

APPARENT SURVIVAL OF SNOWY PLOVERS VARIES ACROSS YEARS AND
BETWEEN SEXES IN COASTAL NORTHERN CALIFORNIA

By

Justin A. Windsor

A Thesis Presented to

The Faculty of Humboldt State University

In Partial Fulfillment of the Requirements for the Degree

Master of Science in Natural Resources: Wildlife

Committee Membership

Dr. Mark Colwell, Committee Chair

Dr. Daniel Barton, Committee Member

Dr. Luke Eberhart-Phillips, Committee Member

Erin Kelly, Graduate Coordinator

May 2020

ABSTRACT

APPARENT SURVIVAL OF SNOWY PLOVERS VARIES ACROSS YEARS AND BETWEEN SEXES IN COASTAL NORTHERN CALIFORNIA

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Adult survival is one of the most influential vital rates affecting population growth of iteroparous organisms. Survival often varies annually due to environmental stochasticity. However, drastic variations in annual adult survival rates can have overwhelmingly negative impacts on population viability and growth. In many wild avian populations, adult survival varies between sexes and may owe to unequal risks associated with reproductive roles or predation; this is particularly true among shorebirds. I used mark-resight data from a 19-year study of Western Snowy Plovers (*Charadrius nivosus nivosus*) in coastal northern California to investigate sex-specific apparent survival of the adult population (N=387). I reported apparent survival (ϕ) along with standard error (\pm SE) and 95% confidence intervals, as well as beta estimates (β) with 95% confidence intervals. Apparent survival varied substantially among years (min $\phi = 0.44 \pm 0.07$; 0.30-0.57 to max $\phi = 0.82 \pm 0.06$; 0.64-0.94), with the minimum occurring in the middle of the study (2006-07) and the maximum occurring in 2009-10. Furthermore, apparent survival varied between sexes, whereby males had higher overall apparent survival (0.72 ± 0.03 ; 0.30-0.93) than females (0.68 ± 0.03 ; 0.26-0.91). Average known lifespan of Snowy Plovers within the study was 3.5 ± 2.1 years, with males living longer on average (4.3 ± 2.8

years) than females (3.6 ± 1.9 years). Overall population growth remained stable ($\bar{\lambda} = 1.05 \pm 0.13$ to 1.10 ± 0.12) across the course of the study. Years of substantially low adult survival have directly reduced overall growth potential for the local population. High temporal variance in adult survival produces increased variance in annual population growth rates, with possible implications for extinction risk. Reduced survival in adult female Snowy Plovers has been shown to influence the adult sex ratio of the population, as observed in other *Charadrius* populations, however that was not evident in this study. Application of demographic parameters in future population viability and growth models will provide a comprehensive understanding of population dynamics and will inform progress toward the recovery of the Pacific Coast population.

ACKNOWLEDGEMENTS

I express tremendous gratitude to my advisor Dr. Mark Colwell, whose profound expertise, delightful disposition, and supportive counsel was necessary to my success. I owe substantial respect and thanks to Dr. Dan Barton, who not only guided me through the intricacies of modern statistical modeling and inference, but also inspired me to think critically beyond traditional ecological knowledge. I am also indebted to Dr. Luke Eberhart-Phillips for his support, and whose growing body of literature on *Charadrius* plovers provided me a firm foundation to build upon. To Elizabeth “Lizzie” Feucht, your unyielding devotion, knowledge, and labors for the local population of plovers is unmatched, thank you for your guidance. I give thanks to my fellow lab mates in the Shorebird Ecology lab, Jeremy Pohlman, Katelyn Raby, and Chelsea Polevy, all of which provided me support and comfort throughout my graduate experience. Furthermore, I thank my graduate colleagues: Claire Nasr, Brian Fagundes, Deven Kammerichs-Berke, and Owen Hardy for their moral support throughout our shared coursework. I also thank Dr. Eleanor Gaines for her counsel and research, as it helped to guide my own.

I extend appreciation to my funders and the managers of the coastal northern California Western Snowy Plover Recovery Unit 2: Susie Tharatt and John Hunter from U.S. Fish and Wildlife service, Jessie Irwin with the Bureau of Land Management, Amber Transou at California Department of Parks and Recreation, and the National Park Service. I would like to thank the folks at Wildland’s Conservancy, Emily Afriat-Hyman and Alex Blessing, for their logistical support in the field. I am indebted to all my

predecessors who labored for the recovery, for my work could not have transpired without their tireless efforts. I acknowledge California Department of Fish and Wildlife, Humboldt County Parks, and Humboldt State University, for their contributions. I appreciate my mentors: Dr. Rick Golightly and Gerry McChesney, who guided me toward advancing my education at Humboldt State University

I share my love and appreciation for my grandmother, who cultivated my passion for birds at a young age. I owe thanks to my childhood best friend, Matthew Chappell, who encouraged me to study and approach a career in the field of wildlife. Finally, I must profess my undying gratitude and boundless love for my partner, Dr. Elizabeth McCallion, whose love, encouragement, and support has not only facilitated my success, but has also shaped me to be a better person.

TABLE OF CONTENTS

ABSTRACT.....	ii
ACKNOWLEDGEMENTS	iv
TABLE OF CONTENTS.....	vi
LIST OF TABLES	viii
LIST OF FIGURES	ix
LIST OF APPENDICES.....	x
INTRODUCTION	1
METHODS	7
Study Area	7
Field Methods	7
Data Set.....	10
Longevity Distribution.....	10
Survival Analysis	11
Annual Population Growth Rate.....	13
RESULTS	15
Longevity Distribution.....	15
Apparent Survival	15
Annual Population Growth Rate.....	19
DISCUSSION	21
Sex-specific Survival	21
Annual Variation in Survival.....	24

CONSERVATION IMPLICATIONS	28
LITERATURE CITED	30
APPENDIX A.....	38
APPENDIX B	41
APPENDIX C	43
APPENDIX D.....	45
APPENDIX E	47

LIST OF TABLES

Table 1. Adult survival estimates from studies of various plover species, estimation method, and regions (Dinsmore 2019).....	5
Table 2. Selection table for Cormack-Jolly-Seber models used to estimate adult apparent survival of Snowy Plovers in coastal northern California from 2001-2018. Models contain annual variation (yr), additive variation between sex and year (sex+yr), sex variation (sex), linear constrained annual variation (Y), quadratic constrained annual (YY), and interactive variation between sex and year (sex*yr) in survival (ϕ) where encounter probability varies annually in a quadratic trend (YY).	17
Table 3. Annual population growth rates (λ) of Snowy Plovers in coastal northern California derived from algebraic method using fecundity (b) with survival estimates (ϕ) and observed consecutive population counts from 2001-18.....	20
Table 4. Top models describing variation in encounter probability (p) for Snowy Plovers in coastal northern California. Encounter probability (p) structures follow: no effect [·], year [yr], sex [sex], additive [sex+yr], linear constraint [Y], additive sex with linear year constraint [sex+Y], quadratic year constraint [YY], and additive sex and quadratic constraint on year [sex+YY].....	40
Table 5. Annual counts of Snowy Plovers in Humboldt County, Mendocino, and Del Norte Counties (RU2) from 2001-19 (Feucht et al. 2020) including philopatric and immigrant (imm.) individuals and derived male adult sex ratios.	42
Table 6. Annual estimates for apparent survival (ϕ) using shrinkage estimates (\tilde{S}) from variance components and encounter probability (p) of male and female adult Snowy Plovers in coastal northern California from 2001-18, based on the top model (ϕ [sex + yr] p[YY]).....	43

LIST OF FIGURES

Figure 1. Principal breeding locations of Snowy Plovers in coastal northern California where observers collected mark-resight data on individually marked birds, 2000-19. See Colwell et al. (2017a) for details.....	8
Figure 2. Longevity distributions of male and female immigrant (above) and local (philopatric) adult Snowy Plovers in coastal northern California, 2001-19.	16
Figure 3. Male and female apparent survival estimates (ϕ ; with 95% CI) derived from shrinkage estimates (S) of top model ($\phi[\text{sex+yr}] p[\text{YY}]$) for Snowy Plovers in coastal northern California, 2001-19.	18
Figure 4. Quadratic constrained annual variation in encounter probability estimates of Snowy Plovers with 95% confidence intervals from 2001-18 in coastal northern California.	39
Figure 5. Annual population growth rates of Snowy Plover derived using algebraic and consecutive population count methods from 2001-18 in coastal northern California.	46
Figure 6. Adult longevity distribution of male and female local (philopatric) adult Snowy Plovers monitored in coastal northern California from 2001-19.	48

LIST OF APPENDICES

Appendix A: Encounter probability.....	38
Appendix B: Annual breeding population and adult sex ratios	41
Appendix C: Estimates of apparent survival and encounter probability.	43
Appendix D: Annual population growth rates	45
Appendix E: Longevity distributions.....	47

INTRODUCTION

Worldwide, 48% of shorebird populations are in decline, while only 16% are increasing (International Wader Study Group 2003). Quantification of vital rates (i.e., productivity and survival) that affect population growth is necessary for effective management for populations of concern. For many populations, an understanding of demography is incomplete (Mendez et al. 2018); for others, conservation planning has not prioritized vital rate analyses, thus hindering productive management outcomes (Heppell et al. 1996, Johnson et al. 2010). This emphasizes the importance of obtaining comprehensive population vital rates to implement effective management strategies for endangered and threatened populations.

