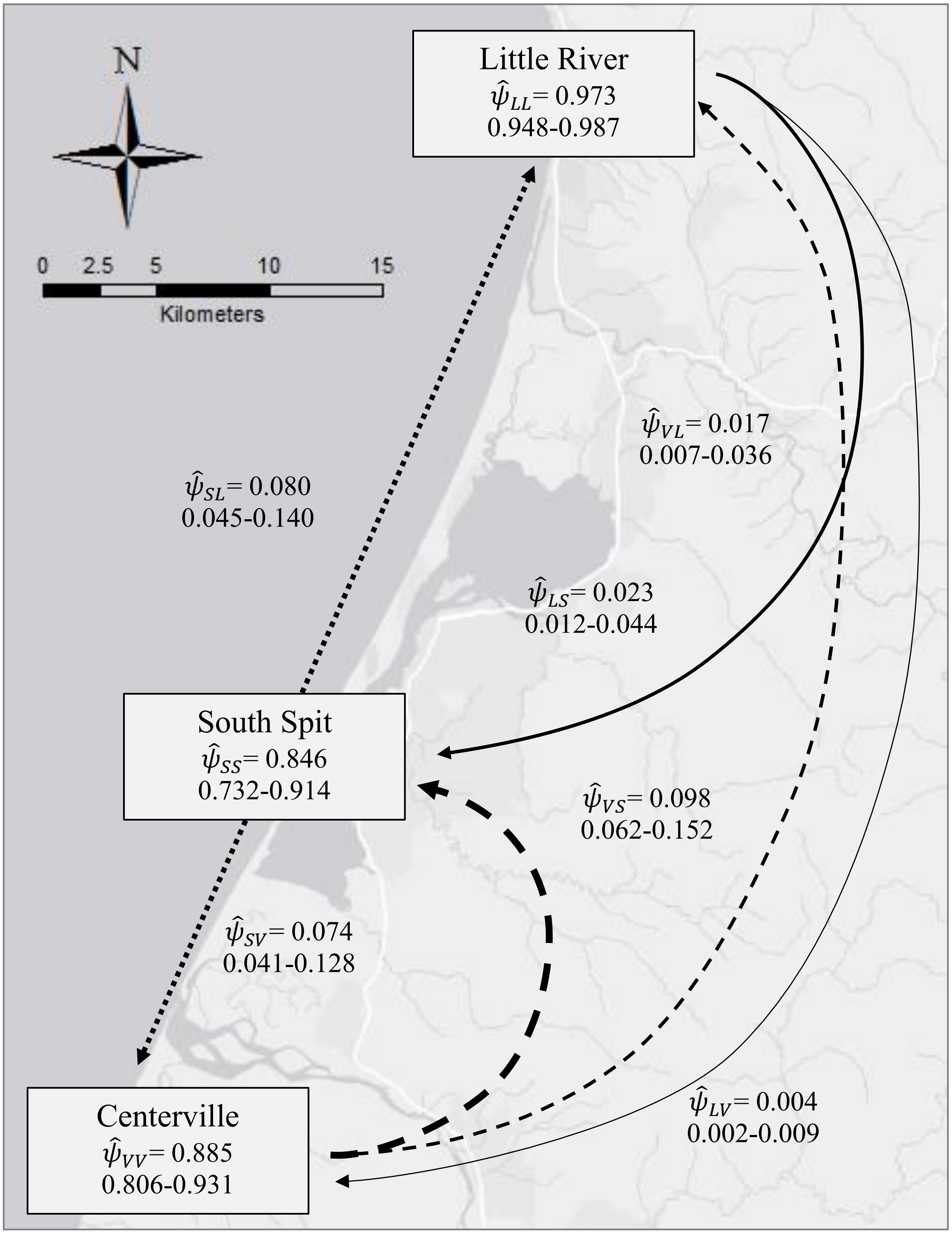

Figure 4. The movement and residency (estimate and 95% CI) of plovers varied by transect location.

