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Cross-seasonal effects, where conditions in one season can have consequences in a following season, can have population-level implications for migratory species. To assess the presence of cross-seasonal effects on a migratory dabbling duck population, we examined the relative importance of habitat conditions in multiple seasons on the subsequent productivity of Northern Pintail (*Anas acuta*) that winter in the Pacific Flyway of North America. Our results indicate that during the period from 1961-2013 habitat conditions during spring staging in Southern Oregon North East California (SONEC) influence the subsequent productivity of pintail, and that the influence of habitat conditions during spring migration was stronger than the relationship between productivity and conditions on the breeding ground and wintering grounds. The association of pintail productivity with habitat conditions differed between early (1961-1985) and recent (1986-2013) time periods for all seasons. Cross-seasonal relationships were comparatively strong in the early years, and weakened or dissolved during the later years, which may indicate a change in how the pintail population is responding to environmental change throughout their annual cycle.

Evidence for Cross-Seasonal Effects: Insights from Long-term Data on Northern Pintail

by
Megan Zarzycki

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APPROVED:

Major Professor, representing Wildlife Sciences

Head of the Department of Fisheries and Wildlife

Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Megan Zarzycki, Author

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INTRODUCTION

Conditions and events in one season that interact to influence changes in reproduction or behavior of a species in another are termed seasonal interactions or cross-seasonal effects (Myers 1981, 1983, Webster et al. 2002). One of the earliest described occurrences of cross-seasonal influences in migratory birds was identification of the critical role of pre-laying nutrient reserves on reproductive performance in Lesser Snow Geese (*Chen caerulescens caerulescens*) (Ankney & MacInnes 1978), and later the role of winter habitat conditions on subsequent reproduction in Mallards (*Anas platyrhynchos*) and Northern Pintails (*Anas acuta*; Heitmeyer & Fredrickson 1981, Kaminski & Gluesing 1987, Raveling & Heitmeyer 1989). From a conservation perspective, an understanding of cross-seasonal influences is a critical mechanism linking habitats on breeding, migration, and wintering grounds that can galvanize actions to coordinate conservation policy across large geographic scales and political boundaries (Jones & Creswell 2010).

Since early work in the 1970s, many subsequent studies have expanded our understanding of cross-seasonal effects on diverse groups of birds, including Black-throated Blue Warblers (*Dendroica caerulescens*) (Sillett et al. 2000), Barn Swallows (*Hirundo rustica*) (Saino et al. 2004), American Redstarts (*Setophaga ruticilla*) (McKeller et al. 2013), and Eurasian Oystercatchers (*Haematopus ostralegus)* (Duriez et al. 2012), but waterfowl continue to be an ideal model species group for exploring the role of cross-seasonal effects on the population dynamics of migratory birds (Nichols 2007, Jónsson 2009). Waterfowl undergo highly visible migrations and congregate in large numbers on wintering and migration areas. Additionally, their importance as a game species has led to a large body of research and monitoring such that for many species in North America there is extensive documentation of vital rates, distribution, and movements throughout the annual cycle. Although evidence for cross-seasonal effects from weather and habitat conditions during the non-breeding season for waterfowl is extensive at the individual level (Sedinger & Alisaukas 2014), it remains difficult to measure effects on a population level and comparatively few studies have linked habitat conditions during spring migration to productivity (Anteau & Afton 2004). The critical importance of nutrients acquired during spring migration and staging however has been well-documented in waterfowl (Ankney & Alisauskas 1991, Alisauskas & Ankney 1992), and improved body condition and nutritional state over winter and especially in spring allows for earlier migration and nest initiation, which has been shown to improve reproductive effort of females (Devries et al. 2008, Arnold et al. 2010).

Northern pintail are capitol breeders who spend a larger proportion of their annual cycle in non-breeding habitats, so nutrient acquisition and body condition carried over from these areas is likely of considerable importance to population productivity (Cox et al. 1998). Consistent with those linkages, Raveling and Heitmeyer (1989) found a direct correlation between winter habitat conditions in California’s Central Valley and the juvenile to adult age ratio in birds harvested by hunters the following fall. A recent reanalysis and expansion of the original Raveling and Heitmeyer paper found that despite widespread changes to habitat since 1989, the presence of cross-seasonal effects between wintering grounds and breeding productivity remains (Osnas et al. 2016). While that work confirmed pintail can be influenced by winter habitat conditions, how the relationship may have changed over time and the importance of habitats used during migration were not considered. In the 28 years since Raveling and Heitmeyer’s (1989) original publication habitat conditions on both the breeding and non-breeding grounds have undergone large, landscape-level changes in composition influenced by many factors including agricultural practices, urban encroachment, habitat restoration activities, and climate change.