Adult survival has a substantial effect on population growth rate in long-lived species with slow reproductive rates (Crone 2001). This is particularly true among shorebirds, where adult survival parameters show the highest elasticity when modeling population viability (Plissner and Haig 2000, Sæther and Bakke 2000, Sandercock 2003). While facilitating adult survival can be difficult in practice and most management efforts are focused on increasing nest and chick survival, understanding variation in adult survival is crucial when designing and obtaining recovery objectives for threatened populations. Furthermore, survival may vary between groups (i.e., males and females, or age classes), over time, and across space (Sandercock 2003, Mullin et al. 2010, Stenzel et al. 2011, Colwell et al. 2013, Mendez et al. 2018). Identifying such variations is needed

to accurately track the progress of a population and to apply effective management schemes.

Sex-specific survival has been documented in many wild bird populations (Horak and Leberon 1998, Kenward et al. 1999, Eeva et al. 2009); this is particularly true for many shorebird populations (Mendez et al. 2018, Eberhart-Phillips et al. 2018, Dinsmore 2019). Sex-specific adult survival may result from differences in reproductive roles (e.g. mating competition, parental investment, or predation pressures; Liker and Székely 2005, Donald 2007, Székely et al. 2014). Differences in dispersal strategies between males and females can further complicate estimates of apparent survival (Sandercock et al. 2005, Mendez et al. 2018) or introduce additional sources of sex-specific mortality (Donald 2007, Eberhart-Phillips et al. 2017). Some studies indicate that differences in sex-specific adult survival may skew adult sex ratios (ASR) in bird populations, which can influence population dynamics (Donald 2007, Stenzel et al. 2011, Eberhart-Phillips et al. 2017). Therefore, quantifying survival estimates for males and females is crucial, not only in understanding overall demography, but also the potential to influence ASRs.

Mark-recapture data acquired over a sufficiently long time series can provide evidence for annual variations in survival and improve our understanding of population dynamics (Anderson et al. 1994). Annual survival rarely remains constant and often varies from year to year in wild populations owing to environmental stochasticity (Schmutz 2009). However, vital rates with the greatest contribution to population growth, in this case adult survival, should exhibit the lowest variance through evolutionary mechanisms and substantial temporal variation in adult survival can increase variance in

population growth rates (Pfister 1998). As managers aim to increase population growth by focusing resources on recruitment (i.e., nest survival and juvenile survival), repeated episodes of low adult survival can limit progress made from reproductive contributions and stifle growth.

The Snowy Plover (*Charadrius nivosus*), is a small shorebird widely distributed in the Americas, with three distinct subspecies (Page et al. 2009). In 1993, the U.S. Fish and Wildlife Service (USFWS) listed the Pacific coast population as threatened under the Endangered Species Act (USFWS 2007). The Snowy Plover in northern California occupies open sparsely vegetated habitats, primarily ocean-fronting beaches (Page et al. 2009, Brindock and Colwell 2011). The listed population is partially migrant, with some individuals residing year-round at sites, whereas others undertake short-distance, seasonal movements to locations other than where they breed (Stenzel et al. 1994, Colwell et al. 2007b). Researchers have characterized the plover's mating system as serial polyandrous, whereby females often desert partners post-hatch in search of new mates (Stenzel et al. 1994, Eberhart-Phillips 2019). Males and females share incubation of a 3-egg clutch for approximately one month, with males typically providing sole care of precocial, nidifugous chicks for an additional month. The breeding season spans early March (first eggs laid) to mid-September (last chicks fledged), which allows males and females to successfully breed up to two and three times, respectively (Warriner et al. 1986). The non-territorial breeding system of the Snowy Plovers facilitates short- and long-distance dispersal of individuals both within and between years, with females tending to disperse further than males (Stenzel et al. 1994, Paton and Edwards 1996).

Estimates of adult survival exist for various plover species (Table 1); some highlight variation between the sexes (Mullin et al. 2010, Stenzel et al. 2011, Colwell et al. 2013, Eberhart-Phillips et al. 2017) and among years (Dinsmore 2008, Stenzel et al. 2011, Saunders et al. 2014, Gaines et al. 2020). The need for updated estimates that examine demographic variations is necessary to understand long-term survival, and to a greater extent population growth. Furthermore, estimating adult survival parameters for localized populations provide a comprehensive understanding into demographic variations across the range and viability of subpopulations (e.g., recovery units). A recent study of Snowy Plovers from the neighboring population in Oregon (RU1), indicated increasing annual adult apparent survival coinciding with partial interval (2000-14) of this study (Gaines et al. 2020). Therefore, my objectives were to estimate adult apparent (i.e., annual) survival and explore variability across time and between sexes, and to draw comparisons of annual variability in survival from this population to those reported by Gaines et al. (2020). Furthermore, I aimed to derive comparative estimates for annual population growth rates and briefly describe the adult longevity distribution of philopatric breeders observed within the coastal northern California population.

Table 1. Adult survival estimates from studies of various plover species, estimation method, and regions (Dinsmore 2019).

Species	Region	Male	Female	Estimation Method	Source
Wilson's Plover (<i>Charadrius wilsonia</i>)	North Carolina, USA	0.77	-	Apparent (CJS)	DeRose-Wilson et al. (2013)
Semipalmated Plover (<i>Charadrius semipalmatus</i>)	Manitoba, Canada	0.71-0.87	-	Apparent (CJS)	Nol et al. (2010)
Piping Plover (<i>Charadrius melodus</i>)	North Dakota, USA	0.66	-	Apparent (CJS)	Root et al. (1992)
	North Dakota, USA	0.74	-	Apparent (CJS)	Larson et al. (2000)
	USA	0.56-0.81	-	True (Barker)	Roche et al. (2010)
	Great Lakes, USA	0.74	0.725	Apparent (CJS)	Saunders et al. (2014)
Mountain Plover (<i>Charadrius montanus</i>)	Montana, USA	0.74-0.96	-	Apparent (CJS)	Dinsmore (2008)
Snowy Plover (<i>Charadrius nivosus</i>)	California, USA	0.743	-	Return Rate	Page et al. (1983)
	Utah, USA	0.58-0.88	-	Apparent (CJS)	Paton (1994)
	California, USA	0.61	0.50	Apparent (CJS)	Mullin et al. (2010)
	California, USA	0.73	0.693	True (Barker)	Stenzel et al. (2011)
	Oregon, USA	0.61-0.77	-	Apparent (CJS)	Gaines et al. (2020)

Species	Region	Male	Female	Estimation Method	Source
Snowy Plover (<i>Charadrius nivosus</i>)	Sinaloa, Mexico	0.63-0.74	0.62-0.74	Apparent (CJS)	Eberhart-Phillips et al. (2017)
Kentish Plover (<i>Charadrius alexandrinus</i>)	Netherlands	0.65	0.73-0.91	Apparent (CJS)	Foppen et al. (2006)
Ringed Plover (<i>Charadrius hiaticula</i>)	Netherlands	0.61-0.82	-	Apparent (CJS)	Foppen et al. (2006)
White-fronted Plover (<i>Charadrius marginatus</i>)	South Africa	0.86	0.93	Apparent (CJS)	Lloyd (2008)

METHODS

Study Area

I studied a color-marked population of Snowy Plovers in Humboldt County, CA. I acquired data derived from a 19-year study ending in 2019 across 11 locations in Recovery Unit 2 (RU2; Figure 1). RU2 encompasses Mendocino, Humboldt, and Del Norte counties; it is one of six designated recovery units along the Pacific coast of the United States (USFWS 2007). During the study period, most plovers in RU2 bred in Humboldt County (Colwell et al. 2017a). For the survival analysis, I excluded observations from sites in Mendocino County, where limited and variable survey efforts compromised data quality. Observers surveyed approximately 100 km of ocean-fronting beaches, riverine gravel bars, and coastal lagoons, in areas of sparse vegetation favored by breeding plovers (Colwell et al. 2017a). For details on habitat, see Colwell et al. (2010, 2011, and 2017a).