Weather covariates in models with additive seasonal and annual effects had greater relative support than the additive model without weather covariates by both AICc and deviance. The best supported survival model with weather covariates included the number of cold days (minimum temperature ≤ 2.3℃) and the total precipitation per season throughout the study. However, both covariates only weakly affected apparent survival: an increase in the number of cold days had a weak positive effect on survival ($\beta = 0.025$; CI -0.085–0.133), while the total precipitation had a slight negative effect on survival ($\beta = -0.024$; CI -0.071–0.023).

The month-long survival estimates varied seasonally (Figure 5), with lowest apparent survival during the winter (i.e., December – March) compared with breeding and fall (i.e., April – November). Apparent survival varied from 0.94 (0.89-0.98) to 1.00 (0.99-1.00; Figure 5) during the study, except for the final interval ($\hat{S} = 0.84$; 0.76-0.90). The average seasonal estimates reflected a similar pattern in which survival estimates are lowest for the February through March (0.89; 0.85-0.92) and higher from April through November (0.97; 0.95-0.99).

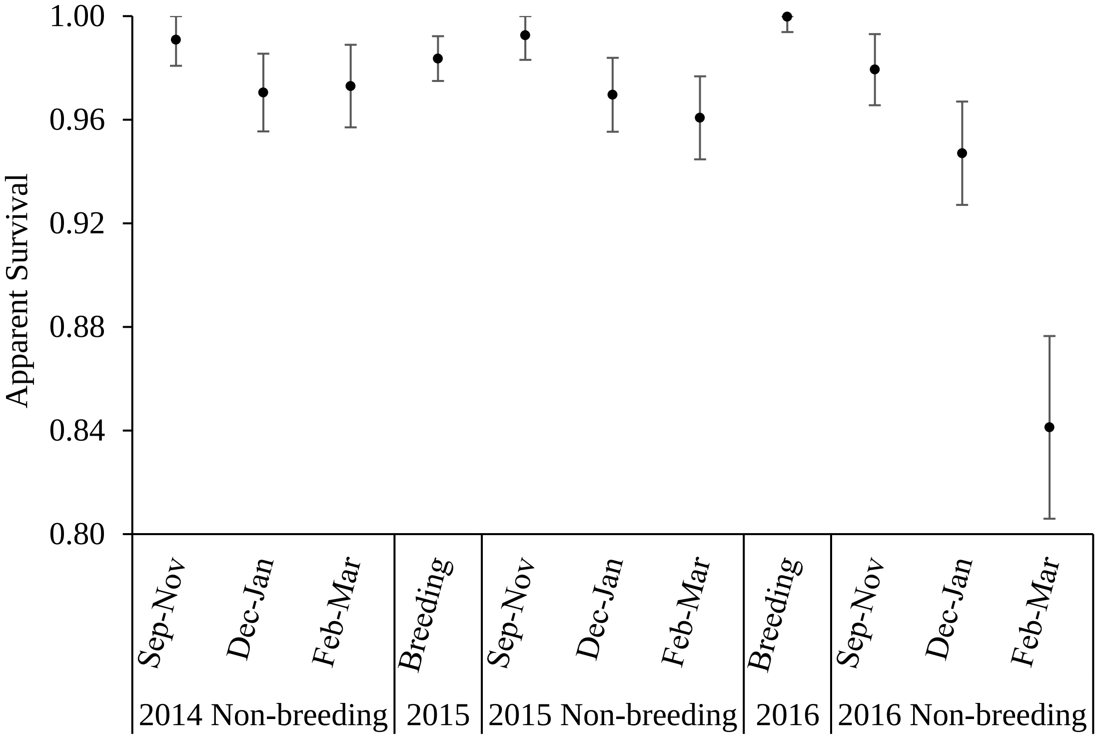

Figure 5. Monthly survival estimates (± CI) for Snowy Plovers varied by year.