Here we further test for the occurrence of cross-seasonal effects in Northern Pintails, examining how breeding productivity may be influenced by environmental conditions experienced throughout their annual cycle. Specifically, our objectives were to test: 1) if habitat conditions on a major spring staging area are associated with subsequent breeding productivity; 2) compare the relative importance of wetland habitat conditions during winter, spring staging, and breeding grounds on productivity; and 3) if the relationship between habitat conditions during winter and pintail productivity has changed since the original analyses in Raveling and Heitmeyer (1989).

LITERATURE REVIEW

IMPORTANCE OF THE NON-BREEDING SEASON

Seasonal habitats may be altered by environmental conditions on local and larger climatic scales, and even slight changes in climate patterns may cause large effects on populations (Aubry et al. 2013). For waterfowl, environmental variability operating through local weather patterns, large-scale climate fluctuations, and direct habitat changes have all been found to impact populations throughout their annual cycle (Almaraz & Amat 2004, Ward et al. 2005, Sedinger et al. 2006, Morrissette et al. 2010).

Across North America, changes in the abundance and distribution of waterfowl have been widely linked to changing environmental and habitat conditions, both through natural processes (environmental stochasticity) as well as human-induced changes (habitat modification, harvest) (Fleskes et al. 2005, Almaraz et al. 2012, Aubry et al. 2010). Land-use changes have influenced the productivity and survival of many species utilizing and occupying agricultural habitats, while changes in the abundance and persistence of wetland habitats has been implicated in declines of wetland dependent species (Fleskes & Gregory 2010). Additionally, changes in climatic conditions have been linked to changes in the demography and distribution of some species of waterfowl, for example, through changes in the frequency of severe weather events and invertebrate food availability (Frederiksen et al. 2008). Much of this work has focused on capital breeders that rely on stored reserves from non-breeding grounds, such as geese and eider species, but the population level consequences of seasonal interactions in dabbling ducks remains less well understood (Gill et al. 2001, Gunnarsson et al. 2005, Reudink et al. 2009).

The use of stored nutrient reserves has been documented in several dabbling duck species, mainly mallards and pintails, but the extent to which dabbling duck females may rely on stored nutrient reserves and their contribution to egg laying incubation varies greatly interspecifically (Devries et al. 2008, Arnold et al. 2013). Reliance on endogenous reserves for breeding and clutch size is highly correlated with stored nutrient levels, which are generally acquired over winter and at spring staging grounds (Mann & Sedinger 1993, Esler & Grand 1994, Dubovsky & Kaminski 1994). Poor body condition at the onset of breeding can result in decreased fledging success (Lehikoinen et al. 2006) and delayed and non-breeding in waterfowl (Coulson 2013), and nest success declines with initiation date through the breeding season (Klet & Johnson 1982, Greenwood et al. 1995, Emery et al. 2005). Despite variation in stored nutrient levels between dabbling duck species, improved body condition over winter allows for earlier migration and nest initiation, which has been shown to improve reproductive effort of hens (Howerter et al. 2014). The body condition of female mallards (*Anas platyrhynchos*) at arrival on the breeding grounds has been found to positively correlate with clutch size, nesting propensity, and the timing of nest initiation and hatch, all influencing subsequent reproductive success, demonstrating the importance of late winter and early spring nutrient acquisition in a temperate breeding dabbling duck (Krapu 1981, Devries 2008).

Historically pintail showed changes in population size that were directly correlated with breeding ground wetland conditions, however unlike other duck species this relationship has degraded since the 1980's (Nicolai et al. 2005). The failure of the pintail population to respond to improved conditions on the breeding grounds has drawn the focus more closely to the role of the non-breeding season, as well as the influence of anthropogenic changes to their habitat and management (Mattsson et al. 2012). Pintail also spend a larger proportion of their annual cycle in non-breeding habitats than most dabbling duck species, so winter and spring survival and body condition is likely of more importance to subsequent breeding attempts than for other duck species (Cox et al. 1998), influencing reproductive output and potentially recruitment and population growth rates (Blums 2002, Blums & Clark 2004).