Field Methods

In a collaborative effort, multiple groups including federal agencies (United States Fish and Wildlife Service, Bureau of Land Management, and National Park Service), state entities (Humboldt State University, California State Parks, California Department of Fish and Wildlife), and private consultants worked to mark virtually the entire breeding population (Colwell et al. 2017a). Researchers captured adult plovers using

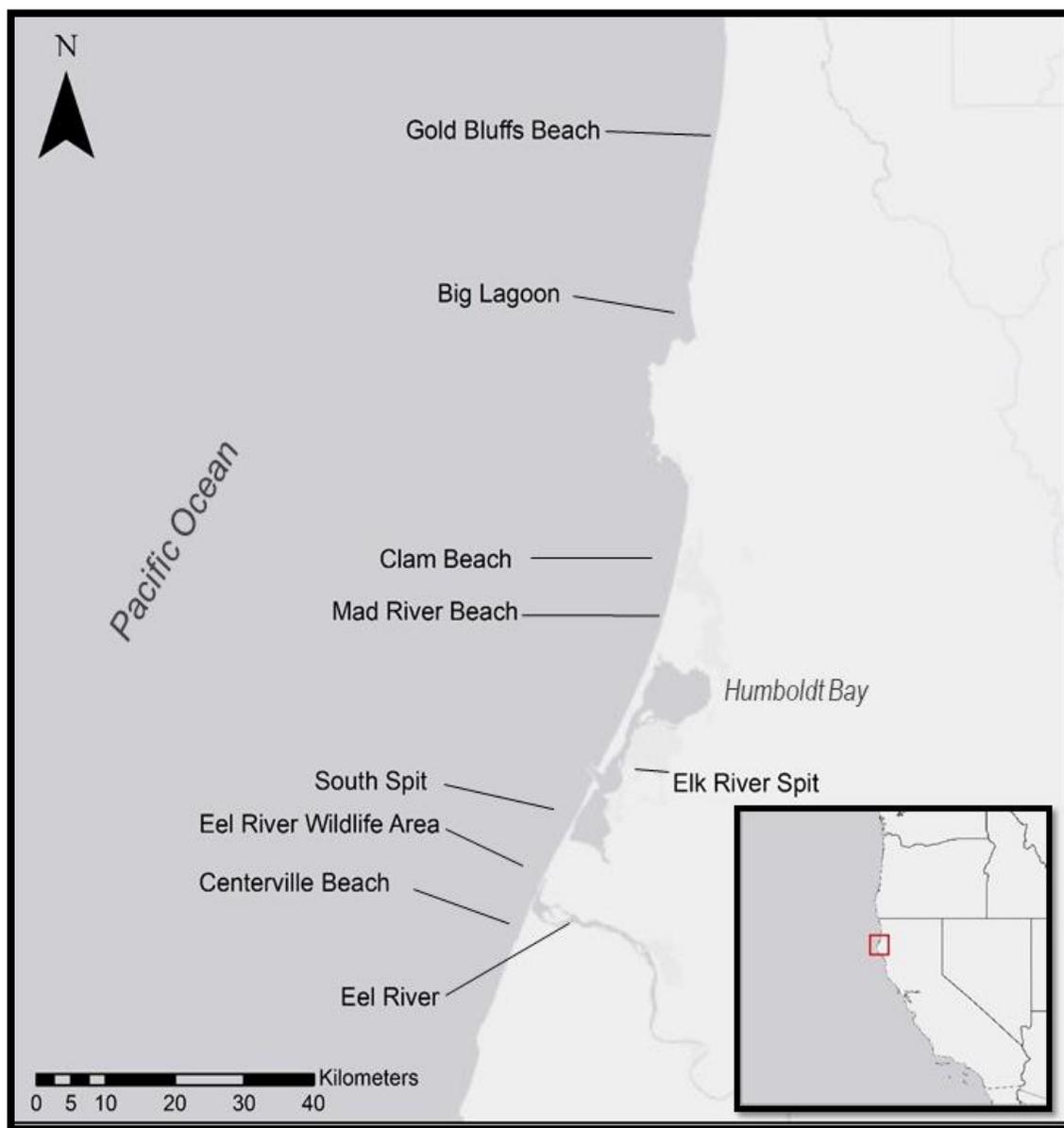


Figure 1. Principal breeding locations of Snowy Plovers in coastal northern California where observers collected mark-resight data on individually marked birds, 2000-19. See Colwell et al. (2017a) for details.

noose mats, walk-in traps, or mist nets during incubation or early chick rearing (DeJoannis 2016, Papian 2018). Researchers fitted adults with a single numbered USFWS metal band wrapped in colored tape, and three colored plastic bands, which provided a unique identifier for each individual. Banding of chicks included a brood-specific, single color-taped USFWS metal band. When young (i.e., yearling) or immigrant plovers were recruited into the breeding population, researchers recaptured and outfitted them with an adult color band combination. Researchers reused combinations after a minimum of 5 years lapsed with no encounter, and reused combinations were applied to the opposite sex individuals to avoid misidentification.

Observers conducted surveys during the breeding season, from mid-March until the end of August, or until the last chick fledged. Typically, observers surveyed sites during the early morning hours on a weekly or bi-weekly rotation. The primary objective was to locate, identify, and sex all plovers based on plumage (Pyle 2008) and banding records. Observers recorded location data using personal data assistants (PDA) equipped with Global Positioning System (GPS), and later used Garmin handheld GPS devices both referenced using World Geodetic System 1984 [WGS 84] in Universal Transverse Mercator [UTM] Zone 10 North units (Colwell et al. 2017a). Researchers worked under federal (USFWS Recovery #TE-73361A-1; US Geological Survey Bird Banding #23844 and #10457), state (California Department of Fish and Wildlife Scientific Collection #SC-0496; California Department of Parks and Recreation Scientific Research #18-635-009), and university (HSU IACUC #14/15.W.07-A and #14/15.W.08-A) permits and protocols.

Data Set

I collated individual encounter histories based on observations spanning 19 years (2001-19). I derived individual encounter histories denoted as a series of detections (indicated by “1”) and non-detections (indicated by “0”), limited to an encounter window between 1 April – 31 July for each annual occasion across the study. I used only after hatch year, adult encounters for the survival analysis, excluding chick encounters from the data set. I verified all encounters by comparing field notes with detailed summaries of individual encounters across all years. I excluded observations of individuals with incomplete observations (i.e., partial band reads) or single, unsubstantiated sightings per encounter window. For estimating annual population growth, I incorporated juvenile survival estimates derived from the previous work of Mullin et al. (2010) during 2001-07 study in Humboldt County. I compiled annual fledged chick counts, as well as annual breeder counts from 2001-2018.

Longevity Distribution

I described the adult longevity distribution and derived naïve longevity of Snowy Plovers in coastal northern California (RU2) by compiling banding and encounter histories for all philopatric breeding plovers, from 2001-19. I collated records of individuals encountered across the entire recovery unit of locally hatched plovers that went on to breed within the study area. I summarized longevity as the frequency of individuals encountered as breeding for one, two, or additional seasons, serving as naïve

longevity, rather than true longevity, as I could not account for imperfect detection and permanent emigration.

Survival Analysis

I included encounters between 1 April and 31 July, which coincided with the peak of breeding when movement is minimal (Gaines et al. 2020) across 18 annual intervals. I excluded observations from Mendocino County, due to inconsistencies in survey efforts over the years; this accounts for differences in sample size between the survival analysis and sample used to derive population growth rates and longevity records. I implemented an information-theoretic approach to model selection and inference as described by Burnham and Anderson (2002). I used the Cormack-Jolly-Seber (CJS; Cormack 1964, Jolly 1965, Seber 1965) model in program MARK (White and Burnham 1999) to estimate adult apparent survival (ϕ) and conditional encounter probability (p). I estimated apparent survival, rather than true survival, due to an inability to separate permanent emigration from mortality.

I applied sex as a grouping variable owing to unequal risks associated with sex-specific roles, as multiple studies indicate variation between male and female apparent survival estimates (Paige et al. 1983, Mullin et al. 2010, Stenzel et al. 2011, Colwell et al. 2013, Eberhart-Phillips et al. 2017). I defined a fully time-dependent model, encompassing an 18-year interval, with the interactive effect of sex on survival and encounter probabilities ($\phi[\text{sex*yr}] p[\text{sex*yr}]$), where the effect of sex varies by year, to

serve as the global model. I used this global model to test goodness-of-fit using the median \hat{c} procedure in Program MARK (Cooch and White 2015).

I implemented a sequential modeling approach by first determining the most supported structure for encounter (p), followed with a comparison of survival (ϕ) structures (Leberon et al. 1992). This procedure reduced the number of models compared in order to avoid spurious results that might otherwise arise from comparing all possible models at once (Burnham and Anderson 2002, Doherty et al. 2012). I defined various structures for encounter probability (p ; no effect [·], year [yr], sex [sex], additive [sex+yr], interaction [sex*yr], linear constrained [Y], and quadratic constrained [YY] time trends across years) while maintaining a fully time-dependent function on survival (ϕ [yr]) for each model. This “step-down method” is sometimes favored over the use of lower dimensioned models where survival contains no effect (Leberon et al. 1992). I used the most parsimonious model from the first sequence, then compared structures for survival probability (ϕ ; no effect [·], sex [sex], year [yr], additive [sex+yr], interaction [sex*yr], linear constraint [Y], and quadratic constraint [YY] time trends across years). I followed an approach similar to Gaines et al. (2020) such that I could directly compare results between the two studies.

