

MOLT IN INDIVIDUALS: A DESCRIPTION OF PREALTERNATE MOLT
PHENOLOGY IN A POPULATION OF SNOWY PLOVERS IN HUMBOLDT
COUNTY, CALIFORNIA

By

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ABSTRACT

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Molt in birds is an essential physiological process. Intrinsic and extrinsic conditions, such as age, sex, location, or food stress, may cause individual variation in molt phenology. This study describes the timing of prealternate molt in western snowy plovers (*Charadrius nivosus nivosus*) wintering in Humboldt County, California, USA. Between July 2014 and April 2015, I photographed uniquely marked plovers twice a month and assigned dates of initiation and completion. I modeled sex, age, hatch date, and breeding location as predictors of molt phenology. I observed prealternate molt from October to April, which is earlier than previously described. Males began molting an average of 71 days earlier than females, and birds that breed in northern California began molting an average of 43 days earlier than those that breed in Oregon and Washington. Earlier initiation was correlated to longer molt duration, which suggests that males need more time than females to complete alternate plumage.

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INTRODUCTION

Feathers define birds, and they form an integral part of the taxon's ecology. The feather coat can function in several ways, including thermoregulation, flight, dynamic streamlining, camouflage, buoyancy, sensation, water-proofing, and communication (Amadon 1966, Spearman and Hardy 1985). Feathers are complex structures composed mainly of proteins called keratins (Proctor and Lynch 1993). Color is produced either by light interactions with surface structures or by the deposition of pigments (Fox 1976, Burkhardt and Finger 1991). The most common feather pigment is melanin, which can produce colors from brownish-red to brown and black, and often serves as a background in structural color (Finger *et al.* 1992). Bright or saturated colors are physiologically costly to produce (Jawor and Breitwisch 2003, Griggio *et al.* 2009). Feathers are relatively durable and strong, but they are degraded by ultraviolet radiation, parasites, and abrasion, resulting in reduced effectiveness (Amadon 1966, Burt and Ichida 1999). To maintain the functional efficiency of the feather coat, birds must replace their feathers (Howell 2010).

Molt in birds is the process of feather replacement, which is generally periodic (Watson 1963, Voitkevich 1966). Feathers are typically replaced during discrete periods of every year, rather than continuously. Molts may be complete, replacing all feathers, or they may involve only certain groups of feathers on the bird's body (Ginn and Melville

1983). The latter type of molt may be termed limited, partial, or incomplete, dependent on its extent (Pyle 2008).

Molt in birds has been catalogued differently by various researchers, and the complexity of the subject has engendered multiple schemes of nomenclature. A coat of feathers has been described in reference to seasonality (*e.g.*, "summer plumage", "perennial plumage"), different ages of the feathers in the coat (*e.g.*, "simple" vs. "compound" plumage), or stages in the species' life-history (*e.g.*, "postnuptial" or "off-season"; Dwight 1902, Humphrey and Parkes 1963, Stresemann 1963, Cramp and Simmons 1983). I use the term 'plumage' to mean the appearance, or complete feather coat, of a bird, and I will use the Humphrey-Parkes scheme to describe molts and plumages.

All species have at least one plumage, called the basic plumage. Some species wear a secondary plumage for part of every year, known as the alternate, and a few of these insert yet a third plumage, the supplemental. Molts are named for the plumages they produce (Figure 1). In most species, the prebasic is the only complete molt (Howell 2010). In the temperate Northern Hemisphere, basic plumage often coincides with nonbreeding periods, and alternate plumages with breeding seasons (Humphrey and Parkes 1959, Pyle 2008). Therefore, molts can appear as brackets to the reproductive season (Figure 2; Dwight 1902). In many species, including the snowy plover, first-year birds undergo a different progression of plumages than their older conspecifics, which

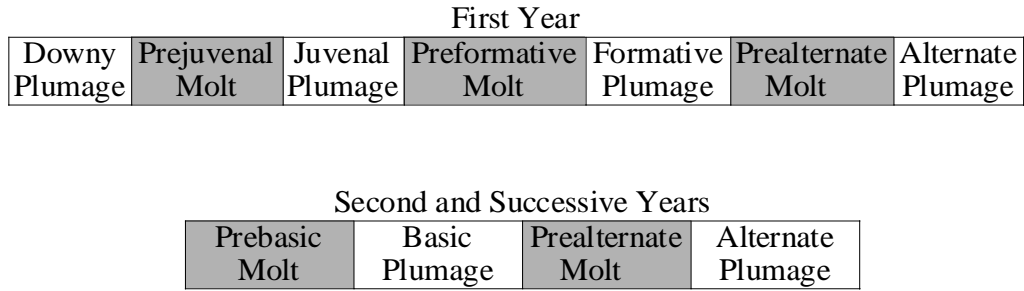


Figure 1. Example progression of plumages and molts in snowy plovers, beginning with the chick stage. The definitive molts and plumages are repeated through successive years (Pyle 2008).

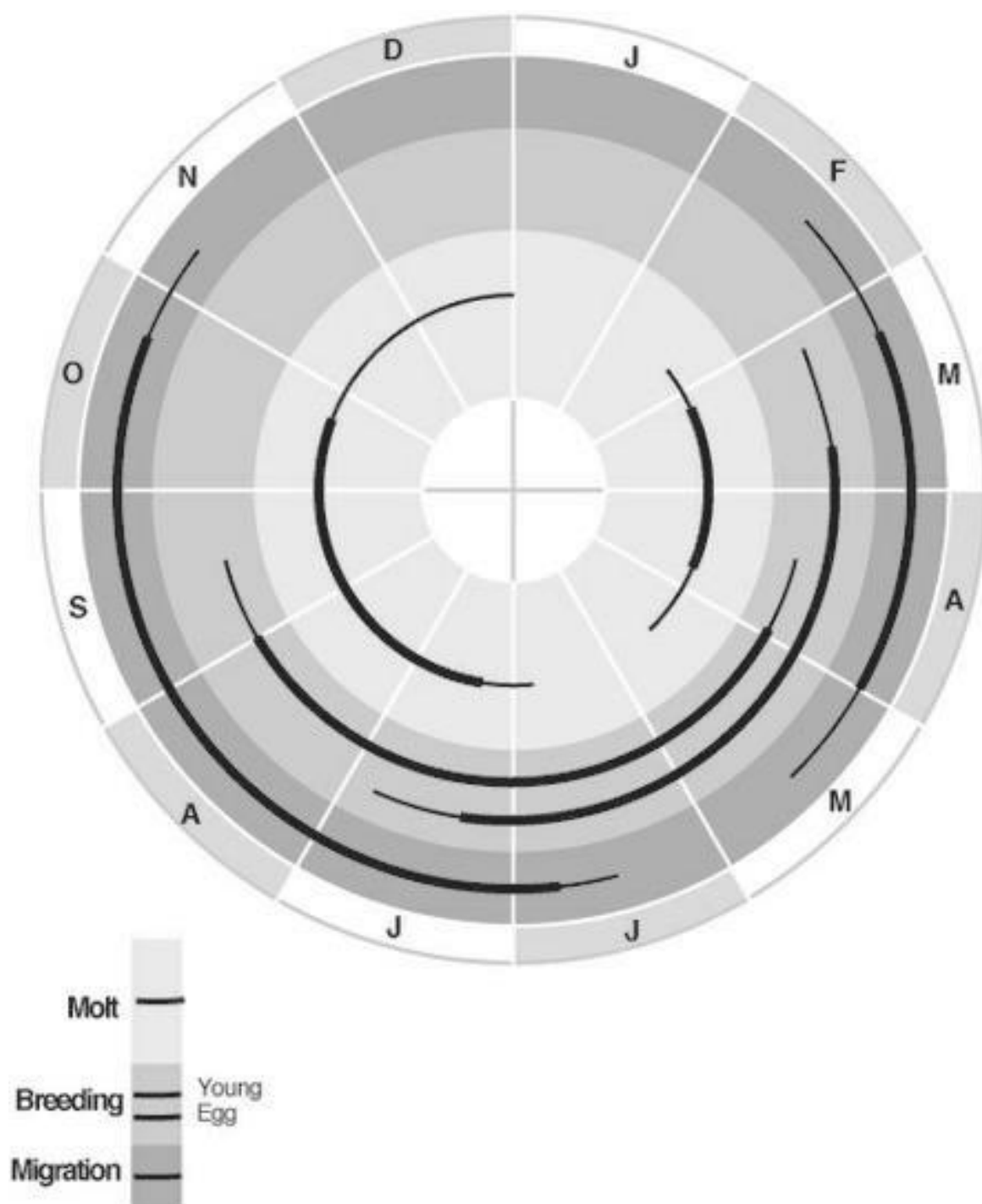


Figure 2. The phenology of molt, breeding, and migration in the snowy plover (from Page et al. 2009).

repeat the same molts, called definitive molts, from year to year after they reach the second prebasic molt in their second year of life (Howell *et al.* 2003).

Molt Physiology

The physiological processes of breeding, molt, and migration are triggered by environmental cues that act on endogenous clocks in birds in the wild (Gwinner 1986). While more variable conditions such as rainfall or food availability have been observed to act on these internal rhythms, especially in the tropics, the process of molt is strongly tied to a response to daylengths, or photoperiodism (Zann *et al.* 1995, Dawson *et al.* 2001, Scheuerlein and Gwinner 2002). A bird's year appears to be split into two parts, breeding and nonbreeding, by photoperiodicity. Short daylengths precede a period of gonadal maturation brought on by high levels of Gonadotrophin-Releasing Hormone (GnRH), and long daylengths mark a return to low levels (Dawson *et al.* 2001). Photoreceptors in the eyes, the pineal glands, and in the brain synchronize the internal clock to variant daylengths (Gwinner and Brandstätter 2001). GnRH, among other functions, stimulates the release of thyroxine, a hormone that regulates growth of feathers (Dawson 2008). The symmetry of flight feather loss and regrowth is mediated by the nervous system (Kuenzel 2003). In passerines, a decrease in photoperiod coincided with the "complete" molt (*sic*; presumed prebasic), while an increase in photoperiod coincided with the "partial" molt (*sic*; presumed prealternate; Leshner and Kendeigh 1941). The tropics experience daylengths with less annual variation than do higher latitudes, so that

winter daylengths in the Northern Hemisphere are longer at low latitudes and summer daylengths are longer at high latitudes, with symmetry around the solstices. Therefore, the latitude where a bird lives should have a distinct effect on photoperiodicity. For example, yellow warblers (*Setophaga petechia*) were documented to begin prebasic molt earlier than conspecifics eight degrees of latitude to the north (Ryder and Rimmer 2003). A population of bar-tailed godwits (*Limosa lapponica*) that breed in northern Alaskan were found to have longer prealternate molts than those of more southern breeding grounds (Conklin and Battley 2011). Blue tits (*Cyanistes caeruleus*) exposed to rapidly decreased photoperiods increased their molt speed in comparison to those exposed to more slowly decreased daylengths (Griggio *et al.* 2009). Photoperiod should be expected to affect physiological responses differently in conspecifics in different latitudes for all or part of their year, *i.e.*, residents vs. migrants, so that molt phenology would likely be affected by these different schedules.