WEATHER EFFECTS ON WATERFOWL

The influence of weather on wetland dependent species is likely a reflection of the role local climate plays in altering the quality and quantity of wetland habitats across broad spatial scales (Johnson et al. 2005). Variation in temperature and precipitation regimes can cause considerable annual and seasonal differences in abundance, distribution, and persistence of wetland habitats in both breeding and non-breeding seasons (Haukos & Smith 1993, 2003, Sorenson et al. 1998). These fluctuations can lead to a myriad of climate-driven changes in habitat and food availability, including plant species and aquatic invertebrates that many waterfowl species rely on (van der Valk 1989, Johnson et al. 2005). Changes in resource and habitat availability can act on wildlife populations through a wide range of mechanisms (Norris & Marra 2007), and in waterfowl weather variables such as precipitation have been tied to changes in survival (Blums et al. 2002), body condition (Bergan & Smith 1993, Smith & Sheeley 1993), and reproductive success (Jonsson et al. 2009, Jonsson et al. 2013).

Climate change is predicted to disproportionately influence wetland habitats due to their sensitivity to alterations in weather patterns, and may cause changes in hydrology, biogeochemistry, and function (IPCC 2014). Spring melt of snowpack is a major contributor to wetland areas and flooded fields that are heavily used by pintail for spring staging and migration, such as southern Oregon northeastern California (SONEC) (Bishop & Vrtiska 2008, Fleskes & Gregory 2010). In the past 100 years, snowpack in the Pacific Northwest has decreased upwards of 10 percent (Mote et al. 2005). This reduction in snow derived water may reduce available habitat during a critical period for pintail, and may be exacerbated by changes in precipitation, temperature, and drought frequency in the area. Potential effects of weather on population size and success could increase with widespread global climate change, as changes in means and variance of temperature, precipitation, and weather extremes are predicted (Mote & Salathe 2010, McIntyre et al. 2014). In order to understand the potential effects of climate change on population dynamics, the effects of historical and naturally-occurring climate fluctuations must be explored (Stenseth et al. 2002, Lande et al. 2003).

Waterfowl species reliance on wetland and flooded habitats makes them especially vulnerable to drought, which reduces water availability and can restrict summer irrigations, reduce seed production, and delay fall flooding (Johnson et al. 2005). Drought may reduce habitat availability and increase the prevalence of disease outbreaks, such as avian cholera and botulism, which can cause mass mortality events in the non-breeding season (Sorenson et al. 1998). Drought may lead to immune-suppression, increased energy costs, and the concentration of large numbers of waterfowl in small areas, leading to rapid infection rates and movement among populations (Hestbeck 1995, Traill et al. 2009) and difficulties in finding food for many species of waterfowl (Bataille & Baldassarre 1993). During the breeding season, Krapu et al.

(1983) found that clutch size was reduced during dry years. Wintering waterfowl habitat in the Central Valley of California is especially vulnerable to drought, as during dry spells water resources are strictly managed, and allocations to managed wetland habitat are some of the first to be reduced. Historically during drought periods water allocations were decreased by as much as 75 percent (Miller et al. 1986). This reduction in available habitat and food resources can lead to starvation, increased predation and disease, and ultimately reduced survival or poor body condition (Blums et al. 2002), potentially resulting in widespread breeding failure or population declines (Newton 1998).

ANTHROPOGENIC AND MANAGEMENT INFLUENCES

For species such as waterfowl that are using highly modified habitats that have undergone extreme anthropogenic land-use and management changes, environmental variability owing to climate may not adequately reflect changes in the population dynamics of these species. Human-driven changes such as harvest, large-scale habitat modifications, and management of their populations and habitats throughout the annual cycle may instead be the drivers behind changes in dabbling duck numbers (Tucker et al. 1994, Fasola et al. 2010). Despite massive losses of natural wetlands, this widespread loss has been somewhat offset by the creation of alternative habitat in artificial wetlands by humans (Elphick 2000, Elphick & Oring 2003, Tourenq et al. 2001). Among these, the conversion and production of agricultural crops such as rice are unique in creating wetland habitat as well as providing a high-energy and abundant food source for many wetland species (Brouder & Hill 1995). Land-use changes and management targeted at increasing these agricultural areas may have dramatically altered the relationship between winter habitat conditions and the population dynamics of waterfowl species that use them (Fleskes et al. 2005, Stafford et al. 2006). Increasingly most energy requirements of wintering waterfowl are still met in agricultural habitats, mainly flooded rice fields (Fleskes et al. 2005, Moon & Haukos 2006), and waste grain fields such as corn, which in some non-breeding areas can make up over 90% of the diet composition of pintails (Pearse et al. 2011).