I constructed models in Program MARK using parameter index and design matrices. I chose the logit link function for each model created using the design matrix and sin link functions for models with identity matrices. I used Akaike’s Information Criterion (Akaike 1992, Burnham and Anderson 2002) corrected for small sample size (AICc) to rank and compare models. I deemed models that fell within seven $\Delta AICc$ units

from the model with the lowest AIC_C as candidate models (Burnham and Anderson 2002). I did not draw conclusions from nested models with an additional parameter ranked as competitive (within $2 \Delta AIC_C$) that lacked improvement in model deviance to avoid uninformative parameters (Arnold 2010). I used estimates from the variance components procedure in Program MARK to estimate annual survival probabilities with standard error ($\pm SE$) and 95% confidence intervals, and their mean (\bar{S}). The variance components method produces a shrinkage estimator of survival (\tilde{S}) that represents process variance (i.e., variance among years), while removing sample variance (i.e., variance due to imperfect encounter probability; Burnham and White 2002). I report beta estimates ($\hat{\beta}$) for competitive models along with 95% confidence intervals to show the effects of covariates, and only consider each significant if the confidence intervals do not overlap zero.

Annual Population Growth Rate

I estimated annual growth rate (λ) in two ways. First, I derived an algebraic annual growth rate using the following equation (Pulliam 1988).

$$\lambda = b\varphi_{Juv} + \varphi_{Ad}$$

I derived two variations of algebraic growth rates for comparison using both male and female parameters by incorporating the adult apparent survival estimates (φ_{Ad}) generated in MARK for each respective sex and year of the study. I used an overall estimate for juvenile apparent survival (φ_{Juv}) of 0.40 as previously reported by Mullin et al. (2010). I

used per capita reproductive success (PCRS) as the fecundity term (b) for each year, where PCRS is the ratio of fledged chicks per breeding individual (either male or female respectively). I derived a third growth rate using the ratio of consecutive annual counts (N_{t+1}/N_t) of adult breeding plovers, which includes those lost or gained through emigration and immigration.

RESULTS

Longevity Distribution

Over 19 years, observers marked and resighted virtually all breeders in RU2. I use only locally hatched, philopatric breeders (N=142) of known age to derive naive longevity, including 80 males and 62 females. Longevities varied greatly among individuals and between sexes (Figure 2). Philopatric breeders (i.e., yearlings hatched and remained in RU2) had a mean (\pm SD) life span of 4.0 ± 2.4 years, ranging from 1 to 19 years. Overall, males had a higher mean lifespan (4.3 ± 2.8 years), than females (3.6 ± 1.9).

Apparent Survival

The global model fit the data with minimal over-dispersion ($\hat{c}=1.03$). I adjusted \hat{c} to match the estimate derived from the previous test (median \hat{c}); subsequently, model ranking did not change. I compared models using quasi Akaike's information criterion adjusted for small sample size and overdispersion (QAIC_c; Burnham and Anderson 2002). The top two ranked models included quadratic annual effect (YY) on encounter probability. The top model included annual variation with an additive effect of sex on apparent survival ($\phi[\text{sex+yr}] p[\text{YY}]$); the second ranked model ($\Delta\text{QAIC}_c=0.14$) contained annual variation in survival alone ($\phi[\text{yr}]$), with nearly equal model weight ($w_i=0.53$ and 0.47 respectively; Table 2).

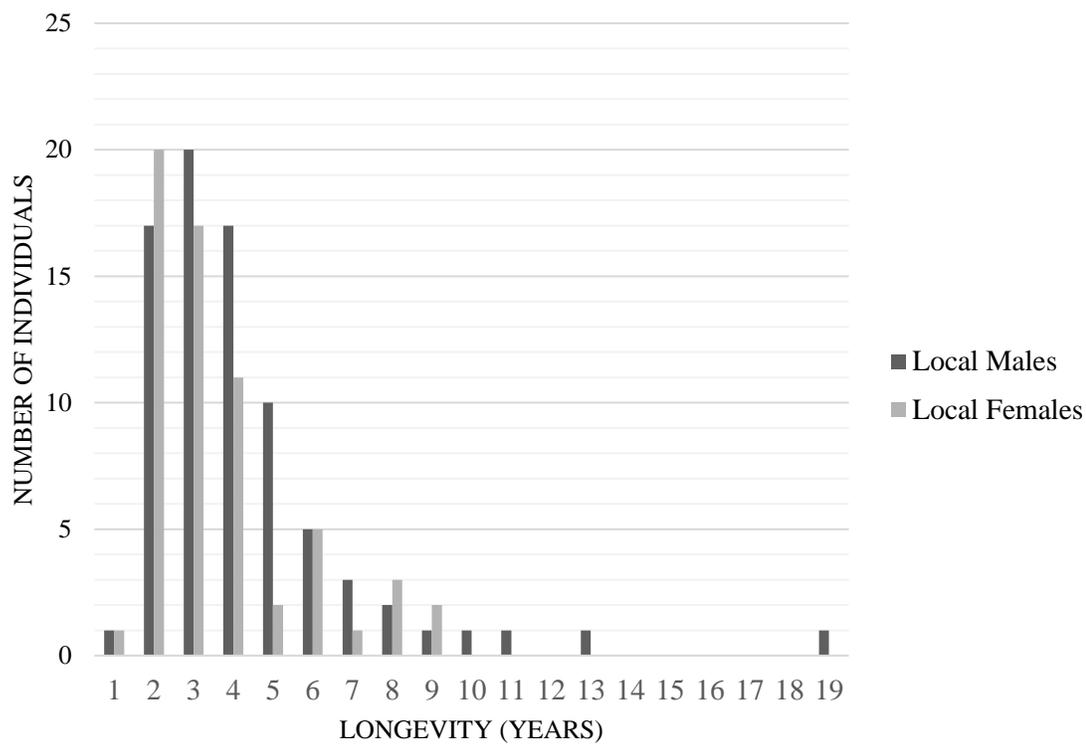


Figure 2. Longevity distributions of male and female (philopatric) adult Snowy Plovers in coastal northern California, 2001-19.

No other models were competitive ($\Delta\text{QAIC}_C \leq 2$) or fell within the candidate set ($\Delta\text{QAIC}_C \leq 7$). I derived shrinkage estimates from the top model indicating substantial annual variation in survival (min $\phi = 0.44 \pm 0.07$; 0.30-0.57 to max $\phi = 0.82 \pm 0.06$; 0.64-0.94) with an additive effect of sex (Figure 3), where none of the 95% confidence intervals spanned zero. Male survival (0.72 ± 0.03 ; 0.30-0.93) was greater ($\beta_{\text{Male}} = 0.21$, 95% CI 0.06 to 0.48) than female survival (0.68 ± 0.03 ; 0.26-0.91). Mean apparent survival for all adults was 0.69 ± 0.02 (0.26-0.93) across all years.

Table 2. Selection table for Cormack-Jolly-Seber models used to estimate adult apparent survival of Snowy Plovers in coastal northern California from 2001-2018. Models contain annual variation (yr), additive variation between sex and year (sex+yr), sex variation (sex), linear constrained annual variation (Y), quadratic constrained annual (YY), and interactive variation between sex and year (sex*yr) in survival (ϕ) where encounter probability varies annually in a quadratic trend (YY).

Model Structure	QAIC _C	ΔQAIC_C	w_i	K	Deviance
$\phi(\text{sex}+\text{yr}) \text{p}(\text{YY})$	1614.49	0.00	0.52	23	531.42
$\phi(\text{yr}) \text{p}(\text{YY})$	1614.63	0.14	0.48	22	533.67
$\phi(\text{sex}) \text{p}(\text{YY})$	1628.34	13.85	0.00	5	582.38
$\phi(.) \text{p}(\text{YY})$	1629.21	14.72	0.00	4	589.27
$\phi(\text{sex}+\text{Y}) \text{p}(\text{YY})$	1629.69	15.20	0.00	6	581.70
$\phi(\text{Y}) \text{p}(\text{YY})$	1630.44	15.95	0.00	5	584.47
$\phi(\text{YY}) \text{p}(\text{YY})$	1630.48	15.99	0.00	6	582.49
$\phi(\text{sex}*\text{yr}) \text{p}(\text{YY})$	1635.26	20.77	0.00	41	513.66