Birds experience significant change in reproductive hormone levels between nonbreeding and breeding seasons as gonads swell to functional sizes (Dawson *et al.* 2001). Numerous studies have noted that reproductive hormone levels either affect molt or show correlation with it. For example, high levels of testosterone delayed prebasic molt (Schleussner *et al.* 1985, Nolan *et al.* 1992), while decreases in prolactin occurred concurrently with its onset (Farner and Gwinner 1980, Szelényi and Péczely 1988, Gwinner 2003, Hahn *et al.* 2004, Dawson 2006, Dixit and Sougrakpam 2013, Mazzaro *et al.* 2013). Supplemental testosterone spurred prealternate molt in basic-plumaged

Wilson's phalaropes (*Phalaropus tricolor*), but prolactin and estradiol had no effect (Johns 1964). Prolactin, high levels of which coincides with parenting behaviors such as nest or brood defense and provisioning, remains at significant levels until the young are fledged (Dawson *et al.* 2009). In experimental manipulations of starlings (*Sturnis vulgaris*) that examined photoperiod, gonadal regression, and peak prolactin as predictors of prebasic molt initiation, Dawson (2006) found that the only consistent link was with the last. However, there has been much less study around the triggers of prealternate molt, as may be seen from this literature review, and its causes still appear murky.

Birds expend more energy during molt (Fox and Kahlert 2005). Molt is often sequential to other energy-demanding processes, such as migration or reproduction (Ginn and Melville 1983, Grubb 2005, Conklin *et al.* 2011, Dawson 2008). Sequential schedules in the annual year appears to be adaptive, as shown by occasional species in which breeding and molt overlap in very specific patterns, such as primary molt in incubating females that are fed by their mates (Rogers *et al.* 2014), or protracted molt (Newton and Rothery 2005, Crossin *et al.* 2012, Johnson *et al.* 2012, Flockhart 2013). Individuals that do not complete each process in time to prepare for the next may be in poor condition to breed (Rohwer *et al.* 2011), or may be lost to predation or exhaustion during migration (Barshep *et al.* 2013). In certain cases of environmental stress, such as food limitation, birds will skip breeding in poor years (Howell 2003, Cubaynes *et al.* 2010), but molt remains an essential part of each year to maintain optimal efficiency of the feather coat. Molt, then, is a major process in a bird's annual year, and is crucial to

individual survival and reproductive success. On the scale of populations, it is an important area of study in ornithology and wildlife conservation (Conklin and Battley 2012, Barshep *et al.* 2013).

Study Population

The snowy plover (*Charadrius nivosus*) is a small shorebird of the Americas. The population along the western coast of North America from Washington to Mexico is considered to be a geographically isolated group, designated as the western snowy plover (*C. n. nivosus*), and listed as threatened in the United States (USFWS 1993, Page *et al.* 2009). Plovers breed along beaches and other suitable nesting areas throughout their range (Warriner *et al.* 1986). In late summer, they begin to form flocks that persist over the winter on marine beaches (Brindock 2009). The species is partially migratory, and individuals from various breeding regions can be found wintering together (Page *et al.* 1995). Until recently, the snowy plover has been taxonomically united with a related species, the Kentish plover (*C. alexandrinus*) of Eurasia (Chesser *et al.* 2011), and some descriptions of the snowy plover may refer to that formerly cosmopolitan species.

Because of the protected status of the western snowy plover, members of the Western Snowy Plover Recovery Team along the Pacific coast monitor their breeding success along the U.S. coast (USFWS 2007). They color-band plovers, giving adults unique color combinations and chicks brood-specific combinations, and record life-history events, such as their hatch dates and breeding efforts (Colwell *et al.* 2015, Lauten

et al. 2013). The west coast is divided into six management units by the species' Recovery Plan: Recovery Units 1-6 (RU1-6); RU1 comprises Washington and Oregon, and Del Norte, Humboldt, and Mendocino Counties in California make up RU2. RU4 spans the coast of California from Sonoma to Monterey Counties (Appendix A; USFWS 2007). Few plovers with bands from the other recovery units have been seen recently in the study area, the north coast of California (pers. obs).

In Humboldt County, recent winter counts (2004-2015) have ranged from 34-150 individuals (J. H. Watkins, pers. comm.). Brindock (2009) conducted regular surveys over two successive winters in Humboldt County and found averages of 33 plovers at Little River State Beach/Clam Beach County Park, 25 on Centerville County Beach, and 7 on the south spit of Humboldt Bay during 2007-2009, which are the wintering sites with highest consistent numbers (USFWS 2014).

Snowy plovers molt completely once a year, which results in the basic plumage. They also undergo a prealternate molt that involves mostly body feathers (Palmer 1967, Prater *et al.* 1977, Pyle 2008). Snowy plovers in basic plumage are white below, with brownish-gray upperparts. In alternate plumage, the forecrown, auriculars, and patches on the sides of the neck become brownish-black or black. In females, these patches may be limited in both size and saturation, so that a plover's alternate plumage may appear similar to her basic plumage. The dark facial markings of plovers are caused by deposition of melanin in feathers (Bokony *et al.* 2003). Males show blacker feathers in

larger extents, and may develop a pinkish color over the crown and nape (Figure 3; Bent 1929, Cramp and Simmons 1983, Pyle 2008).

Snowy plovers undergo the definitive prebasic molt between July and November. Their definitive prealternate molt occurs between November and May (Prater *et al.* 1977, Ginn and Melville 1983, Pyle 2008). Though the natural history of the species has been detailed by many researchers, their observations cumulatively describe a broad window for this molt, while showing some disagreement. Before beginning this study, I had observed snowy plovers in Humboldt County in prealternate molt in November, which is earlier than either bracket given by North American authorities (Table 1).

Chicks hatch in northern California from April to August (Warriner *et al.* 1986, Page *et al.* 2009) in downy plumage. They complete the prejuvenal molt in 28-33 days (Warriner *et al.* 1986). A partial, preformative molt follows the completion of the prejuvenal molt, from August to December or March. They undergo their first prealternate molt in the next few months, and follow definitive plumages thereafter (Pyle 2008). Therefore, plovers of all ages are in prealternate molt in the winter.

Hatch-year birds show consistently higher mortality rates for a variety of potential reasons (Goss-Custard 1984, Kus *et al.* 1984, Warriner *et al.* 1986, Sandercock *et al.* 2005). Hatch-year plovers complete one more molt (the partial preformative) than after-hatch-year plovers, which may present them with an additional energetic burden. Late-hatched chicks molt into their juvenal plumage later in the calendar than early-

hatched chicks, and might show a comparative delay in the preformative molt. I



Figure 3a) An adult snowy plover in basic plumage on 6 Dec 2014 at Centerville Beach, CA; b) An adult female snowy plover in alternate plumage on 5 April 2015 at Little River State Beach, CA; c) An adult male snowy plover in alternate plumage on 14 March 2015 at Centerville Beach, CA.

Table 1. Phenology of prealternate molt in snowy plovers. Molt descriptions were made from North American and European observations, since the taxon was classified as a subspecies of *Charadrius alexandrinus* from 1958 to 2011. Works marked with an asterisk (*) refer to earlier works in the table.

Author	American	European
Ridgway and Friedmann 1919		“winter/summer” terminology
Bent 1962 (reprint of 1929 edition)	“early spring”	
Palmer 1967	March	
Glutz von Blotzheim 1972*		Nov-Mar
Oberholser 1974	“winter/nuptial” terminology	
Prater <i>et al.</i> 1977*		“winter/summer” terminology; males begin Nov-Dec
Cramp and Simmons 1983*		(Nov) Dec-Feb (Mar)
Ginn and Melville 1983		Mar-May
Pyle 2008*	Jan-Apr	
Page <i>et al.</i> 2009*	Feb-Apr	

hypothesized that a chick hatched in the early part of the breeding season would continue to be early with other processes throughout its first year, as found in great tits (*Parus major*; Bojarinova *et al.* 1999) and inferred in marbled murrelets (*Brachyramphus marmoratus*; Gutowsky *et al.* 2010), and might retain an early molt date in subsequent years.

Speeds of molt may be limited by intrinsic and extrinsic factors. Rohwer and Rohwer (2013) found that the rate of molt in flight feathers in many species is largely limited by the number of feathers that grow simultaneously. Ralph (1969) noted that darker blacks and browns resulted from longer periods of oxidation in the molecular construction of melanin. Vágási *et al.* (2010) saw smaller melanized 'badges' in house sparrows (*Passer domesticus*) that showed accelerated molt in experimental conditions as compared to unmanipulated sparrows with typical molt phenology. In collared flycatchers (*Ficedula albicollis*), feather growth rate reflected forage quality during winter molt (Hargitai *et al.* 2014). These findings support the idea that extensive dark markings, which typically signal high quality in an individual (Prum 2012), require more time to grow. Plovers in winter flocks feed in groups undifferentiated by age or sex (pers. obs.), so that neither sex has an advantage in forage. Male plovers, therefore, would potentially have longer prealternate molt durations than females.

Snowy plovers have a polygamous mating system: they usually form more than one pair-bond per season in sequential breeding attempts (Page *et al.* 2009). Breeding season begins in March with courtship activities in males such as vocalizing, posturing,

defending territory or potential mates from other males, and scraping. A female may respond by scraping with a male. Mate selection may even begin in the flock before courtship behavior is apparent. The female tends to abandon the brood for the male to raise, and she seeks a new mate among those plovers that are not engaged in breeding attempts (Warriner *et al.* 1986). These are likely to be few in number in RU2, considering the limited and dispersed local breeding population (Colwell *et al.* 2015). In Kentish plovers, where the pattern of polygamy is similar, female re-mating times increased with later date in one season (Székely *et al.* 1999). Therefore, females would have the best chance of selecting mates at the beginning of breeding season. A male may be able to fledge two clutches per season if he begins at the start of the season, so that timely completion of prealternate molt could affect his productivity. Early initiation of molt would be advantageous in allowing timely completion of more richly colored plumage.

Molt Assessment

Typically, researchers assess molt in captured birds by scoring the growth of flight feathers or estimating the percentage of growing body feathers (Ginn and Melville 1983, Underhill and Zucchini 1986, Gratto-Trevor 2004). Studies of captured birds have rendered a great deal of information on molt, but capture-based methods do not usually allow regular observations of the same bird during the same season. The circumstance of a color-banded population of resident birds presents an excellent opportunity to describe

molt as observed in free-living individuals. Prebasic molt is dominated by flight feathers, which could only be examined in this species by capture, since their flight is abrupt and fairly rare. However, as a threatened population, any research that involves western snowy plovers must minimize impact on their fitness (USFWS 2007). Prealternate molt in snowy plovers largely involves feathers on a bird's head and neck, and it occurs well after the critical enterprise of reproduction is finished. I used the opportunity of a population of marked birds with known histories to observe the phenology of prealternate molt in individuals through photographs.

Study Objectives

I documented the initiations and completions of prealternate molt in a population of uniquely identifiable snowy plovers in Humboldt County, California, during one nonbreeding season. Then, from molt observations in known individuals, I examined whether the demographic variables of sex, age, hatch date, and breeding location offer predictive power on either initiation timing or duration. Lastly, I looked for a relationship between molt initiation and duration to explore whether molt rate followed demographic lines.

METHODS

I documented prealternate molt in banded snowy plovers wintering in Humboldt County, California, by photographing them at regular intervals over one nonbreeding season. From these photographic series, I assigned dates of molt initiation and completion to each plover. Then I used demographic data gathered through separate monitoring efforts to model molt phenology in terms of four covariates: sex, age, hatch date, and breeding location, and regressed duration with initiation.

Field Methods

From mid-July 2014 to mid-April 2015 a second observer and I surveyed 2.5-km transects at each of three study sites in central Humboldt County, California: Little River State Beach/Clam Beach County Park, the Mike Thompson Wildlife Area on the south spit of Humboldt Bay, and Centerville County Beach (Figure 4). I scheduled surveys twice each month, as near as possible to the 1st and 15th days. We began surveys immediately after sunrise, and finished in three hours or less. We attempted to record the color combinations of all the snowy plovers we observed.