Management of waterfowl during the non-breeding season has revolved around the creation of regionally based Joint Venture partnerships in the mid-1980s and 1990s that serve as a vehicle for habitat delivery programs. These regional Joint Ventures have implemented large-scale wetland improvement projects including artificial flooding and waterfowl friendly agricultural practices to improve habitat and resource availability in the non-breeding season. Conservation and management actions undertaken by these Joint Ventures have worked to enhance habitat conditions, and Thomas et al. (2009) found that the body condition of several waterfowl species has improved during winter in the California Central Valley since the inception of the Joint Venture.

Hunting pressure varies spatially and temporally, and may differentially impact wintering pintail populations depending on geographic region, harvest regulations, and natural habitat conditions (Miller et al. 1995, Cox et al. 1998, Fleskes et al. 2007). In years of poor wetland habitat conditions, birds may be concentrated in managed and artificially flooded areas, often areas of high hunting pressure such as refuges or private duck clubs and can be a significant source of mortality for wintering pintails (Cox et al. 1998, Fleskes et al. 2002, Moon & Haukos

2006). While direct hunting pressure may be low, the impact of harvest regulations may increase depending on location and habitat conditions (Moon 2004).

METHODS

STUDY SPECIES AND SYSTEM

Pintail are a mid-sized dabbling duck that relies on wetland and adjacent upland habitats throughout their annual cycle. Historically pintail were one of the most abundant dabbling ducks in North America, but since 1955 their population has varied from a high of 9.9 million birds in 1956 to a low of 1.8 million in 1991 (Hestbeck 1995). Current population numbers estimate a breeding population of 2.6 ± 0.2 million birds, which is 34% below the long-term average and well below the North American Waterfowl Management Plan goal of 5.5 million birds (USFWS 2014). While they remain the most abundant duck species in the Pacific Flyway, wintering bird numbers are only 25% of counts recorded in the 1970's (Fleskes et al. 2002). Our model system included the key breeding, winter, and spring migration areas of the Pacific Flyway of North America used by pintail as outlined in Mattsson et al. (2012). The winter range was the California Central Valley. Between 50-65 percent of the continental pintail population winters in the Pacific Flyway, and of those more than 90 percent occur in the Central Valley of California (Voelzer et al. 1982, Miller et al. 2005). The California Central Valley encompasses three major regions: the Sacramento Valley, the San Joaquin Valley, and the Delta and Suisan Marsh area where the Sacramento and San Joaquin river systems meet, and averages 40 miles wide and 450 miles north to south (CVJV 2006). The breeding range for this population of birds ranges from Alaska to the northern Great Plains, with the largest concentrations in the Prairie Pothole region and Alaska (Austin & Miller 1995), and includes strata 26-40 of the breeding pair survey from the Prairie Pothole region of the United States and Canada (USFWS 2014). Our breeding and wintering locations were the same as those used in previous studies of cross-seasonal influences in pintail (Raveling and Heitmeyer 1989, Osnas et al. 2016). In addition to those analyses, we added a major spring migration stopover area in southern Oregon and northeastern California (SONEC). SONEC encompasses 70,491 km2 over a series of major wetland complexes, including the Klamath Basin, in the intermountain regions of southern Oregon, northeastern California, and a small portion of northwestern Nevada (Fleskes & Yee 2007). The SONEC region is located directly between the California Central Valley and the breeding grounds, and 75-85% of birds wintering in the Central Valley migrate directly to SONEC (Miller et al. 2005), with birds staying up to two months in the area before leaving for the breeding grounds (Miller et al. 2005). Wetland habitats in SONEC are largely dependent upon winter and spring rainfall and snowmelt, and consist of naturally occurring and managed wetland habitats, such as wet meadows, small wetlands, and irrigated pastureland (Bishop & Vrtiska 2008, Ivey & Paullin 1985, Fleskes & Gregory 2010).

DATA USED IN ANALYSIS

We used population-level data available from the USFWS Harvest Surveys and the Waterfowl Breeding Population and Habitat Survey (WBPHS; USFWS 2014) for metrics related to pintail population size, reproductive performance, and wetland habitat conditions on the breeding grounds during the period 1961-2013. Breeding population size was defined as the population estimate from the breeding pair survey from strata 26-40. We used data on age ratios in the fall harvest (juvenile:adult) in the Pacific Flyway (Alaska, Arizona, California, Idaho, Nevada, Oregon, Utah, Washington, and portions of Colorado, Montana, New Mexico, and Wyoming west of the Continental Divide) as a measure of breeding productivity (Raveling and Heitmeyer 1989, Runge and Boomer 2005, Osnas et al. 2016). These data have been collected annually by the Parts Collection Survey (PCS) since 1961. Age ratio is calculated by dividing the number of immature wings by the number of adult wings (sexes are combined). The parts are obtained from hunters through the Parts Collection Survey and have been aged and sexed by experts in waterfowl identification. The Parts Collection Survey is based on a voluntary survey of selected migratory bird hunters in the United States.