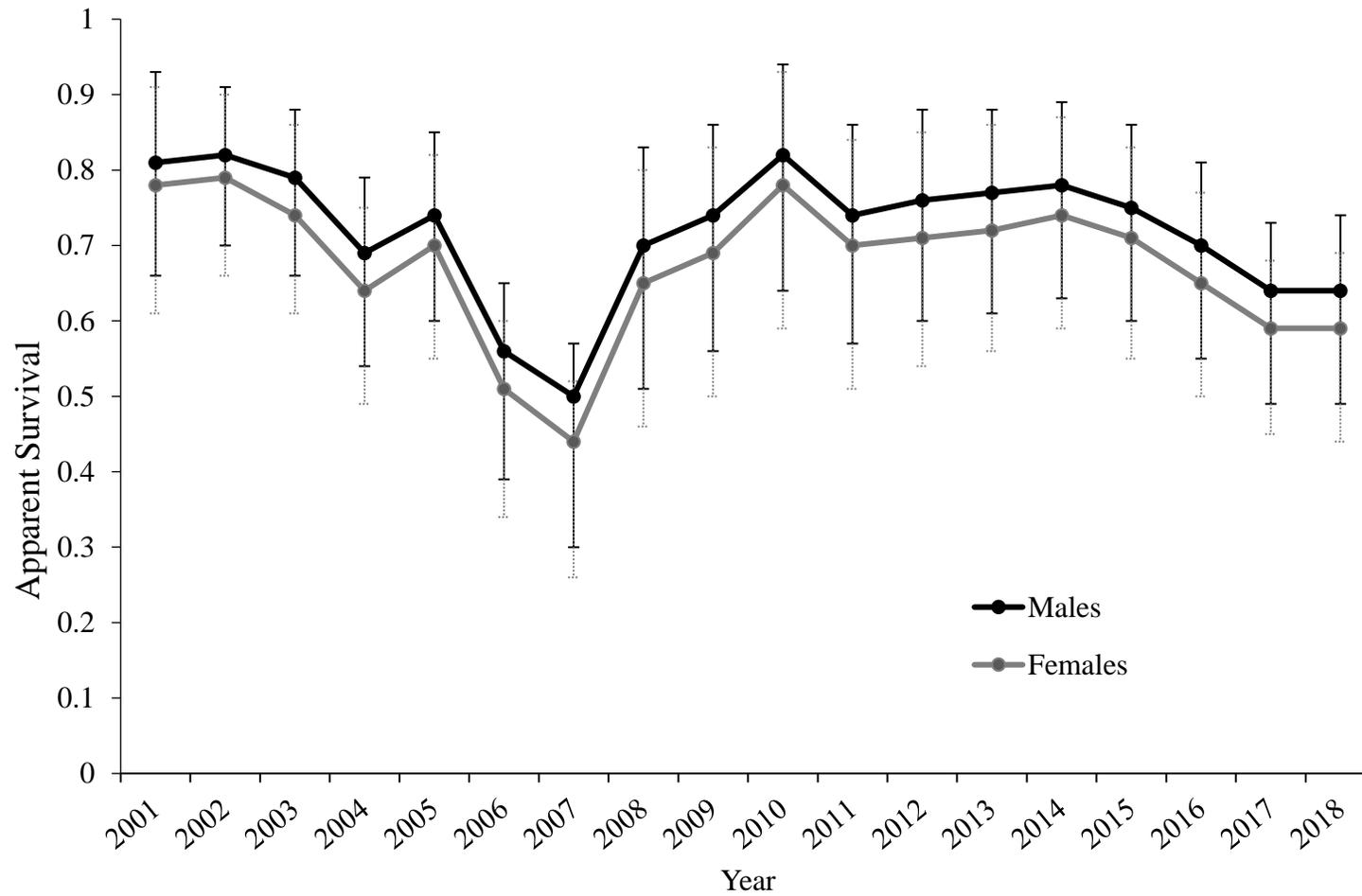


Figure 3. Male and female apparent survival estimates (ϕ ; with 95% CI) derived from shrinkage estimates (\tilde{S}) of top model ($\phi[\text{sex+yr}] p[\text{YY}]$) for Snowy Plovers in coastal northern California, 2001-19.

Annual Population Growth Rate

I used all fledged chicks (N=442) and breeding adults (N=396; 173 males and 223 females) within RU2 from 2001-18, from which I derived annual population growth rates, including immigrant breeders. Annual growth rates from each method varied year to year (Table 3). The mean annual growth rate across all years using female PCRS (i.e. chicks fledged per female) and apparent survival estimates was stable ($\bar{\lambda}_{Female}=1.05\pm 0.13$); the average population growth rate acquired using male PCRS and survival was slightly higher ($\bar{\lambda}_{Male}=1.10\pm 0.14$). Mean overall estimated growth rate from consecutive annual censuses was $\bar{\lambda}=1.06\pm 0.28$, nearly equal to both algebraic terms.

Table 3. Annual population growth rates (λ) of Snowy Plovers in coastal northern California derived from algebraic method using fecundity (b) with survival estimates (ϕ) and observed consecutive population counts from 2001-18.

Year	Consecutive ^a Counts	λ_{Male}	SE	ϕ_{Male}	λ_{Female}	SE	ϕ_{Female}
2001	1.30	1.33	0.14	0.81	1.34	0.13	0.78
2002	1.08	1.01	0.14	0.82	1.05	0.13	0.79
2003	0.87	1.20	0.14	0.79	1.20	0.13	0.74
2004	1.34	1.10	0.14	0.69	1.03	0.13	0.64
2005	0.89	1.06	0.14	0.73	1.06	0.13	0.69
2006	0.89	0.82	0.14	0.56	0.84	0.13	0.51
2007	0.50	0.78	0.14	0.50	0.79	0.13	0.44
2008	1.20	1.08	0.14	0.70	0.86	0.13	0.65
2009	0.52	1.10	0.14	0.74	1.14	0.13	0.69
2010	1.68	1.14	0.14	0.82	1.08	0.13	0.78
2011	1.08	0.90	0.14	0.74	0.96	0.13	0.70
2012	1.12	1.11	0.14	0.76	1.08	0.13	0.71
2013	1.15	1.03	0.14	0.77	1.11	0.13	0.72
2014	1.19	1.04	0.14	0.78	1.04	0.13	0.74
2015	1.18	1.11	0.14	0.75	1.07	0.13	0.71
2016	1.00	1.19	0.14	0.70	1.12	0.13	0.65
2017	0.87	1.09	0.14	0.64	1.07	0.13	0.59
2018	1.14	1.30	0.14	0.64	1.09	0.13	0.59
$\bar{x} \pm SE$	1.06 \pm 0.28	1.10	0.14	0.72 \pm 0.03	1.05	0.13	0.69 \pm 0.02

^aGrowth rate derived from consecutive year counts $\frac{N_t}{N_{t-1}}$

^bAlgebraic estimates (λ) based on fecundity(b) and apparent survival estimates for juveniles ($\phi_{Juv} = 0.40$; see Mullin et al. 2010) and adults (ϕ_{Ad}).

DISCUSSION

I present two primary findings from this study. First, I found survival varied annually (ranging from 0.44 ± 0.06 to 0.82 ± 0.05), with the minimum occurring during 2006-07 interval, and the maximum occurring during the 2009-10 interval. Second, sex-specific annual variation in survival exists between male and female Western Snowy Plovers. Males had higher mean apparent survival (0.72 ± 0.03) than females (0.68 ± 0.03).

My overall estimates of adult apparent survival for males and females extends and improves earlier estimates for the RU2 population (Mullin et al. 2010), and were similar to the estimates of true survival (M: 0.73, F: 0.69) derived via the “Barker” method, reported by Stenzel et al. (2011) in a longterm study in central coastal California. In the Oregon population, Gaines et al. (2020) estimated overall adult apparent survival to be 0.71, higher than overall survival in this study (0.69 ± 0.02). Mean survival was higher for White-fronted, Wilson’s, Piping, Mountain and Semipalmated plovers (Table 1).

Sex-specific Survival

Variation in survival between sexes extends across 41 avian families, where female mortality is higher than males (Liker et al. 2005). Sex-specific adult survival was evident in my study as in other studies of *Charadrius* plovers. For instance, males had higher survival than females in Piping (Saunders et al. 2014) and Mountain plovers (Dinsmore et al. 2008). However, the opposite was true for Kentish (Foppen et al. 2006) and White-fronted Plovers (Lloyd 2008) as females had higher survival than males.

Other studies of Snowy Plovers indicated lower survival in females compared to males (Stenzel et al. 2011, Eberhart-Phillips et al. 2017), whereas Paton (1994) and Gaines et al. (2020) found no difference in survival between sexes.

Sex-specific survival in adult birds is associated with differential costs in reproductive decisions between sexes, such as competition for mates and parental care roles (Liker et al. 2005). Other hypotheses for higher female mortality in birds suggest disadvantages in smaller body size, heterogamy, and greater demands from reproductive effort (Donald 2007). While male-male competition likely increases mortality in polygynous bird species, increased mortality is not associated with female-female competition of polyandrous species (Liker et al. 2005). Owens and Bennett (1994) found that parental care during post-hatching phases biased mortality, as Liker et al. (2005) further substantiated this. In polyandrous breeding Snowy Plovers, females have greater propensity to disperse between breeding sites in search of new mates, sometimes at great distances; increased movement could expose females to higher risks of predation, whereas males typically remain localized and secretive while tending chicks (Warriner et al. 1986, Stenzel et al. 1994, 2007, Colwell et al. 2007a, 2007b, Eberhart-Phillips et al. 2017). Interestingly, Colwell et al. (2013) indicated that current or cumulative reproductive effort was positively associated with improved adult survival. In Kentish Plovers, there were no sex-biased differences in energetic costs accrued during parental care (Amat et al. 2000). These evidentiary differences convolute our understanding and limit any single hypothesis as to what precisely drives sex variation in adult survival of birds.