Apparent survival during each non-breeding season studied (i.e., 2014, 2015 and 2016) is a derived parameter, which is the product of the seasonal survival estimates. Apparent survival during the 2014 and 2015 non-breeding seasons was relatively high and very similar ($\hat{S}$ = 0.88, 0.82–0.92 and $\hat{S}$ = 0.86, 0.81–0.88, respectively) compared with the 2016 non-breeding season ($\hat{S}$ = 0.60, 0.58–0.61). Derived annual apparent survival (e.g., September 2014 through August 2015) was very high during the study, and higher in 2015 ($\hat{S}$ = 0.85; 0.81–0.89) compared with 2014 ($\hat{S}$ = 0.81; 0.77–0.84).

I modeled annual apparent survival after correcting for over-dispersion (median-$\hat{c}$ = 1.099). The top model included variation in detection, but constant survival (Table 5). Detection probability was lowest for plovers of unknown age and/or sex ($\hat{p}$ = 0.65, 0.38-

0.85), and higher for adults ($\hat{p}$ = 0.96, 0.86-0.99) and juveniles ($\hat{p}$ = 1.00, 0.99-1.00) Annual apparent survival was high during this study ($\hat{\varphi}$ = 0.85, 0.79-0.90). Apparent survival was highest in juveniles ($\hat{\varphi}$ = 0.90, 0.76-0.96) and adult females ($\hat{\varphi}$ = 0.87, 0.75-0.93) compared to adult male ($\hat{\varphi}$ = 0.80, 0.69-0.88).

Table 5. Model selection table for CJS annual survival analysis.

Survival (φ)	Detection (p)	ΔQAICc	QAICc Weights	Model Likelihood	K	Deviance
Constant	First Age	0.00	0.70	1.00	4	17.85
First Age	First Age	3.75	0.11	0.15	6	17.35
Age	First Age	4.53	0.07	0.10	7	15.97
Constant	Constant	5.16	0.05	0.08	2	27.16
Constant	Time	5.78	0.04	0.06	3	25.71
Group	First Age	6.62	0.03	0.04	8	15.88

DISCUSSION

There are three main findings from this thesis project. First, Snowy Plovers reliably occur at some locations (e.g., Little River State Beach) throughout the non-breeding season, which allows the study of their demography for short intervals. Second, apparent survival was high during the length of the study, but varied throughout the annual cycle. And, finally, weather covariates only weakly affected survival estimates during the study, likely due to relatively mild weather conditions.

Non-breeding Plovers

Snowy Plovers were highly site faithful and predictable at some locations (e.g., Little River State Beach) between non-breeding seasons, similar to other shorebird populations at winter roost sites (Rehfisch et al. 2003). Plovers are known to exhibit high site fidelity to non-breeding locations between years at coarse spatial scales (Page et al. 1995). Plovers not only displayed high site fidelity between consecutive non-breeding seasons, but also demonstrated high site fidelity at small (i.e., 2.5 km transects) spatial scales in northern California. Plovers also demonstrated a high level of site fidelity within non-breeding seasons, and most plovers (87%) were only observed at only one site. This high within-season site fidelity is, again, similar to other shorebirds (Rehfisch et al. 2003, Conklin et al. 2007, Noel and Chandler 2008) and previous plover studies (Brindock and Colwell 2011). Brindock and Colwell (2011) found that plovers occupy short linear stretches of beach in Humboldt County, but there is insufficient data to describe home ranges in this project. Yet, the high predictability of plovers at locations between and within non-breeding seasons may facilitate more accurate measures of demographic parameters.

As a partial migrant (Page et al. 2009), the listed population segment of Western Snowy Plover consists of a mix of migrants and year-round residents. Most (62%) of the non-breeding population were migrants and were never observed breeding in the recovery unit (i.e., for northern California). The remaining plovers were year-round residents in the area. Migrant plovers were primarily short-distance migrants, which is consistent with previous descriptions (Page et al. 2009). The greatest observed migration distance during this study was about 900 kilometers. Migration is known to be a period of low survival in many species of birds (Sillette and Holmes 2002, Alerstam et al. 2003). The propensity to migrate varies in Western Snowy Plover, and both residency and migration are maintained within the population, suggesting there may be different advantages to both strategies.