We calculated weather covariates for wintering and spring staging time periods that served as measures of wetland habitat conditions in each season. For all weather covariates, monthly values from select weather stations were gathered from NOAA's National Climatic Data Center's (NCDC) archive. We used six California Central Valley stations (Sacramento Airport, Corcoran, Stockton Airport, Los Banos, Chico, and Fairfield), and six SONEC region stations (Squaw Butte, Hart Mountain, Fort Bidwell, Susanville Airport, Silver Lake, Klamath Falls) from the NOAA's weather station network, which were chosen in an attempt to provide broad geographic coverage of the areas. The California Central Valley stations were the same as used in Osnas (2016). We selected the six SONEC stations from the list of stations that had a continuous data record back to at least 1960.

We used a measure of total rainfall during winter and spring and total snowfall in SONEC as our measures of wetland habitat availability (Raveling & Heitmeyer 1989, Osnas et al. 2016). For each station total precipitation was summed for the season of interest, October-February in the California Central Valley and October-April in SONEC, then summed across stations. In addition to precipitation, we included several additional weather variables in both wintering and migration areas that we hypothesized may represent habitat conditions at a different temporal or spatial scale than precipitation, this included the Palmer Drought Severity Index as a standardized measure of drought conditions, and the average number of days below freezing as an indicator of extreme temperatures that may limit bird access to shallow water habitats. Given snowfall is an important contributor to water availability in SONEC, we also included total winter snow in SONEC from October-April as a weather variable. Finally, we used May pond numbers and the mean latitude of the breeding population of pintail, which is the centroid of the breeding population during the annual surveys, as indicators of breeding ground wetland habitat conditions. The mean latitude metric has been used in several analyses of pintail age ratios (Sheaffer et al. 1999, Runge and Boomer 2005), with a higher mean value indicating comparatively poor wetland habitat conditions due to drought in the Prairie Pothole region that force birds to fly farther north to find suitable breeding conditions.

STATISTICAL ANALYSES

We used multiple linear regression analyses to examine the effects of explanatory weather variables on pintail breeding productivity. Prior to analyses, all explanatory and response variables were examined for outliers and normalcy, then standardized to a mean of zero and unit variance, which simplifies interpretation of relative effect sizes, and because there was no time when the age ratio was zero (Zuur 2010). We used Pearson correlation coefficients to look for correlation among explanatory variables and did not use correlated variables ($r > 0.70$) in the same model. We hen created competing models, from which we selected the best explanatory or set of explanatory variables.

We first used the full dataset (1961-2013) and tested for a relationship between spring habitat conditions and pintail productivity using an information theoretic approach. We combined our five explanatory variables into 18 candidate models that included the null, all possible combinations of main effects. We also included select interaction terms between precipitation and snowfall and the size of the breeding population as the recent reanalysis by Osnas et al. (2016) found an interaction in winter between the influence of habitat conditions and pintail population size. We selected the best model using Akaike's Information criterion adjusted for small sample sizes (AICc) and model weights (w_i). We considered all models within two AICc values of the best model as competitive (Akaike 1973, Burnham & Anderson 2002) and evaluated beta values and their 85% confidence intervals to determine the strength and direction of effects and to ensure changes in AICc values were not the result of simply adding uninformative variables (Arnold 2010).

We next compared the best model for spring habitat attained above against the best models for winter and breeding seasons to compare the relative influence of each season on productivity. We identified the best winter model by combining our four explanatory variables into 15 models, and the best breeding model by combining two variables into three models. Our final model set for this analysis contained the top model for all three seasons and the null. Our decision making criteria for identifying the best model was as stated above.

Finally, we broke the dataset into two blocks of years, 1961-1985 and 1986-2013, and asked if the relationship between important explanatory variables identified above and pintail productivity had changed with time. The early time period 1961-1985 corresponded to the years analyzed in Raveling and Heitmeyer's original paper and served as a fundamental comparison between our analysis that work, while the second block of years was used to test if relationships had changed from the early to late time periods. The latter period has included a number of shifts in both the environment that pintail use throughout their annual cycle, as well as their relationship to it. Historically pintail and other dabbling ducks showed changes in population size that were closely tied to breeding ground May pond counts (USFWS 2014), however for several duck species including pintail, this relationship has degraded since the 1980's, despite increasing wetland habitat quality on the prairies and an increase in abundance of other duck species (Miller and Duncan 1999, Podruzny et al. 2002, Nicolai et al. 2005). Additionally, the North American Waterfowl Plan was created in 1986 and subsequently the creation of regional Joint Ventures such as California's Central Valley Joint Venture in 1988 have improved habitat and resource availability in the non-breeding season (Fleskes et al. 2005).