On each survey, I photographed banded snowy plovers with a Canon EOS 500D or EOS 550D camera, with a Rokinon 500 mm f/6.3 lens plus 2x converter plus Canon EOS mount converter, or a Canon EF 100-400 mm f/4.5-5.6 L lens. I recorded some images in RAW format and the rest were made as in-camera jpegs at the highest

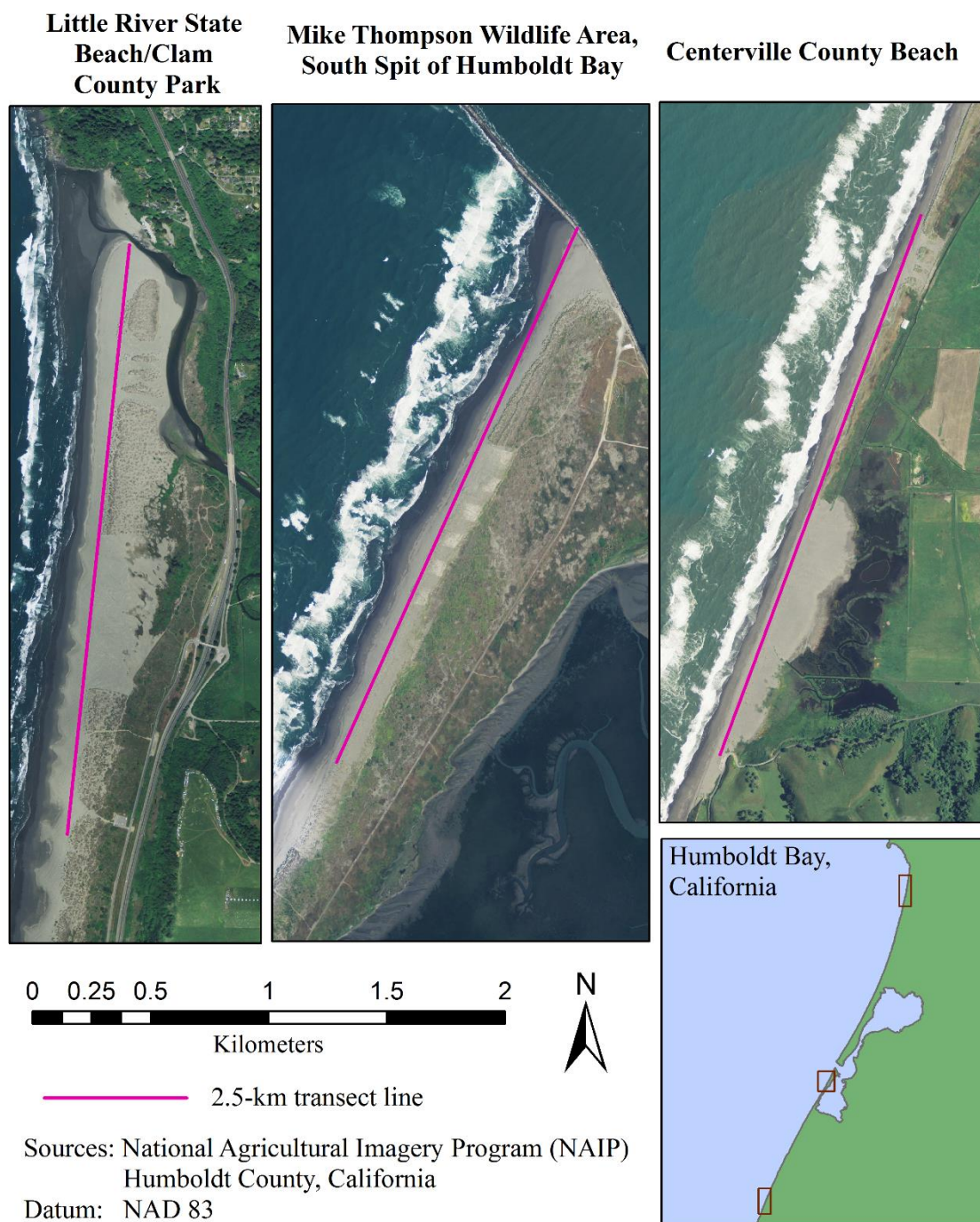


Figure 4. The three transect survey locations, from north to south, for snowy plovers in Humboldt County, CA, from Jul 2014 to Apr 2015.

quality. Image sizes ranged from three to eight megabytes for jpegs and 20 to 40 megabytes for RAW images. It was sometimes necessary to make additional photographs on other occasions, due to poor weather conditions or time constraints. Photographs showed the bird's bands, or I inferred band combinations from other photographs. I conducted this research under Humboldt State University Institutional Animal Care and Use Committee protocol #14.15.W07-A.

I sorted images to create a chronological series of photographs of each uniquely marked individual (Appendix B). I cropped photographs so that they contained only one plover, which occupied roughly one-eighth to one-third of the frame. I adjusted some photographs by changing the exposure, contrast, or color temperature of the whole frame, or selectively moderating light or dark areas to improve marginal images, but I minimized post-processing to preserve original data.

For each photograph series, I determined an initiation date as the median between the dates of the first image where alternate feathering appeared, and that of the previous image (Table 2). If I could not assign an initiation date in a series, I removed the individual from the sample. I determined a completion date in the same way if the photograph series included at least two images of the completed alternate plumage (Appendix C). I converted molt initiation and completion dates to days after 30 September 2014.

Table 2. An example of the calculation of median initiation and completion dates in snowy plovers in Humboldt County, CA, from Oct 2014 to Apr 2015. Photo ‘b’ is the first image to show molt prealternate molt in a series, and Photo ‘a’ is the previous image in the series, with a span of 14 days, inclusive. The median day between the two dates 1/2/15 and 1/15/15 fall on 1/9/15 when the half-day is rounded up.

Date	1/2/15	1/9/15	1/15/15
Photo number	a	median	b

Analyses

Since the process of assigning initiation and completion dates from an examination of photographs may introduce subjectivity, a second analyst performed the same process on a sample of the photo series. Then I treated each series of photographs as a set of assays for each analyst, and ranked as first the photograph assigned as the first image to show prealternate molt. I ranked the adjacent two photographs next (*i.e.*, before and after), since they were both just as close to being selected (Figure 5). I compared the results of the two analysts with Kendall's Rank Correlation Coefficient (Siegel 1956; Appendix D). I did not test observer reliability on assigned dates of molt completion.

First, I tested my data's distribution for normality by examining a histogram of the frequency of residual values and a quantile-quantile plot of theoretical versus sample quantiles. Then I modeled four covariates against initiation date and duration of molt in two separate analyses with additive linear regression ("lm" function) in R (R 3.1.1 GUI 1.65 Mavericks build, www.r-project.org, accessed 11 July 2014; Table 3). I checked the fit of the global model in each analysis with a scatter plot of theoretical vs. sample residual values. I arrived at coefficient estimates by model-averaging four candidate models of initiation and three models of duration with the "model.sel" and "model.avg" functions, which use AIC with small-sample bias adjustment, or AICc, to select the best model (Bartoń 2015). These functions calculate confidence intervals from model-

photo number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
rank	9	8	7	6	5	4	3	2	1	2	3	4	5	6	7	8

Figure 5. An example arrangement by one analyst of a photo series of 16 images when the 9th is selected as the first image in prealternate molt in an individual snowy plover in Humboldt County, CA, from Oct 2014 to Apr 2015. The next adjacent numbers, 8 and so on.

Table 3. Models used to estimate initiation day and duration of prealternate molt in snowy plovers in Humboldt County, CA, from Oct 2014 to Apr 2015.

Structure
initiation day ~ sex + age + hatch day + breeding location
initiation day ~ sex + age + breeding location
initiation day ~ sex + age + hatch day
initiation day ~ sex + age
duration ~ sex + age + hatch day + breeding location
duration ~ sex + age + hatch day
duration ~ sex + age

averaged coefficient estimates and their standard errors. While there are many possible models, given four covariates, I kept the number of models to four for molt initiation and three for molt duration because of the small sample size (Burnham and Anderson 2002). I had noticed the early appearance of prealternate molt in several older male plovers in both the previous year and during the study, so I included both age and sex as predictors in all of my candidate models. I also regressed molt duration with initiation as a univariate linear function ("lm") with an alpha value of 0.05. If early molt initiation is more likely in certain demographic groups, inclusion of initiation as a predictor of duration alongside sex, age, hatch day, and breeding location would introduce autocorrelation. A relationship between duration and initiation would imply that synchronicity in completion dates stems from a mechanistic cause, rather than individual variation.

RESULTS

Observers documented 205 band combinations from July 2014 to April 2015 at the three survey sites (Appendix E). I assessed prealternate molt in a sample of 53 uniquely marked plovers (Table 4). I used 38 of these records with complete demographic data to model prealternate molt initiations, and 11 of these 38 with completion dates to model prealternate molt duration.

Description of Prealternate Molt Phenology

I assigned molt initiation dates for 53 plovers, and completion dates for 17 of these (Appendix F). I observed molt initiations from 9 October to 25 March and molt completions from 17 November to 8 March (Figure 6). I calculated durations from 17 to 123 days (Figure 7, Table 5).

Kendall's Rank Correlation Coefficients

Kendall's Rank Correlation Coefficient is 1 when multiple analysts show perfect agreement and -1 when they show perfect disagreement (Seigel 1966). My assessment of molt phenology from photo series was supported by that of the secondary analyst by a mean value of 0.77 ($n = 10$, 95% CI = 0.24 to 1.3). The sample was mostly male (60%), after-hatch-year (90%), and resident (90%).

Table 4. Demographic composition of the sample of snowy plovers used to describe prealternate molt phenology ($n = 53$) in Humboldt County, CA, from Oct 2014 to Apr 2015. Plovers are categorized by sex, age class, and breeding location.

	After-hatch-year	Hatch-year	totals
Female			
Recovery Unit 1	1	8	9
Recovery Unit 2	11	0	11
Recovery Unit 4	0	0	0
unknown	0	0	0
totals	12	8	20
Male			
Recovery Unit 1	3	6	9
Recovery Unit 2	15	0	15
Recovery Unit 4	0	1	1
unknown	3	1	4
totals	21	8	29
Unknown Sex			
Recovery Unit 1	0	4	4
Recovery Unit 2	0	0	0
Recovery Unit 4	0	0	0
unknown	0	0	0
totals	0	4	4

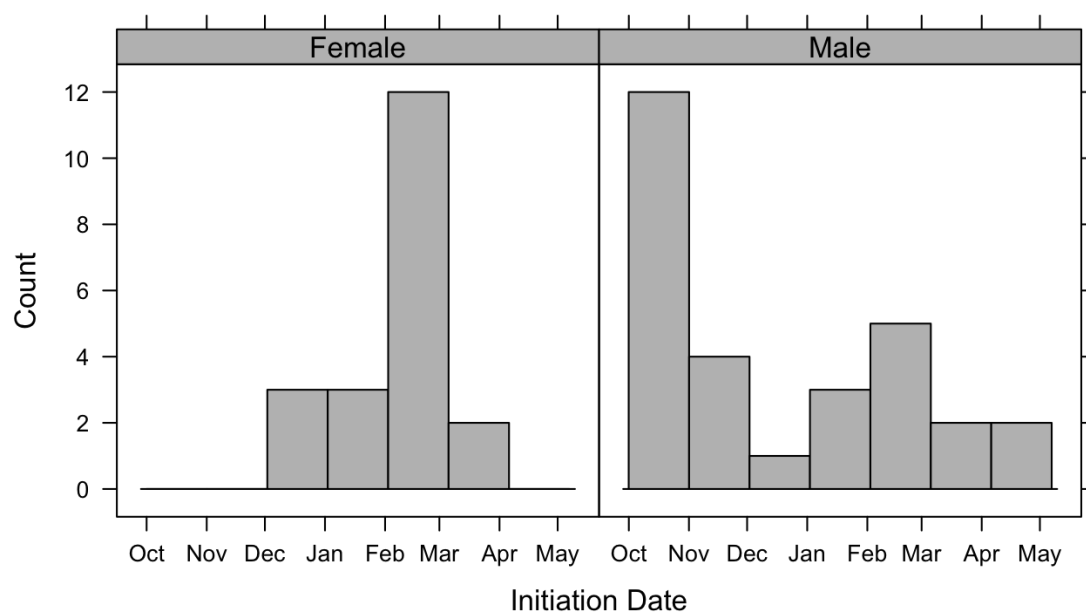


Figure 6. Summary of observed prealternate molt initiations in snowy plovers in Humboldt County, CA, from Oct 2014 to Apr 2015, categorized by sex (20 females, 29 males).