Apparent Survival

Annual apparent survival was higher than previously recorded for the population (Stenzel et al. 2007, Mullin et al. 2010). Previous analyses have studied annual survival using single sampling windows in the breeding season for large populations over many years (Stenzel et al. 2007, Mullin et al. 2010, Stenzel et al. 2011), whereas this project is a detailed analysis of many short intervals from a small population for three years. This project may have produced higher survival estimates because fewer plovers were included in the analysis and most survived, while previous studies included more individuals over long periods. However, the higher survival estimates may simply reflect favorable conditions during the study. This project was conducted during a period of local (Colwell et al. 2017) and range-wide population growth (www.fws.gov/arcata/es/birds/wsp/plover) when survival is expected to be high. Furthermore, measuring apparent survival during the non-breeding season may yield more accurate estimates because of high return rates to non-breeding areas.

Snowy Plover monthly survival estimates were high but variable throughout the study. Apparent survival was lower in December through March compared with April to November when apparent survival was high and seemingly stable. This pattern of lower survival estimates during the winter or non-breeding season has been shown (Stenzel et al. 2007, Mullin et al. 2010, Leyrer et al. 2013, Eberhart-Phillips and Colwell 2014) for shorebirds. Lower apparent survival estimates during the non-breeding season have been due to food limitations (Leyrer et al. 2013) and cold temperatures (Mullin et al. 2010, Eberhart-Phillips and Colwell 2014). Weather weakly affected apparent survival during the study, but it is unknown whether and to what extent other factors such as predation (Cresswell and Whitfield 1994, Lank et al. 2003), food limitation (Warnock et al. 1997, Kober and Barlein 2009, Bowgen et al. 2015), disease (Page et al. 2009), or a combination of these factors (Yasué et al. 2003, Kock et al. 2018) affect survival. The results from this project suggest that weather has a cumulative effect on apparent survival in contrast with previous work with the northern California population (Mullin et al. 2010, Eberhart-Phillips and Colwell 2014). Previous studies have shown that prolonged cold temperatures have a severe and immediate affect on apparent survival (Mullin et al. 2010, Eberhart-Phillips and Colwell 2014), whereas this study found that cold temperatures weakly improved apparent survival. The total precipitation during a survival interval affected survival, which suggests that the number of or intensity of storms may affect survival. Increased precipitation may influence foraging (Warnock et al. 1997) or increase energetic requirements of plovers (Evans 1976).

Apparent survival during the final non-breeding season was much lower than earlier seasons. The lower observed survival estimates may be a result of the study design (i.e., the end of the study and lack of continued data collection) or dispersal. However, it is possible that the estimates reflect a real decrease in survival for plovers in the final season. At least eight year-round resident plovers disappeared in the final two months of study, and few birds were encountered on the final survey occasion (Figure 3). Subsequent return rates to the breeding population were also lower than average (Feucht et al. 2017), and counts of plovers during the 2018 winter window survey were about 30% lower than the previous three winter counts (E. Feucht and J. Miller pers. comm.). Though this hints to a possible mortality event at the end of the 2016 non-breeding season, it is impossible to distinguish mortality from dispersal and the end of data collection.

Environmental Conditions

Several studies of shorebirds (Stenzel et al. 2007, Mullin et al. 2010, Eberhart-Phillips and Colwell 2014) have shown that mortality is episodic, and these events have been attributed to cold temperatures and inclement weather based on anecdotal evidence. Weather only weakly affected apparent survival during the study, which may be due to the relatively mild conditions during the study, or weather may have indirect effects on survival rates. Additionally, weather did not have a detectable acute effect on apparent survival as suggested by previous research (Mullin et al. 2010, Eberhart-Phillips and Colwell 2014). Whether mortality events are caused by weather or if weather conditions simply make plovers more vulnerable to other sources of mortality is unknown.