RESULTS

Pintail breeding productivity showed considerable annual variation during the years of our study with fall age ratios ranging from 0.55 to 2.6 juveniles per adult (mean = 1.04). Weather patterns varied seasonally and annually for each location, encompassing periods of regional drought as well as extreme wetness in all seasons. During spring migration in SONEC, the single variable model with winter snowfall was the best predictor of subsequent pintail productivity (Table 1). No other model was competitive and total snowfall occurred in any model receiving model weight. Pintail productivity was directly related to total snowfall, and confidence limits for the beta estimate did not include zero ($\beta = 0.011$, 95% confidence interval = 0.0086- 0.023; Fig. 1).

There was a clear best model relating weather to productivity for winter and the breeding grounds over all years, 1961-2013. The best single-season model for breeding was the single variable model that included the estimated mean latitude of the breeding population ($B = -5.4$, 95% confidence interval = [-0.77, -0.29]), which received 99% of model weight. Productivity declined as mean latitude increased. The best single-season model for winter was the interaction term between total precipitation and breeding population size with 55% of the model weight; winter rainfall had a positive effect on productivity but only with larger population sizes ($B = 0.35$, 95% confidence interval = [0.14, 0.56]). The additional competitive model with 30% of the model weight included days below freezing, but this additional parameter was uninformative, with 85% confidence intervals that contained zero. Comparing the relative importance of habitat conditions in each season to pintail productivity over all years (1961-2013), spring habitat conditions were a better predictor of pintail productivity than wetland conditions during winter or on the breeding grounds (Table 2). Spring habitat conditions received 99% of the model weight and the models with winter habitat condition and breeding wetland habitat condition were not competitive.

The effects of habitat conditions on productivity varied by time period. From 1961-85, pintail productivity increased with SONEC snowfall and winter rainfall and decreased with increasing breeding latitude, similar to the results above (Table 2). Confidence limits around all betas did not include zero. During the latter period (1986-2013) the relationships between habitat conditions and productivity declined considerably or disappeared (Fig. 2). The null model received the most support, however the model with total SONEC snowfall was competitive. Pintail productivity was no longer associated with breeding latitude or Central Valley rainfall. Spring habitat conditions best explained the variation in productivity of pintail over time with 77% of the model weight in the early years (B = 0.011, 95% confidence interval = [0.0086, 0.023]), but in the late years that declined to 25% of the model weight and the confidence interval around the parameter estimate contained zero (B = 0.0019, 95% confidence interval = [-0.0024, 0.0064]).

To explore possible explanations for the change in relationships between habitat conditions in each season and time period, we plotted our response variable (age ratio in the fall harvest) and key explanatory variables (total SONEC snow, winter rainfall, and breeding latitude) against year and fit regression lines for the early vs. late time periods to look for relationships and patterns. Mean pintail age ratio was higher during the earlier time period (1.01 vs. 0.7), declined with year, and varied over a wider range of values (0.4 – 2.2 vs. 0.5 – 0.9) compared to the later time period (Fig. 3). That pattern was mirrored by total SONEC snowfall, whose mean value was almost two times greater during the early time period (59.4 cm [22.04 – 100.7]) compared to late (30.4 cm [11.3 – 66.8]) period, and whose range declined from 78.7 to 55.6 between early and late time periods. In contrast, winter rainfall varied comparatively little through time and while trends in mean breeding latitude varied within time periods, the mean (54.1 lat. vs. 55.6) and range of values (51.7 – 58.9 vs. 51.7 – 59.8) experienced were similar between time periods.

TABLES

Table 1. Relationship between weather variables on a spring migration staging area in southern Oregon-northeastern California (SONEC) and pintail productivity (indexed by fall age ratios) for 1961-2013. Explanatory variables in models included total non-breeding season (October-April) snow (SNOWFALL), spring (March-April) total rainfall (RAIN), spring Palmer Drought Severity Index score (PDSI), the size of the pintail breeding population (BPOP), and the number of days below 32ºF each spring (FREEZE). We included the intercept-only, null model for comparison and present the number of parameters (K), ΔAIC_c, and AIC_c and model weight (w_i) for each model.