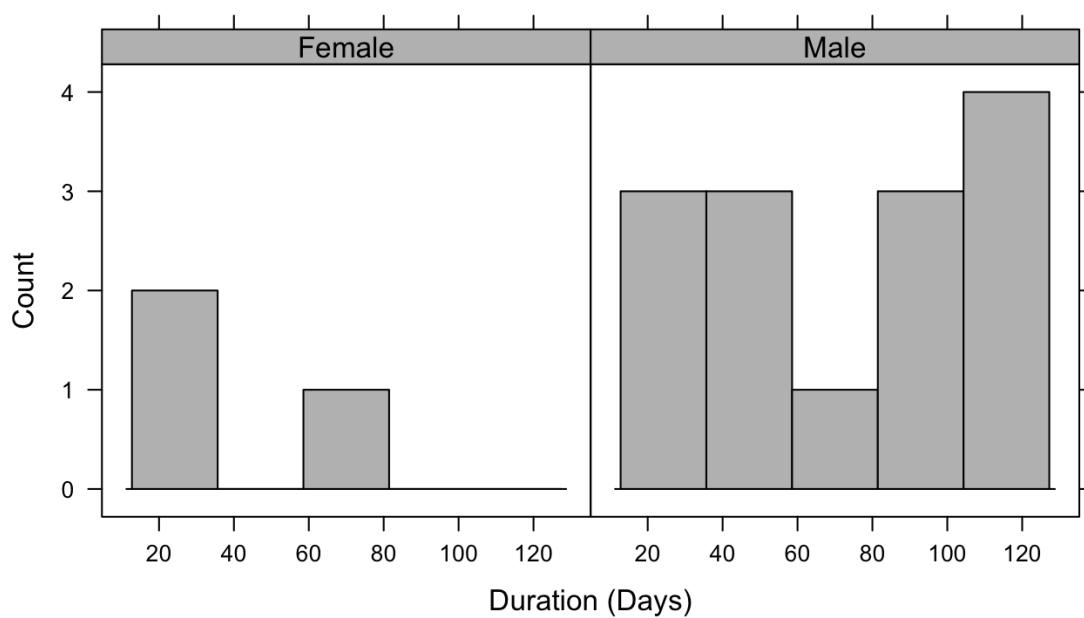


Figure 7. Summary of observed prealternate molt durations in snowy plovers in Humboldt County, CA, from Oct 2014 to Apr 2015, categorized by sex (3 females, 14 males).

Table 5. Summaries of observed initiation and completion dates and calculated durations of prealternate molt phenology in Humboldt County, CA, from Oct 2014 to Apr 2015.

	Minimum	1 st Quartile	Median	3 rd Quartile	Maximum	<i>n</i>
Initiation	10/09/14	10/28/14	01/29/15	02/24/15	03/25/15	53
Completion	11/17/14	01/08/15	02/19/15	03/07/15	03/08/15	17
Duration (days)	17	31	71	103	123	17

Predictors of Molt Initiation and Duration

Two of the four covariates were predictive of molt initiation date: sex and breeding location (Tables 6-7). Males initiated molt 71 days ($n = 38$, 95 % CI = 48 to 94 days) earlier than females, and residents of RU2 initiated molt 43 days ($n = 38$, 95% CI = 13 to 73 days) earlier than plovers that migrated from RU1 (Figure 8). There was only one record in the sample of an RU4 plover (Table 4), so I did not consider the estimate for that breeding location as predictive. I kept the record in the sample, however, for its potential contribution to estimates of sex and age covariates. Hatch day showed a very small, probably positive effect on molt initiation date. For every day later in the season that a plover hatched, molt initiation day was predicted to be 0.3 days later ($n = 38$, 95% CI = 0.04 days earlier to 0.7 days later), after accounting for the effects of other variables.

The model that includes only sex and age as covariates of molt duration was clearly the best in the set (Table 8), but posterior distributions of coefficient estimates did not indicate either negative or positive correlation between duration of molt and either sex or age (Table 9).

Initiation date was strongly predictive of duration. Molt duration was 0.5 day shorter for every day that molt initiation was delayed ($n = 17$, 95% CI = 0.2 to 0.8 day shorter for every day delayed, $F_{1,15} = 11.14$, $r_{adj}^2 = 0.3878$, $P = 0.0045$; Figure 9).

Table 6. Candidate model set for molt initiation phenology in snowy plovers in Humboldt County, CA, from Oct 2014 to Apr 2015, with values for number of parameters (K), AICc, Δ AICc, and Akaike weights, based on AICc. Models are ordered by Δ AICc.

Model Structure	K	Log Likelihood	AICc	AICc Δ	Akaike Weight
initiation day ~ sex + age + hatch day + breeding location	7	-180.53	378.8	0	0.582
initiation day ~ sex + age + breeding location	6	-182.43	379.6	0.77	0.397
initiation day ~ sex + age + hatch day	5	-186.8	385.5	6.69	0.021
initiation day ~ sex + age	4	-191.11	391.4	12.63	0.001

Table 7. Model-averaged coefficient estimates for molt initiation phenology in snowy plovers in Humboldt County, CA, from Oct 2014 to Apr 2015.

Parameter	Estimate	Std Error	Adjusted SE	Lower 95% CI	Upper 95% CI
Intercept	145.94	26.53	27.04	92.94	198.94
Sex (M)	-70.97	11.13	11.54	-93.59	-48.35
Age	-4.47	4.31	4.46	-13.21	4.27
Hatch Day	0.33	0.18	0.19	-0.04	0.7
Breeding Location (RU2)	-42.96	14.76	15.28	-72.92	-13.01
Breeding Location (RU4)	72.64	32.91	34.16	5.69	139.6

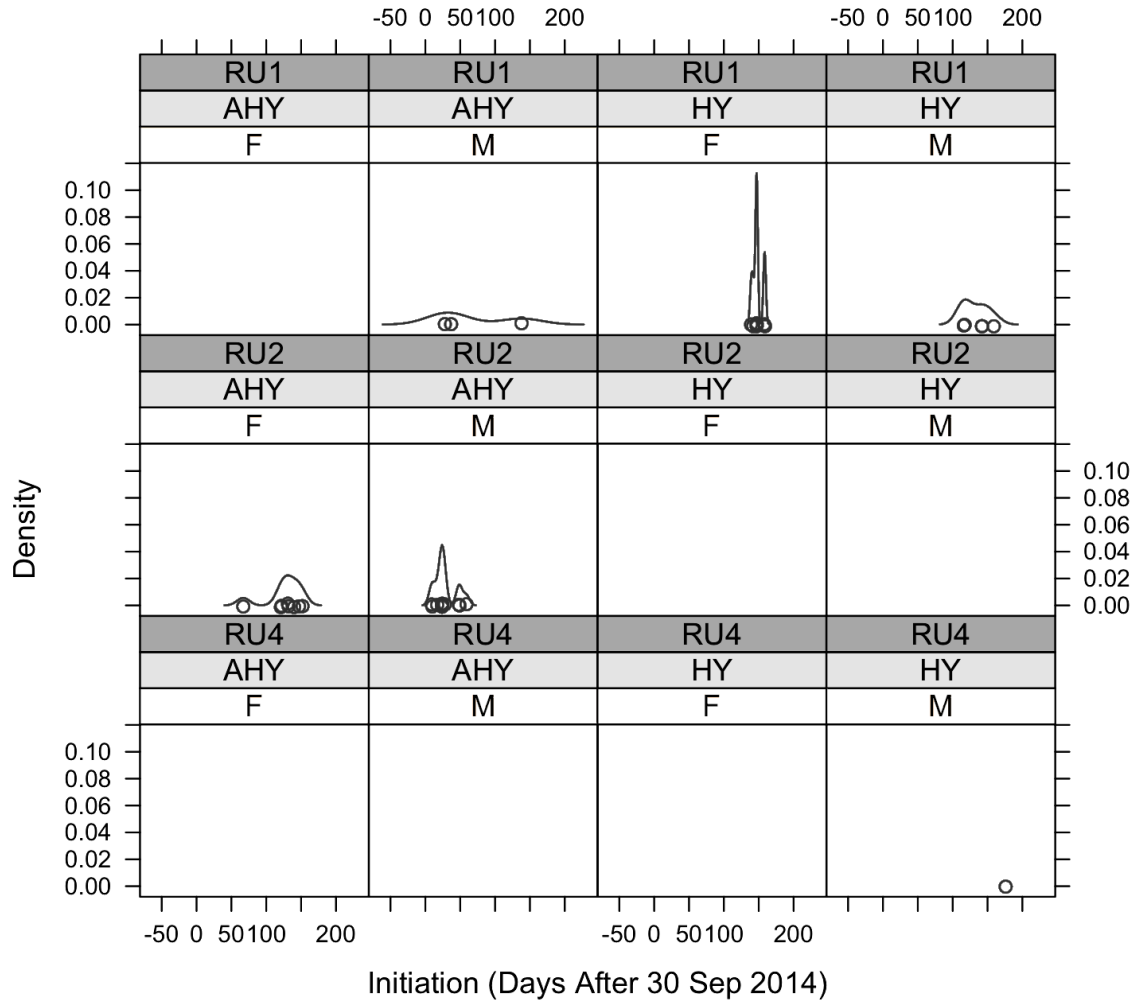


Figure 8. Density plots of prealternate molt initiations by category in snowy plovers in Humboldt County, CA, from Oct 2014 to Apr 2015 ($n = 38$). Each small circle represents one record.

Table 8. Candidate model set for duration of molt in snowy plovers in Humboldt County, CA, from Oct 2014 to Apr 2015, with values for number of parameters (K), AICc, Δ AICc, and Akaike weights, based on AICc. Models are ordered by Δ AICc.

Model Structure	K	Log Likelihood	AICc	AICc Δ	Akaike Weight
duration = sex + age	4	-46.443	108.9	0	0.958
duration = sex + age + hatch day	5	-45.399	115.8	6.91	0.03
duration = sex + age + breeding location	5	-46.337	117.7	8.79	0.012

Table 9. Model-averaged coefficient estimates for duration of prealternate molt in snowy plovers in Humboldt County, CA, from Oct 2014 to Apr 2015 ($n = 11$).