CONSERVATION IMPLICATIONS

The conservation of endangered and threatened species is dependent on the management of factors that limit recovery. The recovery plan for the Western Snowy Plover emphasizes the improvement of productivity (USFWS 2007). While some productivity management techniques may affect survival (e.g., nest exclosures), management could directly target sources of mortality to improve survival. Because apparent survival is predictably lower during the non-breeding season, especially December through March, management directed at protecting non-breeding plovers may improve overall survival in the population.

It is relatively uncomplicated to monitor plovers during the non-breeding season. I recommend that organizations monitoring and managing Western Snowy Plover populations expand their efforts to include surveys of large and predictable non-breeding flocks, so as to refine our knowledge and understanding of survival and episodic mortality events. Integrated population models and Bayesian population viability analyses have been successfully used in Great Lakes' Piping Plovers to identify the limiting factors of population recovery (Saunders et al. 2018). This approach may be used in Snowy Plovers to not only identify what demographic parameter limits recovery, but also identify what factors limit recovery.

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APPENDIX A

Appendix A: Banded snowy plovers.

Though many plovers in the non-breeding flocks were uniquely color banded when they entered the study population, 44 plovers were banded as part of this project. In 2014, 22 plovers were banded, another 19 were banded in 2015 while only 2 were banded in 2016. During the 2016 non-breeding season weather, flock behavior and scheduling challenges reduced both banding effort and success.

Table 6. Plovers banded during the non-breeding season 2014 – 2016.

Date	Band Number (USFWS)	Location	Color Bands	Age	Sex
8/16/2014	2381-05370	CV[1]	WV:YY	AHY	M
8/16/2014	2381-05369	CV	WV:RR	AHY	U
8/19/2014	2381-07631	LRSB[2]	RY:YG	HY	U
9/8/2014	2381-05371	LRSB	WV:BB	HY	U
9/8/2014	2381-05372	LRSB	WV:WW	AHY	F
9/8/2014	2381-05654	LRSB	RY:GG	HY	F
9/8/2014	2381-05669	LRSB	GV:WG	HY	U
9/8/2014	2381-05722	LRSB	GV:WR	HY	U
9/8/2014	2381-05767	LRSB	GV:BY	AHY	F
9/8/2014	2381-07166	LRSB	RY:BB	AHY	M
9/19/2014	2381-65373	CV	WV:GG	AHY	F
9/19/2014	2381-05374	CV	WV:BG	AHY	U
9/19/2014	2381-05375	CV	WV:OB	AHY	U

Date	Band Number (USFWS)	Location	Color Bands	Age	Sex
9/19/2014	2381-05376	CV	WV:YB	AHY	U
9/19/2014	2381-06087	CV	GV:RY	HY	U
9/29/2014	2381-05377	LRSB	WV:BR	U	F
9/29/2014	2381-05378	LRSB	WV:BW	U	U
9/29/2014	2381-06062	LRSB	GY:YR	HY	M
9/29/2014	2381-07422	LRSB	GV:RB	AHY	M
9/29/2014	2381-05609	LRSB	RY:RR	HY	U
9/29/2014	2381-07524	LRSB	GV:YR	HY	F
9/29/2014	2381-05635	LRSB	RY:RW	HY	F
9/29/2014	2381-05848	LRSB	RY:OW	HY	U
9/29/2014	2381-05342	LRSB	WW:OW	AHY	M
9/14/2015	2381-05425	LRSB	WV:BY	AHY	M
9/14/2015	2381-05426	LRSB	WV:GB	HY	U
9/14/2015	2381-08771	LRSB	VW:GY	HY	F
9/14/2015	2381-05355	LRSB	OR:WY	HY	U
9/19/2015	2381-05414	LRSB	GY:OG	HY	U
9/19/2015	2381-05427	LRSB	WV:GR	U	U
9/19/2015	2381-08629	LRSB	GY:YG	HY	U
9/19/2015	2381-07485	LRSB	GY:WY	AHY	U
10/31/2015	2381-05428	CV	WV:GW	U	U
10/31/2015	2381-05430	CV	WV:GY	U	M
10/31/2015	2381-05431	CV	WV:OW	U	U