Model	ΔAIC_c	w_i	K
SNOWFALL	0[a]	0.730	3
*SNOWFALL + BPOP + SNOWFALL * BPOP*	3.34	0.137	5
SNOWFALL + RAIN	5.56	0.045	4
SNOWFALL + PDSI	5.56	0.045	4
SNOWFALL + FREEZE	5.68	0.043	4
Null	40.82	0.000	2

[a] AIC_c value of top model was 0.2

Table 2. Relationship between weather variables during winter, spring staging, and breeding grounds and pintail breeding productivity (indexed by fall age ratios) from 1961-2013. Explanatory variables in models include average non-breeding season (October-April) snow in SONEC (SNOWFALL), winter (October-February) precipitation totals in California (RAIN_CA) and the size of the breeding population (BPOP), and the estimated mean latitude of pintails during the breeding season (MEAN LAT). We defined models ≤ 2.0 ΔAIC values from the best model as competitive. We included the intercept-only, null model for comparison and present the number of parameters (*K*), ΔAIC_c, and AIC_c and model weight (w_i) for each model.

Model	ΔAIC_c	w_i	*K*
All Years: 1961-2013			
SNOWFALL	0.00	0.997	3
MEAN LAT	11.61	0.003	3
*RAIN + CA + RAIN_CA*BPOP*	21.87	0.000	5
Null	40.60	0.000	2
Early Period: 1961-1985			
SNOWFALL	0.00	0.765	3
MEAN LAT	2.37	0.233	3
*RAIN + CA + RAIN_CA*BPOP*	12.07	0.002	5
Null	15.99	0.000	2
Late Period: 1986-2013			
Null	0.00	0.572	2
SNOWFALL	1.63	0.253	3
MEAN LAT	2.52	0.162	3
*RAIN + CA + RAIN_CA*BPOP*	7.56	0.013	5

[a] AIC_c value of top model was 3.2, 13.4, and -23.4.