Estimates of apparent survival confound mortality with permanent emigration (Leberon et al. 1992). The same propensity for female Snowy Plovers to disperse (Stenzel et al. 1994) could drive apparent survival estimates lower than “true” survival, as there is potential for less encounters of females than males (and therefore contribute to the lower survival estimates). Changes in habitat quality, continued nest failure, and reduced mate selection may prompt females to emigrate in search of better opportunities (Stenzel et al. 1994); this may also vary with age and breeding experience. For example, Eberhart-Phillips et al. (2017) found strong sex-specific differences in survival in the interval between fledging and first breeding attempt (i.e., first-winter survival) along the Southern extent of the Snowy Plovers range, indicating different ecological pressures. Additionally, Foppen et al. (2006) reported that yearling female Kentish Plovers exhibited lower apparent survival than older age classes, speculating higher dispersal in yearling females caused lower estimates of apparent survival. While dispersal potentially drives apparent estimates lower in some plovers, reduced survival has been confirmed in some populations of Snowy Plovers; for instance, after accounting for fidelity rates, Stenzel et al. (2011) found true survival for females remained lower than males. However, Gaines et al. (2020) did not report sex-specific variation in adult apparent survival estimates.

Sex differences in survival could have potential implications for the breeding population. Since population growth relies on reproduction (in a closed population), and reproduction relies upon contributions from both sexes, sex variation in survival can influence a shortage of either sex, which can negatively affect population viability

(Engen et al. 2003). Donald (2007) concluded that differences in adult mortality between sexes are more likely contributing to male-skewed adult sex ratios (ASRs) rather than male-skewed ratios of broods among wild bird populations. Differences between sexes in both costs and benefits, in deserting versus providing parental care, arise under biased ASR, facilitating polygamy of the limiting sex (McNamara et al. 2000). It is unknown whether ASR is an evolutionary relic or a driver of the plovers' polyandrous sequential mating system (Eberhart-Phillips 2019). In Snowy Plovers, Stenzel et al. (2011) postulated that male-skewed sex ratios were primarily driven by higher survival among adult males. However, Eberhart-Phillips et al. (2017) reported minimal impacts on ASR from sex-specific adult survival, suggesting sex-specific variation in survival among juveniles contributed the greatest influence on deviations in ASR. While male-skewed ASRs exist in other populations (Sandercock et al. 2005, Stenzel et al. 2011), there was no evidence of male-biased ASR within RU2 (Table 5), as the mean ASR across the study was 0.50.

Annual Variation in Survival

Substantial annual variation in apparent survival existed across years in the local population, as reported in other studies of *Charadrius* plovers (Dinsmore 2008, Roche et al. 2010, Stenzel et al. 2011, Gaines et al. 2020). For subpopulations across the Pacific Coast range, annual variation in adult survival exhibits both similar and contrasting patterns. In central coastal California (RU4), adult survival was variable, but high (0.72 ± 0.02 to 0.80 ± 0.02) for most years, with the exception of one year (1998) in the

middle of the study where survival was particularly low (0.47 ± 0.03 ; Stenzel et al. 2011). In Oregon (RU1), adult survival has increased linearly across years from 0.61 ± 0.03 in 1990 to 0.77 ± 0.01 in 2014 (Gaines et al. 2020). While vital rates are often heterogeneous across a species range due to varying conditions influencing population dynamics (Méndez et al. 2018), subpopulations within relatively close proximity likely exhibit spatial synchrony (Eberhart-Phillips et al. 2015). However, comparisons between the coastal northern California population and the Oregon population reveal disparate demographic pressures at work, as patterns in temporal variation in adult survival estimates, degree of variation, and population counts contrast.

Limited studies address seasonal variation in survival; however, some have found lower survival during winter months. For instance, in Mountain Plovers survival was higher during summer (Miller and Knopf 1993) than winter (Knopf and Rupert 1995). In Snowy Plovers of coastal northern California, Papian (2018) also reported lower overwinter survival, compared to other seasonal intervals. Roche et al. (2010) surmised that differences between wintering locations might explain annual variation in Piping Plover survival. Saunders et al. (2014) associated negative effects on adult survival at wintering locations along the southeastern Atlantic coast of the United States, to increased hurricane activity and Merlin (*Falco columbarius*) populations. For Snowy Plovers in this region, extreme cold temperatures decreased apparent survival estimates (Eberhart-Phillips and Colwell 2014). Anecdotally, during the winter of 2006-07, the local population in northern California experienced a sharp decline coinciding with a year of low apparent survival. In January (2007), approximately 45 marked adults in a local

wintering flock vanished during a prolonged cold spell, several of which were local breeders (Mullin et al. 2010). Contrastingly, ~260 km to the north in the Oregon population, Gaines et al. (2020) reported higher survival and population growth during the same interval, while finding no effect of colder than average winter temperatures and only weak effects of higher winter precipitation on adult apparent survival. Despite these recent findings, observations indicated more extreme cold conditions in northern California than in Oregon during the winter of 2006-07 (Eberhart-Phillips et al. 2016). It is unknown whether extreme weather conditions directly cause mortality or increase susceptibility to other causes of mortality (i.e., disease, starvation, or predation).

Predator management strategies have improved Snowy Plover nest and chick survival (Dinsmore et al. 2014, 2017), but there is little indication that predator removal improves adult survival. Gaines et al. (2020) reported that while years of increased adult apparent survival coincided with increased predator management efforts (i.e., removal), acknowledged that such efforts likely reduced nest failures, which may have falsely improved apparent survival through reductions in permanent emigration. In RU2, managers used predator exclosures from 2001-06 to improve nest success; this practice anecdotally coincided with a declining trend in annual apparent survival. Predator exclosures, while widely used across the range, became controversial as they were associated with adult mortality (Johnson and Oring 2002, Murphy et al. 2003, Neuman et al. 2004, Isaksson et al. 2007) and population decline (Eberhart-Phillips et al. 2015). In the local population, records indicate one depredated adult recovered at an exclosure, while seven other adults disappeared during incubation at exclosed nest sites (Hardy and

Colwell 2008). Such losses incurred within a small population could have pronounced effects on overall annual survival estimates. Gaines et al. (2020) reported negative effects from predator exclosure use on adult apparent survival, depicting an inverse relationship between percent of nests exclosed and survival rates. However, Gaines' study did not directly quantify the effect on individual adult survival.

CONSERVATION IMPLICATIONS

Challenging implications exist regarding the recovery for the Pacific Coast population of Western Snowy Plovers in RU2 given the nature of temporal variation in adult survival. Years of substantially low survival have directly reduced overall population growth rates over the 19-year study. High variability in adult survival increases variance in annual population growth rates, which increases extinction probabilities (Pfister 1998). Differences between consecutive counts and algebraic population growth rates (Table, 3; Figure 5) emphasize the influence of immigration and emigration and the breeding population in RU2 (Colwell et al. 2017a, Eberhart-Phillips and Colwell 2015). Despite successful efforts in recent years to increase per capita reproductive success, population numbers in RU2 remain far below targets specified by the recovery plan (Colwell 2019). Future research would benefit the recovery by collecting and incorporating environmental data into survival models, to identify factors that increase mortality in adults.

Incorporating temporal and sex-specific variations of survival parameters into population viability models will provide comprehensive knowledge of local populations, by identifying specific demographic sources of compromised survival (i.e., female or annual interval). Quantifying population dynamics on the local scale provides insight into localized obstacles that hinder growth, and the respective contributions of each recovery unit within the greater population. Furthermore, gaining perspective on the influence of sex-specific adult survival and its relation to ASR may contribute to our understanding of

the interplay between population dynamics and breeding system evolution. I recommend that managers not only continue facultative management efforts to increase productivity, but also continue extensive banding efforts to extend monitoring and track changes in vital rates and demographics. Future analyses using mark-resight data will reveal frequency of episodic high mortality events in a larger context, extend our understanding of environmental limitations, and provide updated demographic information to incorporate into population viability analyses. Specifically, if managers expand resight efforts beyond breeding intervals, and collect resight data during non-breeding season months and sustain such efforts over time, it would provide a means to target interannual periods of high mortality and more precisely identify the factors responsible. Furthermore, range wide collaboration and unification of mark-resight data would facilitate future analyses that better measure true survival, provide a better picture of dispersal dynamics, and assess the presence of sex-specific survival in the greater population. Such collaboration and data sharing across the recovery would provide a direct means to estimate true survival, site fidelity, site propensity, and dispersal, thus provide a more holistic representation of population dynamics and assist in decision-making to accomplish the recovery of the Pacific Coast population.