Date	Band Number (USFWS)	Location	Color Bands	Age	Sex
11/13/2015	2381-08882	CV	VW:OG	HY	M
11/13/2015	2381-05391	CV	VW:RR	HY	M
11/13/2015	2381-05432	CV	WV:OG	U	U
11/13/2015	2381-05433	CV	WV:OR	U	U
11/13/2015	2381-05434	CV	WV:OY	U	U
11/28/2015	2381-05435	LRSB	WV:RB	AHY	M
11/28/2015	2381-05625	LRSB	VW:RY	AHY	M
11/28/2015	2381-08720	LRSB	VW:RG	HY	U
12/2/2015	2381-05436	CV	WV:WY	U	U
8/7/2016	2381-05416	LRSB	OV:GY	HY	F
8/29/2016	2381-10257	LRSB	OV:GW	HY	M

[1] Centerville Beach

[2] Little River State Beach

APPENDIX B

Appendix B: Environmental Conditions

Weather conditions during the three non-breeding seasons were very different from each other. The 2014 non-breeding season was warm and dry, with a mean temperature of 8.7 ± 3.4ºC and only 79.0 cm of rain recorded from September through March (Figure 8). The 2015 non-breeding season was colder (7.5 ± 3.5ºC) and had greater precipitation (112.2 cm), while the 2016 non-breeding season was the coldest (6.8 ± 3.9ºC) and the wettest (140.7 cm). None of the three years approached the record cold of 2007 (September 2007 to March 2008; 5.66 ± 3.6ºC) and that may be why weather conditions did not have a detectable effect on apparent survival. There is no clear pattern in oscillations of weather conditions from one winter to the next when mean minimum temperature and precipitation are compared (Figure 7).

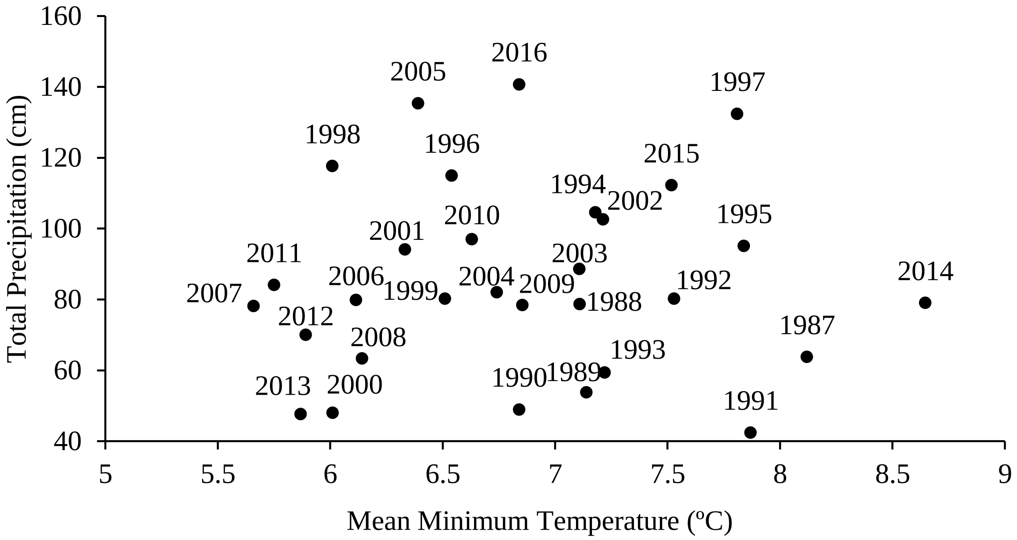

Figure 6. Mean minimum temperature and total precipitation from Sept. 1 through Mar. 31 beginning in 1987.