Parameter	Estimate	Std Error	Adjusted SE	Lower 95% CI	Upper 95% CI
Intercept	1.58	24.58	29.52	-56.27	59.43
Sex (M)	48.55	24.74	29.86	-9.98	107.07
Age	8.52	5.19	6.27	-3.77	20.81
Hatch Day	0.32	0.27	0.34	-0.34	0.99
Breeding Location (RU2)	27.15	31.19	40.91	-53.04	107.34

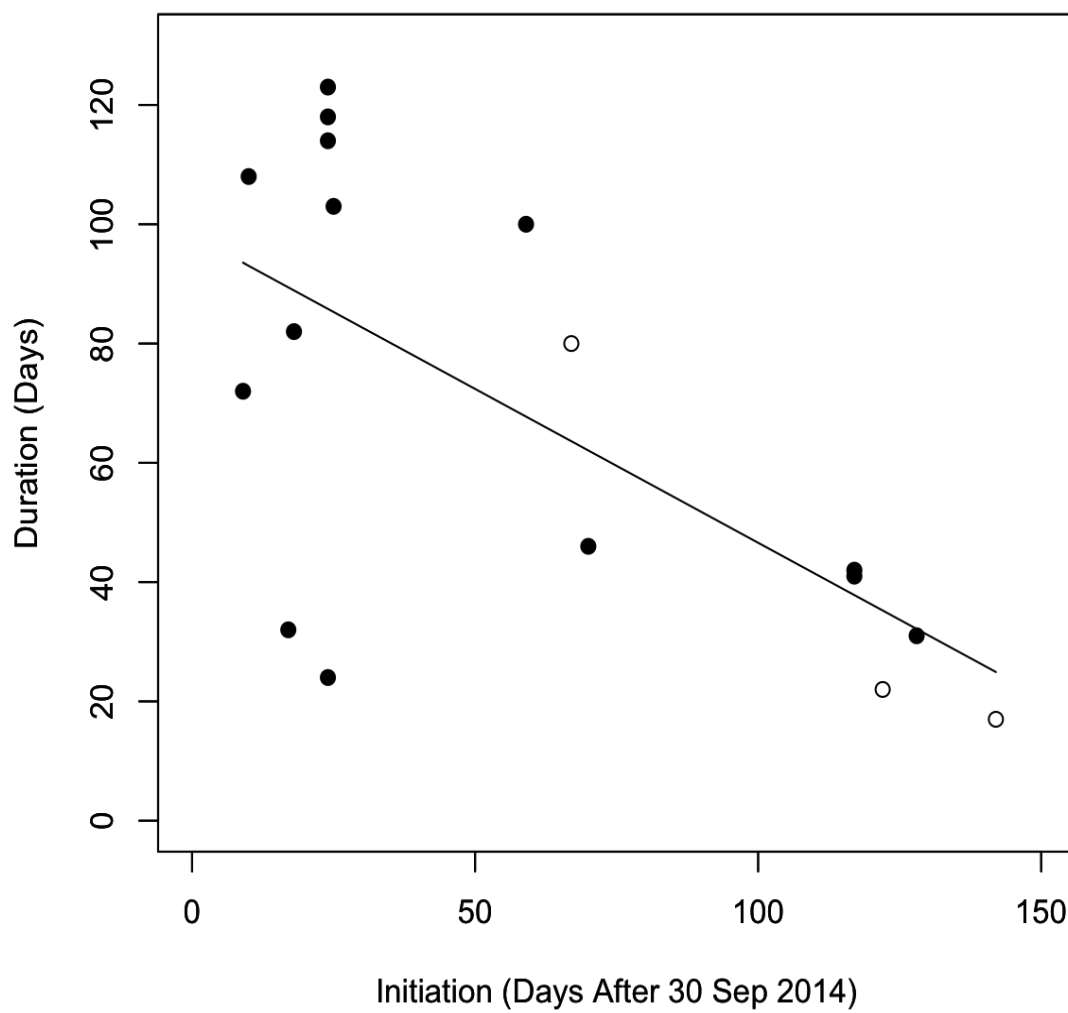


Figure 9. Duration regressed with initiation of prealternate molt in female (○) and male (●) snowy plovers in Humboldt County, CA, from Oct 2014 to Apr 2015.

DISCUSSION

This study enhances current knowledge of prealternate molt phenology in snowy plovers. Authorities on the molt of snowy plovers in North America have defined the period of the prealternate molt to be between January and April (Page *et al.* 2009, Pyle 2008), but my findings suggest that this range needs to be extended to begin in October. Males and residents of RU2 initiated molted earlier than females and migrants from RU1, and individuals that began molt earlier experienced longer durations on average.

Population Phenology of Prealternate Molt

European authors have described the prealternate molt of *Charadrius alexandrinus* with an earlier start than North American (Table 1), though they presumably summarized observations of Kentish plovers. Recent genetic findings have shown that Kentish and snowy plovers are paraphyletic (Küpper *et al.* 2009), so that observations of the Kentish plover's molts are of ambiguous value to describe those of snowy plovers. North American accounts reference museum collections and earlier works on both snowy and Kentish plovers (Palmer 1967, Pyle 2008, Page 2009). In North America, few specimens of western snowy plovers have been collected north of Marin County, California (108; VertNet 2015), and two major resources were written with collections in Texas (Oberholser 1974) and New York (Palmer 1967). Environmental conditions (particularly longer winter daylengths) in the southern areas

where observations or specimens were drawn from, would conceivably affect molt phenology differently than those obtaining in coastal northern California and Oregon, where this study was done.

Environmental conditions can affect physiological processes. For example, temperature, rainfall, or food availability have been shown to have varied impacts on gonadal maturation or egg-laying dates (Dawson 2008). Gonadal maturation may act as an intermediate driver of molt phenology. Since winter flocks of plovers do not appear to be separated by age or sex, show no territoriality around feeding areas, and they stay together in loose flocks on a daily basis (pers. obs.), environmental conditions would be likely to affect prealternate molt phenology on a population-wide scale.

Variation in Prealternate Molt Phenology

This study found an appreciable variety in prealternate molt phenology. This may be partly ascribed to the environmental conditions between two populations (RU1 and RU2), though they are only separated during the breeding season and that separation is neither particularly distinct nor great. If plovers have the same access to food resources and experience the same conditions in the winter flock, the remaining causes for physiological variation within the population are demographic or of individual quality. My finding that certain demographic groups predictably molted earlier implies that molt phenology is not random.

My observation of male-biased molt initiation dates in snowy plovers is surprisingly distinct. Sex difference in molt initiation date is described by some accounts of Kentish plovers, with earlier molt in males (Prater et al. 1977, Cramp and Simmons 1983). Across the plovers and their allies (Charadriidae), I find no mention of similarly biased timing (Howell 2010, Pyle 2008), but earlier molt in males is documented in the more distantly related ruff (*Calidris pugnax*; Montgomery 2015) and in bar-tailed godwits (Piersma and Jukema 1993). Since there is little literature devoted to prealternate molt in shorebirds, sex differences may be widespread, but little known. However, it was somewhat difficult to distinguish the initiations and completions of prealternate molt in some cases. The same feather tracts could look darker or more saturated in different lights or body postures (as evidenced in multiple photos taken on the same day). Some birds showed very subtle molt. The comparison between molt assessments of the same photos by two analysts revealed some subjective variation, especially in females (Appendix D). This could be addressed by an attempt to standardize photos in some way, or with more frequent observations, and may have caused a male-biased phenology to appear more distinct than it is.

I did not attempt to quantify the degree of melanization I observed in individuals in alternate plumage, but there is certainly variation in the saturation and extent of their dark facial markings. If bolder markings take longer to grow, as they do in house sparrows (Vágási *et al.* 2010), duration of molt is probably correlated to this "honest signal", as evidenced by the trend towards shorter durations in females (Figure 7).

Shorter durations in more subtly marked individuals would suggest that duration and extent are linked, as in the preformative molt of first-year wrentits (*Chamaea fasciata*), where late-hatching individuals molt fewer feathers (Elrod *et al.* 2011). Another study might attempt to quantify alternate plumage and correlate its boldness to the duration of prealternate molt.

There was correlation between location and initiation of prealternate molt between plovers documented in RU1 or RU2, with the latter beginning their molt earlier. Plovers in RU2 generally begin breeding in March (Colwell *et al.* 2015), but those in RU1 begin in April (Lauten *et al.* 2013). This study's two regions are adjacent, and large in extent, so that their average photoperiods are similar; this makes location as documented here an imprecise predictor of molt phenology (Appendix A). Also, I continued to record novel band combinations in winter flocks throughout the study period, which implies that individuals travelled singly from their breeding grounds, rather than in large groups (Appendix E). If so, each plover would exhibit a unique photoperiodicity in relation to its location over time. This variety might be significant enough to affect molt phenology in the individual. Earlier molt in more southern residents could be a result of earlier gonad recrudescence in response to favorable breeding conditions, or a direct response to less extreme changes in photoperiod. Further studies could use geolocators on individuals to correlate photoperiods to molt phenology, or study snowy plovers in more widely spaced regions.

Age may be a predictor of molt initiation. This study's sample was small in light of the number of parameters. The first year of molts in plovers is different than successive years, which may cause some variation in phenology between birds in their first year and older birds. Such a logistical trend is implied by a difference in means between the two age groups (Figure 10).

Hatch date was not indicated as a predictor of prealternate molt phenology, regardless of the variety in timing in prejuvenal and preformative molts enforced by a long hatching season. Similarly, though postjuvenile molt (i.e. preformative molt) was influenced by hatch date in blackcaps (*Sylvia atricapilla*), later molts were not (Pulido and Coppack 2004).

Despite significant differences within the population in molt initiation and duration, most of the population completed molt near the same time (Appendix G). Similarly, late initiation of wing molt in bar-tailed godwits was linked to shorter duration (Conklin and Battley 2012). This suggests that synchronization of completion is achieved on either the individual or population level. Individual physiologies may respond to environmental triggers or social cues. Social interaction has been observed to affect molt phenology in some cases (Dawson 2008). Certainly, my results indicate that further research into the physiology of molt phenology is merited.