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APPENDIX A

Appendix A: Encounter probability

Encounter probability was best explained by quadratic constraints on annual variation ($p[YY]$; Figure 4). Quadratic effect of time variation for encounter probability ($p[YY]$) held the majority of the model weight ($w_i = 0.80$). The second ranked model with the additive effect of sex and quadratic constrained annual trend ($sex+YY$) was within $2 \Delta QAIC_C$ with slightly less support ($w_i = 0.25$). These two models were 11 times more likely than the next best model with a linear constrained time trend ($p[Y]$; $w_i = 0.07$). No other models were equally competitive ($\Delta QAIC_C \leq 2$; Table 4); however, models with no effect [\cdot], additive effect of sex and year [$sex+yr$], and sex [sex] all fell within $7 \Delta QAIC_C$. I used the quadratic annual time trend for encounter probability ($p[YY]$) for the following sequence of modeling to compare survival structures.

The overall mean encounter probability was high ($p = 0.89 \pm 0.01$). The relationship was best described by a quadratic annual trend, with the nadir of encounter rates ($p = 0.80 \pm 0.01$) occurring during the middle years (2006-09), when the population was lowest; higher encounter rates ($p = 0.89 \pm 0.02$; 0.96 ± 0.02) occurred at the beginning and end of the study, respectively (Figure 4). The sharp decline in total breeding adults that occurred between 2006 and 2009 (Table 5) likely influenced lower encounter estimates, forcing a decreasing trend that later recovered.

The additive effect of sex and quadratic annual constraints (sex+YY) in encounter probability indicated that female detection probability was slightly less (0.01) than males. However, I found this slight deviation to be inadequate to draw biological conclusions from.

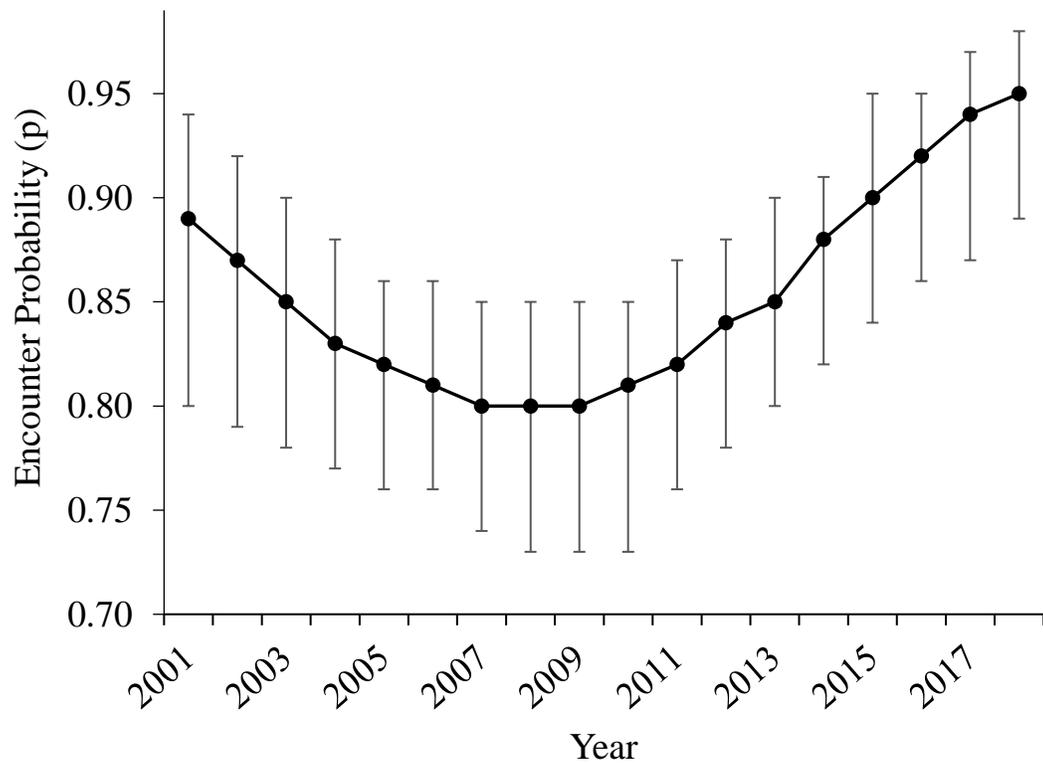


Figure 4. Quadratic constrained annual variation in encounter probability estimates of Snowy Plovers with 95% confidence intervals from 2001-18 in coastal northern California.

Table 4. Top models describing variation in encounter probability (p) for Snowy Plovers in coastal northern California. Encounter probability (p) structures follow: no effect [·], year [yr], sex [sex], additive [sex+yr], linear constraint [Y], additive sex with linear year constraint [sex+Y], quadratic year constraint [YY], and additive sex and quadratic constraint on year [sex+YY].

Model Structure	QAIC _c	Δ QAIC _c	w_i	K	Deviance
$\phi(\text{yr}) p(\text{YY})$	1614.63	0.00	0.59	22	533.66
$\phi(\text{yr}) p(\text{sex+YY})$	1616.38	1.74	0.25	23	533.31
$\phi(\text{yr}) p(\text{Y})$	1619.17	4.53	0.06	21	540.29
$\phi(\text{yr}) p(\cdot)$	1619.32	4.69	0.06	20	542.53
$\phi(\text{yr}) p(\text{sex+Y})$	1621.31	6.39	0.02	22	540.06
$\phi(\text{yr}) p(\text{sex})$	1621.30	6.67	0.02	21	542.43
$\phi(\text{yr}) p(\text{sex+yr})$	1631.30	16.66	0.00	37	518.38

APPENDIX B

Appendix B: Annual breeding population and adult sex ratios

The Recovery Plan for the Pacific Coast population of Western Snowy Plovers designated six recovery units (RU's) across the plovers' range within the United States. Furthermore, the plan set targets for recruitment rates and population numbers for each recovery unit, as well as for the entire population. For RU2, the target was 150 individuals, with 3000 individuals for the greater population held for no less than 10 years (USFWS 2007). More recently, recruitment goals for RU2 have been on track, as substantial habitat restoration efforts have been productive in encouraging high numbers of fledged chicks (Feucht et al. 2020). However, the overall trend of annual counts of breeding adults in RU2 remains far below the objective targets outlined by the Recovery Plan. The population has shown significant variation since 2001 (Table 4). The high variability in breeding adults follows annual variation in adult survival. Dispersal between the Oregon/Washington subpopulation (RU1) and northern California subpopulation (RU2) likely contributed to variations, as well. Adult sex ratios using the number of breeding males and the total breeding counts for the year, reveal relatively equal sex ratio over the years.

Table 5. Annual counts of Snowy Plovers in Humboldt County, Mendocino, and Del Norte Counties (RU2) from 2001-19 (Feucht et al. 2020) including philopatric and immigrant (imm.) individuals and derived male adult sex ratios.

Year	Returning Adult Females	Philopatric Yearling Females	Imm. Females	Returning Adult Males	Philopatric Yearling Males	Imm. Males	Total Breeders	ASR (Male)
2019	15	11	8	25	4 ^a	9	72	0.53
2018	19	4	6	18	5	11	63	0.54
2017	20	4	11	19	5	13	72	0.51
2016	17	7	9	17	6	16	72	0.54
2015	18	1 ^a	11	14	2	15	61	0.51
2014	14	5	6	16	2	8	51	0.51
2013	15	1	7	12	4 ^a	5	44	0.47
2012	14	2	4	11	2	6	39	0.48
2011	11	6 ^a	3	7	2 ^a	7	36	0.44
2010	9	2 ^a	5	10	1	5	32	0.5
2009	9	0	1	6	2	1	19	0.47
2008	9	2	6	8	1	10	36	0.52
2007	9	2	5	8	2	4	30	0.46
2006	18	6 ^a	6	11	4	14	59	0.49
2005	19	6	9	15	4 ^a	13	66	0.48
2004	17	5	15	16	3	18	74	0.5
2003	22	4 ^a	2	16	5	6	55	0.49
2002	19	9	5	20	6 ^a	4	63	0.48
2001	14	7	8	11	2	16	58	0.5

^a Total includes after-second-year (ASY) plover breeding in RU2 for first time

APPENDIX C

Appendix C: Estimates of apparent survival and encounter probability.

Table 6. Annual estimates for apparent survival (ϕ) using shrinkage estimates (\tilde{S}) from variance components and encounter probability (p) of male and female adult Snowy Plovers in coastal northern California from 2001-18, based on the top model ($\phi[\text{sex} + \text{yr}] p[\text{YY}]$).