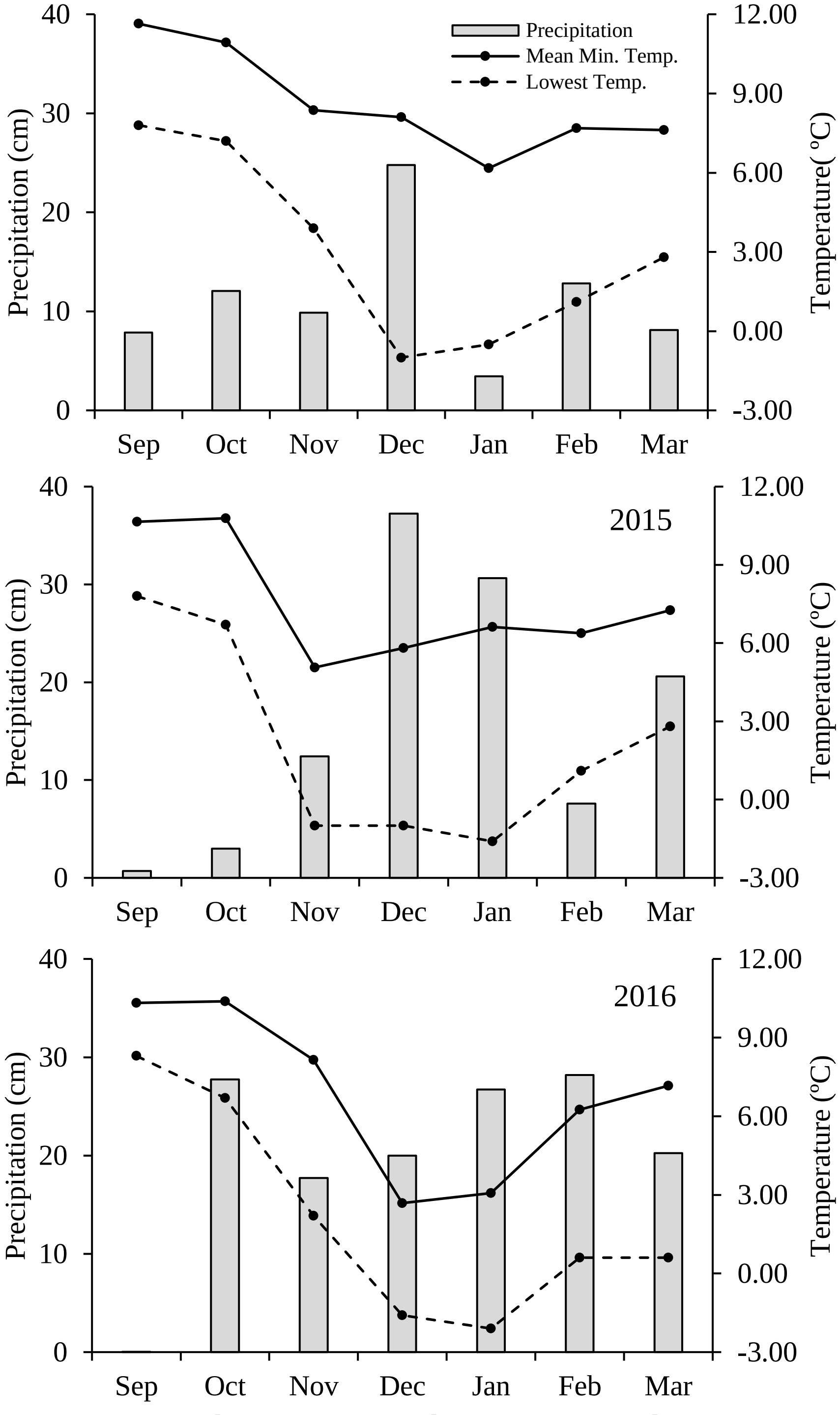

Figure 7. Seasonal variation in total precipitation and minimum temperature in the three non-breeding seasons.