Some plovers raise young late in the season (September; Warriner *et al.* 1986). This may delay prebasic molt, which may carry over in prealternate molt phenology. From other studies of molt, it appears that birds "catch up" with conspecifics after a delay

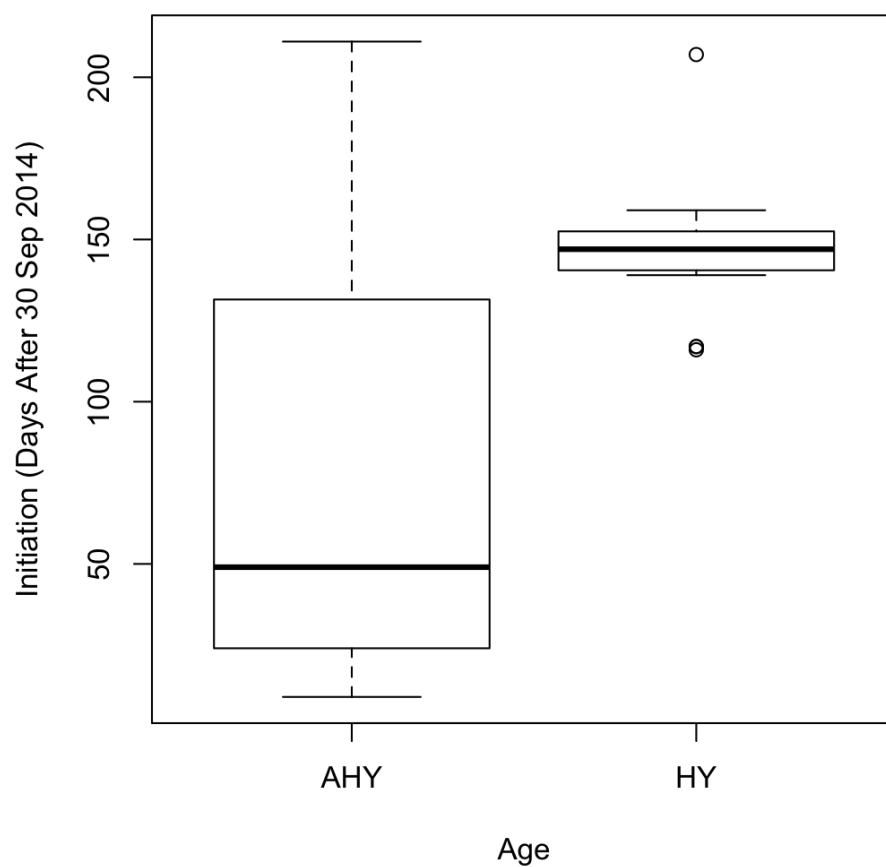


Figure 10. Difference in prealternate molt initiation phenology by age class (AHY = after-hatch-year, HY = hatch-year) in snowy plovers in Humboldt County, CA, from Oct 2014 to Apr 2015 ($n = 38$).

in the molt cycle (Conklin *et al.* 2013), especially when two events, like prebasic and prealternate molt in snowy plovers, are not immediately adjacent. Breeding success and its phenology might be used as a covariate in a future study of molt phenology.

The invertebrate prey of shorebirds have been observed to be less available in winter by burrowing more deeply in the substrate (Goss-Custard 1984). Food limitation has been found to cause either slower growth or lower quality feathers, or both (Grubb 2005), and to delay prealternate molt initiation (Danner *et al.* 2015). Plovers that either begin prealternate molt early or complete it late in spring may take advantage of higher productivity, or higher-quality individuals may forage more efficiently. I did not attempt to measure the quality of new alternate feathers or their extent, both of which may have been affected by shorter durations (Dawson *et al.* 2000, Rohwer and Rohwer 2013). Further research into the year-round availability of prey used by western snowy plovers along their west-coast range and studies of their foraging rates might be useful to predict molt phenology.

The great majority of molt studies have focused on flight-feather molt, which involves the growth of much bulkier feathers than in prealternate molt in snowy plovers. Perhaps the limited prealternate molt does not raise the metabolic rate significantly, and therefore available forage is not critical to prealternate molt. We still know very little about molt and its physiological triggers or costs, so this study poses more questions for further research.

Limitations

This analysis would have benefitted from a larger sample size. There was an indication that age could be predictive of molt phenology and it might have yielded a coefficient estimate with a larger sample. Also, the sample showed unequal representation among demographic categories that may have confounded results (Table 4). Though observers recorded 205 band combinations, many were not useful because of inconsistent observations and duplicate band combinations. In addition, a greater effort to locate birds on alternate sites would have strengthened the photo series of many plovers.

I noticed that the alternate plumage was not yet complete in some plovers I photographed on my last surveys, in mid-April. I removed individuals from the sample because molt was incomplete or not apparent in their last images. This has likely biased my results towards earlier molt in the population. A future study of prealternate molt in snowy plovers should include the month of May, which is specified as the latter part of the molt period in Kentish plovers by Ginn and Melville (1983).

Given the complexities of constructing a frequent, continuous series of high-quality photographs, I would endorse the approach used by Howell *et al.* (1999), in which the authors assessed molt *in situ* in a random sample of birds encountered in a series of visits. Though flocks of wintering plovers in Humboldt are fairly predictable, individuals

are mobile enough to make a study that targets specific plovers and spans many months a challenging task.

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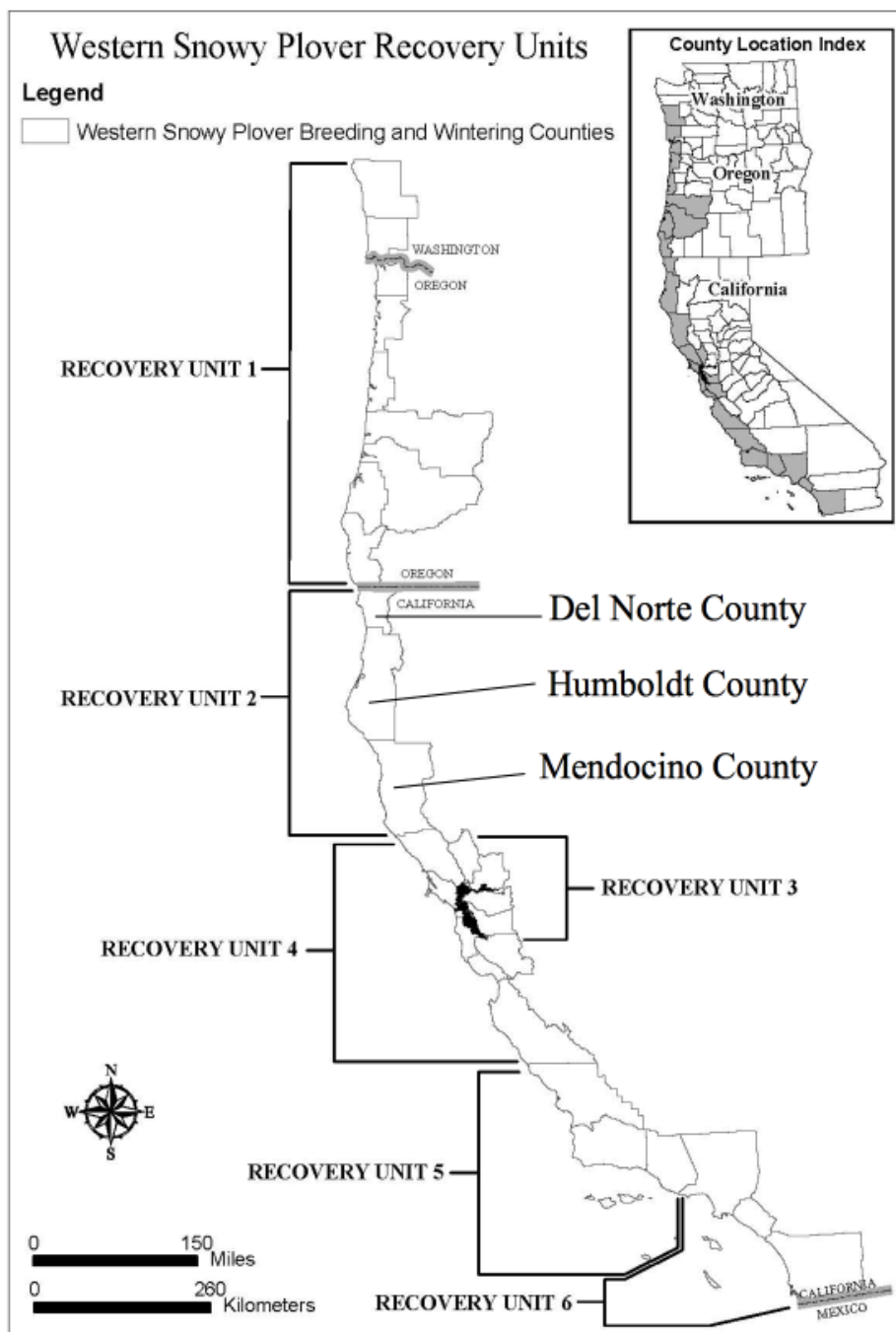
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APPENDIX A

Appendix A. A map of the U.S. range of the western snowy plover, divided into Recovery Units 1-6 (USFWS 2007).



APPENDIX B

Appendix B. Photo series of an exemplar individual, GV:RB. I assigned the 2nd image as the last in basic plumage, and calculated the median date between it and the next (10/16/14 and 11/02/14; median: 10/24/14). I assigned the 11th image (02/20/15; previous: 02/10/15) as the first in alternate plumage, and calculated the median completion date as 02/15/15. I converted median date to the number of days after 30 September 2014, and subtracted initiation date from completion date to get duration of molt.



Appendix B. (continued).



Appendix B. (continued).



Appendix B. (continued).



APPENDIX C

Appendix C. Calculated molt initiation and completion dates. I found the median date between those of the last image in basic plumage and the successive image to arrive at initiation date, and the median date between those of the first image in alternate plumage and the previous image to arrive at the completion date, if possible (continued next two pages).

Initiation of Prealternate Molt					Completion of Prealternate Molt				
Plover Color Combination	Date of Last Image in Basic Plumage	Date of Image After Last Basic Plumage	Median Date of initiation	Days Between Images	Date of Image Proceeding Alternate Plumage	Date of First Image in Alternate Plumage	Median Date of Completion	Days Between Images	Duration of Molt (Days)
WG:YO	10/03/14	10/15/14	10/09/14	12	12/06/14	01/02/15	12/19/14	27	72
X:O	10/04/14	10/16/14	10/10/14	12	01/19/15	02/01/15	01/25/15	13	108
RY:BG	10/15/14	10/22/14	10/18/14	7	01/02/15	01/14/15	01/08/15	12	82
WW:BB	10/16/14	10/18/14	10/17/14	2	11/10/14	11/25/14	11/17/14	15	32
GV:RB	10/16/14	11/02/14	10/24/14	17	02/10/15	02/20/15	02/15/15	10	114
GY:OW	10/16/14	11/02/14	10/24/14	17					
RY:BB	10/16/14	11/02/14	10/24/14	17					
RY:WG	10/16/14	11/02/14	10/24/14	17	12/01/14	12/18/14	12/09/14	17	46
VW:BR	10/16/14	11/02/14	10/24/14	17	11/10/14	11/25/14	11/17/14	15	24
VW:OW	10/16/14	11/02/14	10/24/14	17	02/10/15	02/28/15	02/19/15	18	118
W:BY	10/16/14	11/02/14	10/24/14	17	02/20/15	02/28/15	02/24/15	8	123
OR:YR	10/18/14	11/02/14	10/25/14	15	02/01/15	02/10/15	02/05/15	9	103
B/R/B:B	10/16/14	11/10/14	10/28/14	25					
GY:GR	10/16/14	11/10/14	10/28/14	25					
GY:OB	11/02/14	11/10/14	11/06/14	8					
A/W:Y	11/10/14	11/25/14	11/17/14	15					
GY:GW	11/11/14	11/25/14	11/18/14	14					
GY:BB	11/25/14	12/01/14	11/28/14	6	02/28/15	03/16/15	03/08/15	16	100
GY:BR	11/25/14	12/18/14	12/06/14	23	02/20/15	02/28/15	02/24/15	8	80
OR:WG	12/01/14	12/18/14	12/09/14	17					
WV:YY	12/06/14	12/18/14	12/12/14	12					
GY:BW	12/14/14	01/14/15	12/29/14	31					
GV:BB	01/03/15	01/15/15	01/09/15	12					
Y/L/Y:Y	12/14/14	03/06/15	01/24/15	82					

Appendix C. (continued).