Year	Male ϕ	SE	p	SE	Female ϕ	SE	p	SE
2001	0.81	0.05	0.89	0.03	0.78	0.06	0.89	0.03
2002	0.82	0.05	0.87	0.03	0.79	0.05	0.87	0.03
2003	0.79	0.05	0.85	0.03	0.74	0.05	0.85	0.03
2004	0.69	0.05	0.83	0.03	0.64	0.06	0.83	0.03
2005	0.73	0.05	0.82	0.03	0.69	0.06	0.82	0.03
2006	0.56	0.05	0.80	0.03	0.51	0.06	0.80	0.03
2007	0.50	0.06	0.80	0.03	0.44	0.06	0.80	0.03
2008	0.70	0.06	0.80	0.03	0.65	0.07	0.80	0.03
2009	0.74	0.06	0.80	0.03	0.69	0.06	0.80	0.03
2010	0.82	0.06	0.82	0.03	0.78	0.06	0.82	0.03
2011	0.74	0.06	0.84	0.03	0.70	0.06	0.84	0.03
2012	0.76	0.06	0.85	0.03	0.71	0.06	0.85	0.03
2013	0.77	0.06	0.87	0.02	0.72	0.06	0.87	0.02
2014	0.78	0.05	0.90	0.02	0.74	0.06	0.90	0.02
2015	0.75	0.05	0.92	0.02	0.71	0.06	0.92	0.02

Year	Male φ	SE	p	SE	Female φ	SE	p	SE
2016	0.70	0.05	0.93	0.02	0.65	0.05	0.93	0.02
2017	0.64	0.05	0.95	0.02	0.59	0.05	0.95	0.02
2018	0.64	0.05	0.96	0.02	0.59	0.05	0.96	0.02
Mean	0.72	0.03	0.89	0.01	0.68	0.03	0.89	0.01

APPENDIX D

Appendix D: Annual population growth rates

I estimated algebraic population growth rates using per capita reproductive success (PCRS) as the fecundity term (b), juvenile survival estimates derived from Mullin et al. (2010), and adult apparent survival estimates from my top model with additive effect of sex and year. I derive additional population growth rates with the effect of immigration and emigration accounted for through consecutive annual population counts. Years of declining population growth rates coincide with years of low adult survival (2006 and 07).

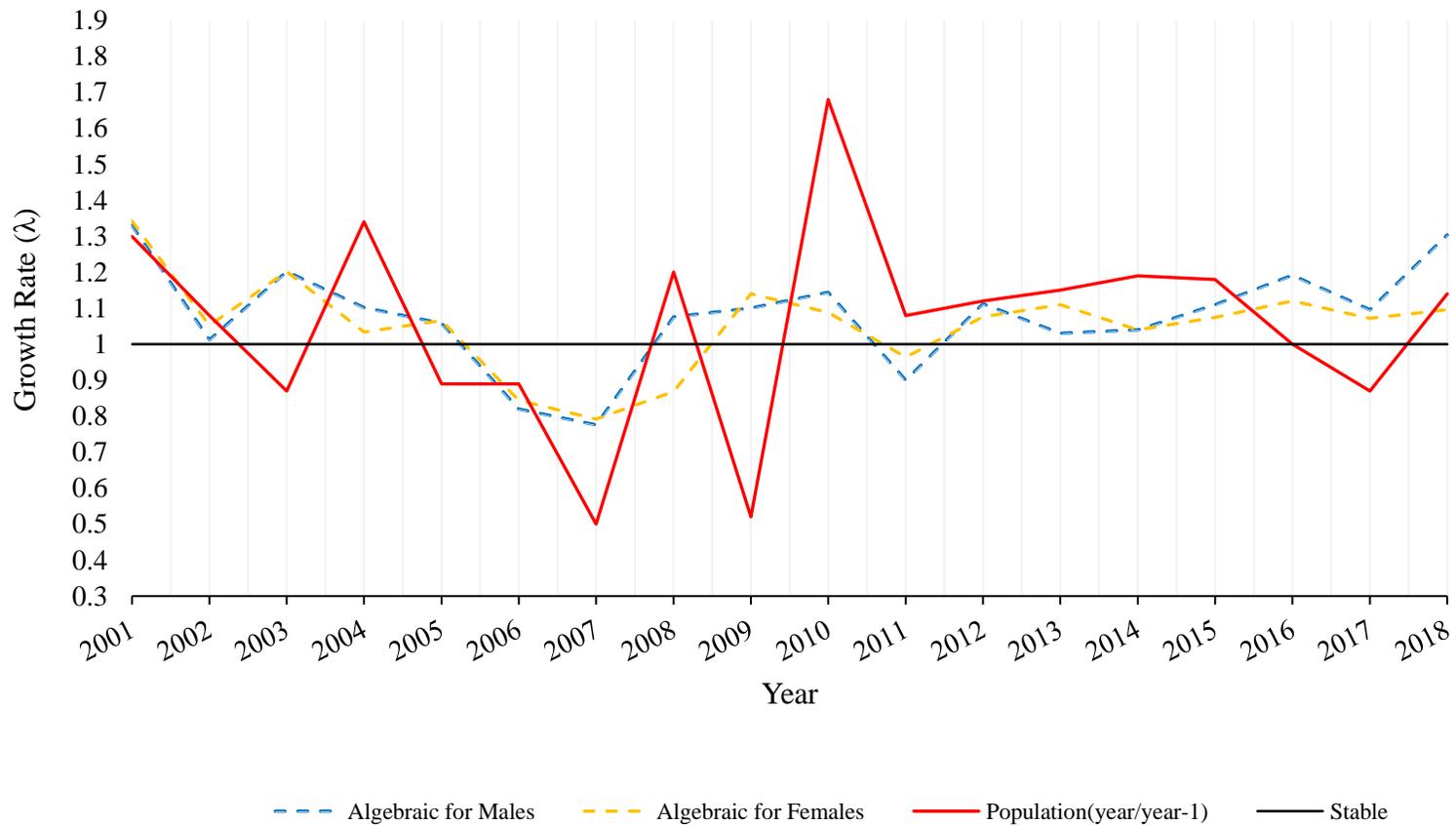


Figure 5. Annual population growth rates of Snowy Plover derived using algebraic and consecutive population count methods from 2001-18 in coastal northern California.

APPENDIX E

Appendix E: Longevity distributions

Compilations of mark–resight records indicate a wide range of ages (Figure 6) within the coastal northern California population (1–19 years). Overall, the average lifespan of plovers in this study was ~4 years. The maximum naive longevity was 19 years for one adult male that hatched within the population in 2001. The oldest male set the longevity record for the species and was the second most prolific breeder within the study; see Colwell et al. (2017). This anecdote is merely one example of how adult survival strongly influences fecundity. However, the concept applied to a broader population context provides evidence as to how adult survival relates to population growth through fecundity. For a small breeding population (19–74), relatively long-lived individuals play pivotal roles in contributing and sustaining the population via reproductive effort over time. As mark–resight efforts continue and management actions evolve future assessments of longevity and adult maximum age structure may consequently reveal a different story, as both are reflections of survival and are subject to change with increased intervals.

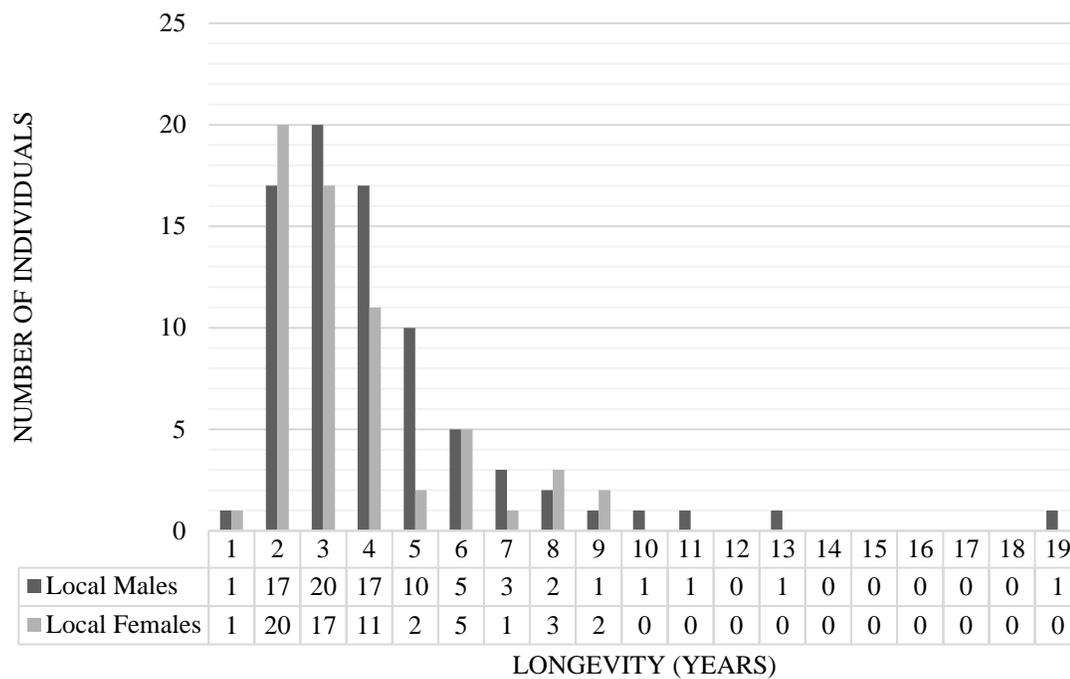


Figure 6. Adult longevity distribution of local (philopatric) male and female Snowy Plovers monitored in coastal northern California from 2001-19.