Plover Color Combination	Initiation of Prealternate Molt				Completion of Prealternate Molt				
	Date of Last Image in Basic Plumage	Date of Image After Last Basic Plumage	Median Date of initiation	Days Between Images	Date of Image Proceeding Alternate Plumage	Date of First Image in Alternate Plumage	Median Date of Completion	Days Between Images	Duration of Molt (Days)
W/L/W:Y	01/19/15	02/01/15	01/25/15	13	02/28/15	03/14/15	03/07/15	14	41
YG:AA	01/19/15	02/01/15	01/25/15	13	02/28/15	03/16/15	03/08/15	16	42
RY:YB	01/14/15	02/14/15	01/29/15	31					
OR:OY	01/19/15	02/10/15	01/30/15	22	02/13/15	02/28/15	02/20/15	15	22
WV:YS	02/01/15	02/10/15	02/05/15	9	02/28/15	03/16/15	03/08/15	16	31
Y/L/Y:V	02/01/15	02/10/15	02/05/15	9					
WV:OS	01/14/15	03/01/15	02/06/15	46	01/14/15	03/01/15	02/06/15	46	0
W/R/W:Y	01/14/15	03/06/15	02/08/15	51	01/14/15	03/06/15	02/08/15	51	0
BL:GY	02/10/15	02/20/15	02/15/15	10					
LB:AY	02/10/15	02/20/15	02/15/15	10					
Y/B/Y:V	02/10/15	02/20/15	02/15/15	10					
AG:AB	02/10/15	02/21/15	02/15/15	11					
RY:GG	02/13/15	02/20/15	02/16/15	7					
A/Y/A:W	02/13/15	02/21/15	02/17/15	8					
B/A:Y	02/10/15	02/28/15	02/19/15	18					
GY:YB	02/10/15	02/28/15	02/19/15	18					
R/A:V	02/10/15	02/28/15	02/19/15	18					
W/R/W:V	02/10/15	02/28/15	02/19/15	18					
Y/W/Y:V	02/10/15	02/28/15	02/19/15	18	02/28/15	03/16/15	03/08/15	16	17
B/O/B:V	02/20/15	02/28/15	02/24/15	8					
L/R:Y	02/20/15	02/28/15	02/24/15	8					
RY:RR	02/20/15	02/28/15	02/24/15	8					
GY:YR	02/21/15	02/28/15	02/24/15	7					
WW:OB	02/21/15	02/28/15	02/24/15	7					
L/R/L:X	02/28/15	03/14/15	03/07/15	14					
GV:WG	02/28/15	03/16/15	03/08/15	16					
GV:WR	02/28/15	03/16/15	03/08/15	16					
O/W:Y	02/28/15	03/16/15	03/08/15	16					
GB:BA	03/15/15	04/04/15	03/25/15	20					

Appendix C. (continued).

	Median Date of Initiation	Days Between Images		Median Date of Completion	Days Between Images	Duration of Molt (Days)
means	01/04/15	16.9		01/27/15	16.3	67
standard deviations	54.121	12.740		37.181	11.595	41.709

APPENDIX D

Appendix D. Sample used to evaluate Kendall's Rank Correlation Coefficients (Kendall's Tau). Demographic categories are F = female, M = male, AHY = after-hatch-year, HY = hatch-year, RU2 or RU4 = Recovery Unit 2 or 4 location in breeding season.

Band Combination	Demographic Category	Analyst 1 initiation image	Analyst 2 initiation image	Kendall's Coefficient
AG:AB	F AHY RU2	13	13	1.00
GB:BA	M HY RU4	8	9	0.90
GV:BB	F AHY RU2	8	11	0.32
GV:RB	M AHY RU2	3	4	0.97
GY:BB	M AHY RU2	7	8	0.73
GY:BR	F AHY RU2	6	6	1.00
GY:OB	M AHY RU2	6	9	0.37
GY:OW	M AHY RU2	4	5	0.91
OR:OY	F AHY RU2	10	12	0.49
OR:YR	M AHY RU2	6	7	0.92
mean				0.77
standard deviation				0.27
mean (female)				0.71
mean (male)				0.80

Appendix E. (continued).

[illegible]

Appendix E. (continued).

Month	Oct				Nov							
Day	15	16	18	22	2	5	8	10	11	15	16	17
A/R:V												
A/W:Y		CN	CN		CN			CN	CN	CN		
A/Y/A:V												
A/Y/A:W		CN	CN		CN				CN	CN		
AG:AB		CN	CN		CN			CN	CN	CN		
B/A:Y						CV			CN		CV	
B/G:Y												
B/O:V		CN			CN							
B/O/B:V			CN		CN			CN	CN			
B/R:V		CN	CN									
B/R:Y		CN							CN			
B/R/B:B		CN	CN					CN				
B/R/B:V												
B/W/B:G		CN										
B/Y/B:G		CN			CN				CN	CN		
B/Y/B:V												
BL:GY		CN	CN		CN			CN	CN			
BS:BW												
BS:GW		CN										
BS:OG		CN			CN			CN		CN		
BS:RW		CN	CN		CN			CN	CN	CN		
BS:WR					CN							
BW:RW												
G/B/G:Y					CN					CN		
G/W:V												
G/W/G:V												
G/Y:V												
G:B		CN										
GB:BA	CV			CV		CV	CV				CV	

Appendix E. (continued).

Month	Nov	Dec						Jan				
Day	25	1	5	6	13	14	18	2	3	14	15	19
A/R:V												
A/W:Y	CN	CN			CN		CN		CN		CN	CN
A/Y/A:V												
A/Y/A:W		CN			CN		CN		CN		CN	CN
AG:AB	CN				CN		CN		CN		CN	CN
B/A:Y		CN					CN		CN		CN	CN
B/G:Y		CN										
B/O:V												
B/O/B:V	CN						CN		CN		CN	CN
B/R:V	CN	CN							CN			
B/R:Y		CN			CN							
B/R/B:B	CN	CN					CN		CN			
B/R/B:V									CN			
B/W/B:G												
B/Y/B:G	CN	CN			CN		CN		CN		CN	CN
B/Y/B:V												
BL:GY	CN	CN			CN		CN		CN		CN	CN
BS:BW												
BS:GW												
BS:OG												
BS:RW	CN	CN					CN		CN			
BS:WR					CN							
BW:RW												
G/B/G:Y	CN	CN					CN		CN		CN	CN
G/W:V												
G/W/G:V												
G/Y:V												
G:B												
GB:BA			CV	CV		CV				CV		

Appendix E. (continued).

Month	Feb					Mar		Apr			
Day	1	10	13	14	28	1	16	4	5	10	12
A/R:V											
A/W:Y			CN		CN						
A/Y/A:V											
A/Y/A:W	CN		CN		CN		CN				
AG:AB											
B/A:Y	CN		CN		CN		CN				
B/G:Y											
B/O:V	CN										
B/O/B:V	CN	CN			CN						
B/R:V											
B/R:Y											
B/R/B:B	CN		CN								
B/R/B:V			CN								
B/W/B:G											
B/Y/B:G											
B/Y/B:V											
BL:GY	CN		CN				CN				
BS:BW											
BS:GW											
BS:OG											
BS:RW											
BS:WR											
BW:RW											
G/B/G:Y	CN		CN		CN						
G/W:V											
G/W/G:V											
G/Y:V											
G:B											
GB:BA								CV		CV	

Appendix E. (continued).

Month	Jul			Aug									
Day	21	28	30	1	4	7	8	11	15	16	18	19	21
GG:RY													
GR:BW													
G(R)S:GW													
GR:YB													
G(W)S:AR		CN			CN	CN		CN			CN		CN
GS:OB													
GS:WO											CN		
GS:WR				CV									CN
G(Y)S:BW							CV		CV				
GV:BB	CN		CN		CN	CN					CN		
GV:BR													
GV:BY											CN		CN
GV:GB													
GV:RB	CN	CN	CN			CN					CN		CN
GV:RY													
GV:WG													
GV:WR													
GV:YR		CN	CN		CN	CN							CN
GW:BW													
GW:GW													
GY:BB													
GY:BR			CN			CN					CN		
GY:GW													
GY:GR	CN	CN	CN			CN		CN			CN		CN
GY:OB												CN	CN
GY:OW	CN	CN	CN		CN	CN					CN		CN
GY:RR	CN	CN	CN			CN					CN		CN

Appendix E. (continued).

Month	Aug	Sep									Oct		
Day	29	2	3	8	16	17	19	21	29	30	1	3	4
GG:RY					CN								
GR:BW													
G(R)S:GW			CV			CV						CV	
GR:YB													
G(W)S:AR		CN			CN			CN		CN			CN
GS:OB													
GS:WO		CN											
GS:WR		CN			CN			CN				CV	
G(Y)S:BW			CV			CV							
GV:BB		CN			CN					CN			CN
GV:BR													
GV:BY		CN		CN	CN								CN
GV:GB													
GV:RB		CN			CN				CN	CN			CN
GV:RY						CV	CV						
GV:WG				CN						CN			CN
GV:WR				CN						CN			
GV:YR									CN				CN
GW:BW					CN					CN			CN
GW:GW													
GY:BB					CN								CN
GY:BR					CN					CN			
GY:GW													CN
GY:GR		CN		CN	CN			CN		CN			CN
GY:OB		CN		CN	CN			CN		CN			CN
GY:OW		CN			CN			CN		CN			CN
GY:RR				CN	CN								

Appendix E. (continued).

Month	Oct				Nov							
Day	15	16	18	22	2	5	8	10	11	15	16	17
GG:RY												
GR:BW		CN										
G(R)S:GW	CV			CV		CV					CV	
GR:YB												
G(W)S:AR		CN	CN		CN			CN	CN			
GS:OB				CV								
GS:WO												
GS:WR				CV		CV	CV		CN		CV	
G(Y)S:BW	CV					CV					CV	
GV:BB		CN	CN		CN				CN			
GV:BR		CN										
GV:BY		CN	CN		CN				CN			
GV:GB												
GV:RB		CN			CN			CN				
GV:RY		CN	CN						CN		CV	
GV:WG		CN			CN				CN			
GV:WR		CN	CN		CN				CN	CN		
GV:YR		CN			CN			CN				
GW:BW			CN		CN				CN			
GW:GW												
GY:BB		CN	CN		CN			CN	CN	CN		
GY:BR		CN	CN		CN				CN	CN		
GY:GW		CN	CN		CN			CN	CN			
GY:GR		CN			CN			CN	CN	CN		
GY:OB		CN	CN		CN			CN	CN	CN		
GY:OW		CN			CN							
GY:RR		CN	CN		CN							

Appendix E. (continued).

Month	Feb					Mar		Apr			
Day	1	10	13	14	28	1	16	4	5	10	12
GG:RY											
GR:BW											
G(R)S:GW						CV					
GR:YB							CN				
G(W)S:AR											
GS:OB											
GS:WO											
GS:WR											
G(Y)S:BW											
GV:BB	CN						CN		CN		
GV:BR											
GV:BY	CN		CN								
GV:GB	CN										
GV:RB	CN		CN		CN		CN		CN		CN
GV:RY											
GV:WG	CN		CN		CN		CN				
GV:WR			CN		CN		CN				
GV:YR											
GW:BW											
GW:GW											
GY:BB	CN		CN		CN		CN		CN		
GY:BR	CN		CN				CN		CN		CN
GY:GW	CN		CN		CN						
GY:GR	CN				CN		CN				
GY:OB	CN		CN								
GY:OW	CN				CN				CN		
GY:RR							CN				

[illegible]

Appendix E. (continued).

[illegible]

Appendix E. (continued).

Month	Nov	Dec						Jan				
Day	25	1	5	6	13	14	18	2	3	14	15	19
GY:WG												
GY:YB		CN					CN		CN		CN	CN
GY:YG												
GY:YR	CN	CN			CN		CN		CN		CN	
L/B/L:V												
L/G/L:V		CN										
L/G:V	CN	CN	CV	CV		CV			CN	CV		
L/O:Y			CV			CV		CV		CV		
L/O:Y												
L:R												
L/R:B, f	CN				CN		CN					
L/R:B, m	CN				CN		CN		CN		CN	CN
L/R/L:V												
L/R/L:X					CN							
L/R:Y	CN	CN			CN				CN		CN	CN
L/W/L:R				CV		CV						
L/Y/L:V					CN				CN			
L/Y:V												
LB:AY		CN			CN		CN		CN		CN	CN
LS:GW												
O/G:Y												
O/L:B						CV						
O/L:Y												
O/R:B												
O/R/O:Y												
O/R:V												
O/R:V	CN	CN			CN		CN		CN		CN	
O/W:Y	CN	CN			CN				CN		CN	CN
O:Y							CN			CV	CN	

Appendix E. (continued).

[illegible]

Appendix E. (continued).

[illegible]

Appendix E. (continued).

Month	Jul			Aug									
Day	21	28	30	1	4	7	8	11	15	16	18	19	21
RY:YW			CN		CN						CN		CN
S:B	CN		CN		CN	CN					CN		CN
S:B													
S:G, f		CN											
S:R													
S:V													
S:V			CN			CN					CN		CN
S:X									CV				
VW:BO													
VW:BR	CN		CN			CN					CN		CN
VW:OW	CN	CN	CN		CN			CN			CN		CN
VW:YB									CV				
VW:YY	CN	CN	CN			CN					CN		
W:BY					CN	CN					CN		CN
W:O											CN		
W/O:Y													
W/A/W:B													
W/A/W:R													
W/A/W:V													
W/A/W:Y													
W/B/W:R													
W/B/W:V			CN			CN							
W/G/W:V													
W/L:V													
W/L/W:Y													
W/L/W:X													
W/O/W:V													
W/R:B													
W/R/W:B								CN					

[illegible]

Appendix E. (continued).

Month	Aug	Sep									Oct		
Day	29	2	3	8	16	17	19	21	29	30	1	3	4
W/R/W:V					CN								
W/R/W:Y													
W:V													
W/Y:V					CN								CN
W/Y/W:R											CV		
W/Y/W:V													
WG:RR													
WG:WV													
WG:YO	CV		CV			CV						CV	
WV:BB				CN						CN			
WV:BG							CV						
WV:BR									CN	CN			CN
WV:BS					CN							CV	CN
WV:BW									CN	CN			CN
WV:BY													
WV:G(G)S							CV					CV	
WV:O(B)S							CV					CV	
WV:OW													
WV:R(R)S	CV		CV			CV						CV	
WV:RW													
WV:WW				CN				CN		CN			CN
WV:YB							CV						
WV:YS													CN
WV:YY			CV			CV	CV					CV	
WW:BB		CN			CN					CN			
WW:BS			CV			CV						CV	
WW:OB		CN						CN		CN			CN

Appendix E. (continued).

Month	Oct				Nov							
Day	15	16	18	22	2	5	8	10	11	15	16	17
W/R/W:V		CN			CN			CN	CN	CN		
W/R/W:Y						CV					CV	
W:V												
W/Y:V		CN	CN									
W/Y/W:R	CV			CV		CV	CV					
W/Y/W:V									CN			
WG:RR												
WG:WV												
WG:YO	CV			CV		CV	CV				CV	
WV:BB												
WV:BG												
WV:BR		CN	CN		CN				CN	CN		
WV:BS	CV			CV		CV	CV				CV	
WV:BW			CN		CN			CN	CN	CN		
WV:BY					CN							
WV:G(G)S	CV			CV		CV					CV	
WV:O(B)S	CV			CV		CV	CV				CV	
WV:OW											CV	
WV:R(R)S	CV			CV		CV					CV	
WV:RW												
WV:WW		CN			CN			CN	CN	CN		
WV:YB												
WV:YS		CN	CN		CN			CN	CN	CN		
WV:YY				CV		CV					CV	
WW:BB		CN	CN		CN			CN	CN			
WW:BS	CV			CV		CV	CV				CV	
WW:OB		CN	CN		CN			CN	CN	CN		

Appendix E. (continued).

Month	Nov	Dec						Jan				
Day	25	1	5	6	13	14	18	2	3	14	15	19
W/R/W:V							CN		CN			
W/R/W:Y						CV				CV		
W:V							CN					
W/Y:V												
W/Y/W:R			CV	CV		CV						
W/Y/W:V												
WG:RR												
WG:WV												
WG:YO			CV	CV		CV	CN	CV		CV		
WV:BB												
WV:BG												
WV:BR					CN		CN		CN		CN	CN
WV:BS			CV	CV		CV						
WV:BW	CN	CN			CN		CN		CN		CN	CN
WV:BY		CN										
WV:G(G)S			CV	CV		CV		CV		CV		
WV:O(B)S				CV		CV		CV		CV		
WV:OW						CV						
WV:R(R)S			CV	CV		CV		CV		CV		
WV:RW						CV						
WV:WW					CN		CN		CN		CN	CN
WV:YB												
WV:YS	CN	CN			CN		CN		CN		CN	CN
WV:YY						CV				CV		
WW:BB		CN			CN		CN		CN		CN	CN
WW:BS				CV		CV						
WW:OB		CN			CN		CN		CN		CN	CN

Appendix E. (continued).

Month	Feb					Mar		Apr			
Day	1	10	13	14	28	1	16	4	5	10	12
W/R/W:V	CN		CN		CN						
W/R/W:Y								CV			
W:V											
W/Y:V											
W/Y/W:R											
W/Y/W:V											
WG:RR											
WG:WV											
WG:YO				CV		CV		CV		CV	
WV:BB											
WV:BG											
WV:BR	CN		CN		CN						
WV:BS											
WV:BW			CN		CN		CN		CN		
WV:BY											
WV:G(G)S				CV		CV					
WV:O(B)S						CV					
WV:OW											
WV:R(R)S											
WV:RW											
WV:WW	CN		CN		CN		CN				
WV:YB											
WV:YS	CN		CN		CN		CN				
WV:YY				CV		CV					
WW:BB	CN		CN				CN		CN		CN
WW:BS											
WW:OB	CN		CN		CN						

Appendix E. (continued).

Month	Jul			Aug									
Day	21	28	30	1	4	7	8	11	15	16	18	19	21
WW:OW			CN			CN					CN		CN
W:Y													
X:O	CN		CN			CN					CN		CN
X:R													
X:R													
X:R, m	CN	CN	CN		CN								
X:S													
X:S (pale)				CV									
X:S, m			CN		CN				CV				
X:W (pale)				CV			CV		CV				
X:W													
X:W													
X:Y													
X:Y				CV									
X:Y, m		CN											
Y:V													
Y/B/Y:B													
Y/B/Y:G			CN										
Y/B/Y:V													
YG:AA													
Y/L/Y:V													
Y/L/Y:Y													
Y/O:B													
Y/O:V					CN								
Y/O/Y:B													
Y/O/Y:V													
Y/R:B, f					CN								

Appendix E. (continued).

Month	Aug	Sep									Oct		
Day	29	2	3	8	16	17	19	21	29	30	1	3	4
WW:OW		CN			CN			CN	CN	CN			CN
W:Y													
X:O		CN			CN			CN					CN
X:R										CN			CN
X:R													
X:R, m													
X:S													CN
X:S (pale)			CV			CV						CV	
X:S, m			CV							CN			
X:W (pale)			CV			CV						CV	
X:W													
X:W												CV	
X:Y													CN
X:Y	CV												
X:Y, m													
Y:V		CN											
Y/B/Y:B										CN			
Y/B/Y:G										CN			
Y/B/Y:V													
YG:AA													
Y/L/Y:V					CN			CN		CN			
Y/L/Y:Y										CN			
Y/O:B		CN											
Y/O:V		CN						CN		CN			CN
Y/O/Y:B													
Y/O/Y:V					CN								
Y/R:B, f					CN								

Appendix E. (continued).

Month	Oct				Nov							
Day	15	16	18	22	2	5	8	10	11	15	16	17
WW:OW		CN										
W:Y												
X:O		CN	CN		CN			CN	CN			
X:R					CN				CN	CN		
X:R									CN			
X:R, m		CN	CN		CN			CN	CN			
X:S		CN			CN				CN			
X:S (pale)												
X:S, m	CV		CN	CV		CV	CV				CV	
X:W (pale)	CV			CV	CN	CV	CV				CV	
X:W		CN							CN			
X:W	CV			CV		CV	CV				CV	
X:Y					CN			CN	CN	CN		
X:Y												
X:Y, m			CN									
Y:V												
Y/B/Y:B												
Y/B/Y:G								CN				
Y/B/Y:V			CN		CN				CN	CN		
YG:AA							CV			CN		
Y/L/Y:V			CN		CN				CN	CN		
Y/L/Y:Y	CV			CV		CV	CV				CV	
Y/O:B												
Y/O:V		CN	CN								CV	
Y/O/Y:B												
Y/O/Y:V												
Y/R:B, f					CN							

[illegible]

[illegible]

APPENDIX F

Appendix F. Data set used to model molt initiation and duration. I calculated duration by subtracting initiation date from completion date. Sex, age, hatch, and breeding location data came from monitoring efforts by the Western Snowy Plover Recovery Team. F = female, M = male, RU1, 2, or 4 = Recovery Unit 1, 2, or 4.

Band Combination	Initiation (Days After 30 Sep 2014)	Duration (Days)	Sex	Age (Years)	Hatch (Days After 1 Mar)	Breeding Location
WGYO	9	72	M	4	65	RU2
XO	10	108	M	2	155	RU2
WWBB	17	32	M	2	52	RU2
GVRB	24	114	M	3	139	RU2
GYOW	24	NA	M	6	162	RU2
RYBB	24	NA	M	3	116	RU2
RYWG	24	46	M	3	148	RU2
VWOW	24	118	M	8	132	RU2
BRBB	28	NA	M	3	138	RU1
GYGR	28	NA	M	5	120	RU2
GYOB	37	NA	M	3	135	RU1
AWY	48	NA	M	2	88	RU2
GYGW	49	NA	M	5	140	RU2
GYBB	59	100	M	3	109	RU2
GYBR	67	80	F	2	42	RU2
YLYY	116	NA	M	1	121	RU1
WLWY	117	41	M	1	125	RU1
YGAA	117	42	M	1	153	RU1
RYYB	121	NA	F	4	114	RU2
OROY	122	22	F	3	77	RU2
WRWY	131	0	F	1	154	RU2
GVBB	132	NA	F	5	89	RU2
LBAY	138	NA	M	2	155	RU1
RYGG	139	NA	F	1	112	RU1
AYAW	140	NA	F	5	140	RU2
BAY	142	NA	M	1	142	RU1
RAV	142	NA	M	1	106	RU1
YWYV	142	17	F	1	100	RU1
BOBV	147	NA	F	1	137	RU1
GYR	147	NA	F	1	131	RU1
LRY	147	NA	F	1	137	RU1
RYRR	147	NA	F	1	101	RU1
WWOB	147	NA	F	2	113	RU2
GYRB	152	NA	F	4	114	RU2
LRLX	158	NA	F	1	73	RU1
GVWR	159	NA	M	1	191	RU1
OWY	159	NA	F	1	131	RU1
GBBA	176	NA	M	1	166	RU4

APPENDIX G

Appendix G. Observed initiation (□) and completion (■) dates of prealternate molt in snowy plovers in Humboldt County, CA, from Oct 2014 to Apr 2015 (n = 53).