FIGURES

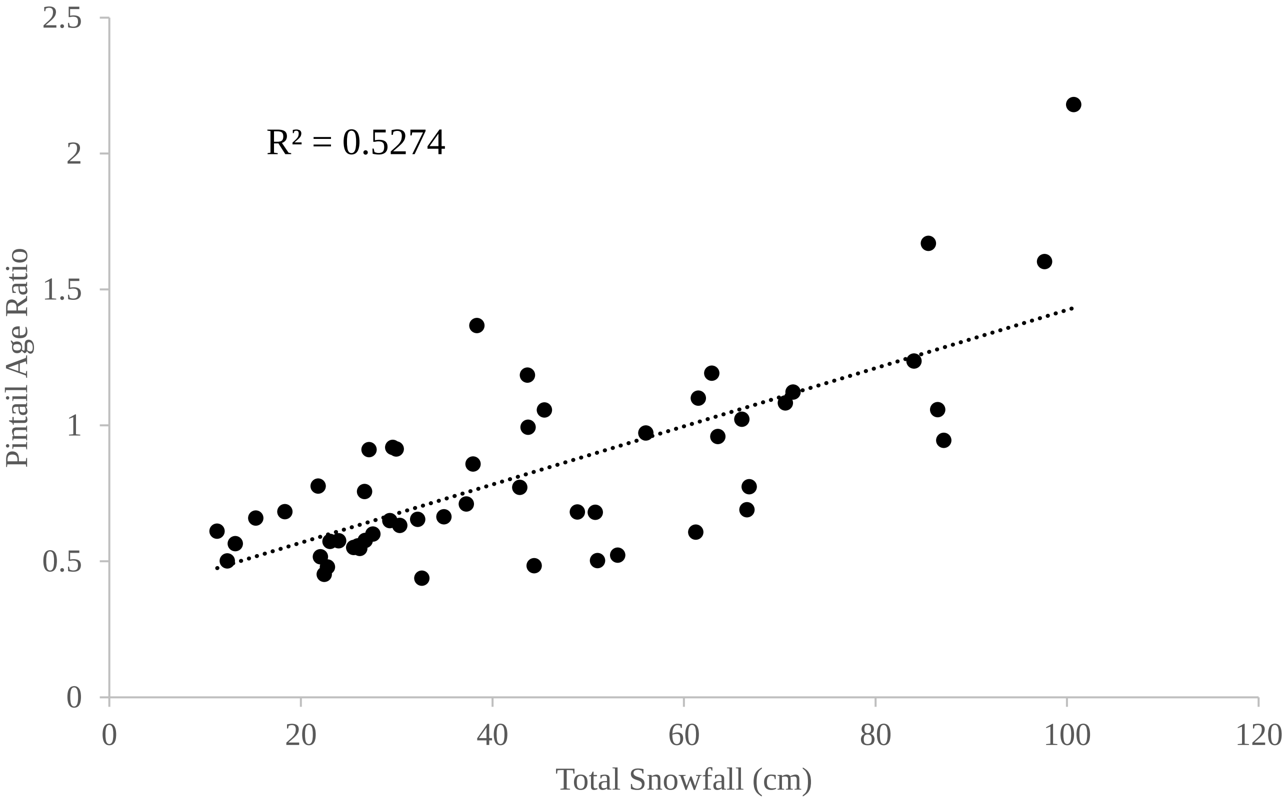

Figure 1. The relationship between pintail productivity and non-breeding season total snowfall in southern Oregon and northeast California (SONEC).

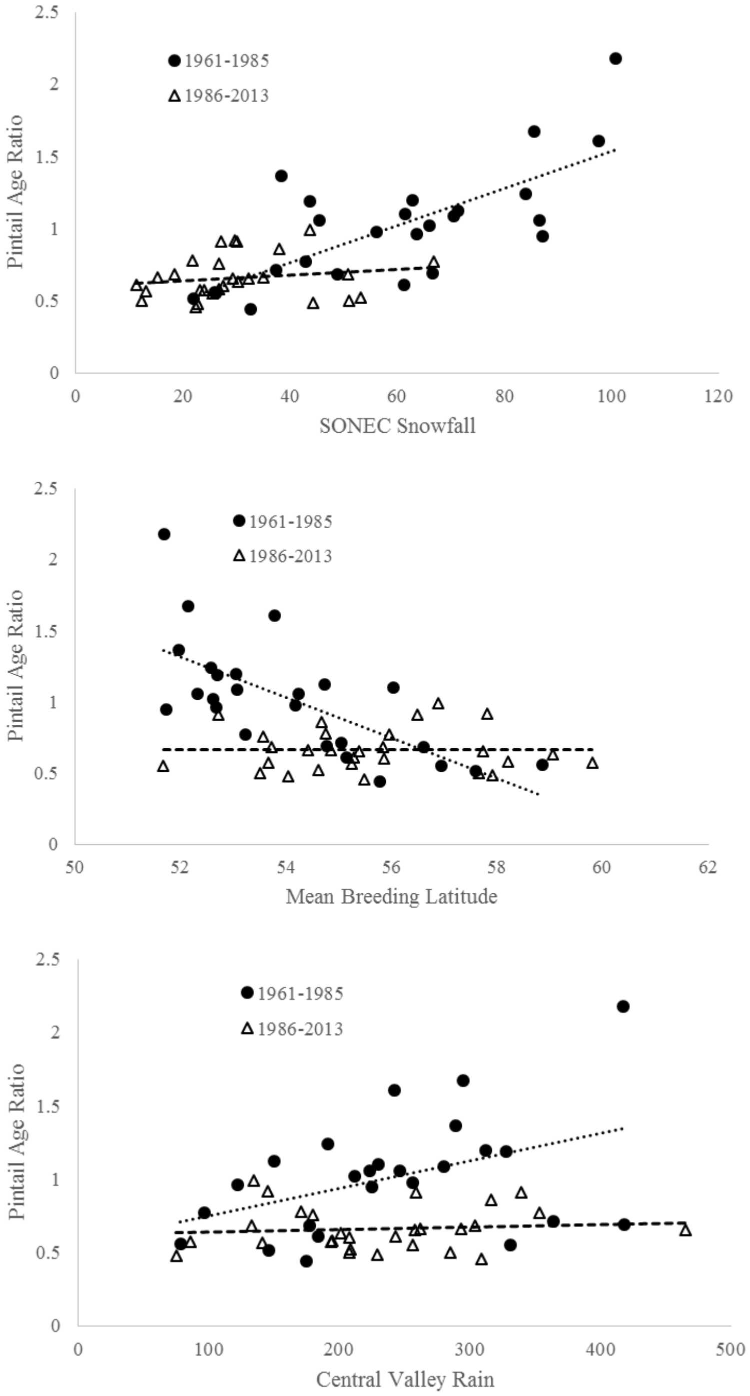

Figure 2. Habitat condition indicator variables, SONEC winter snow, California Central Valley winter rain, and the mean breeding latitude of the pintail population over the years 1961-2013.

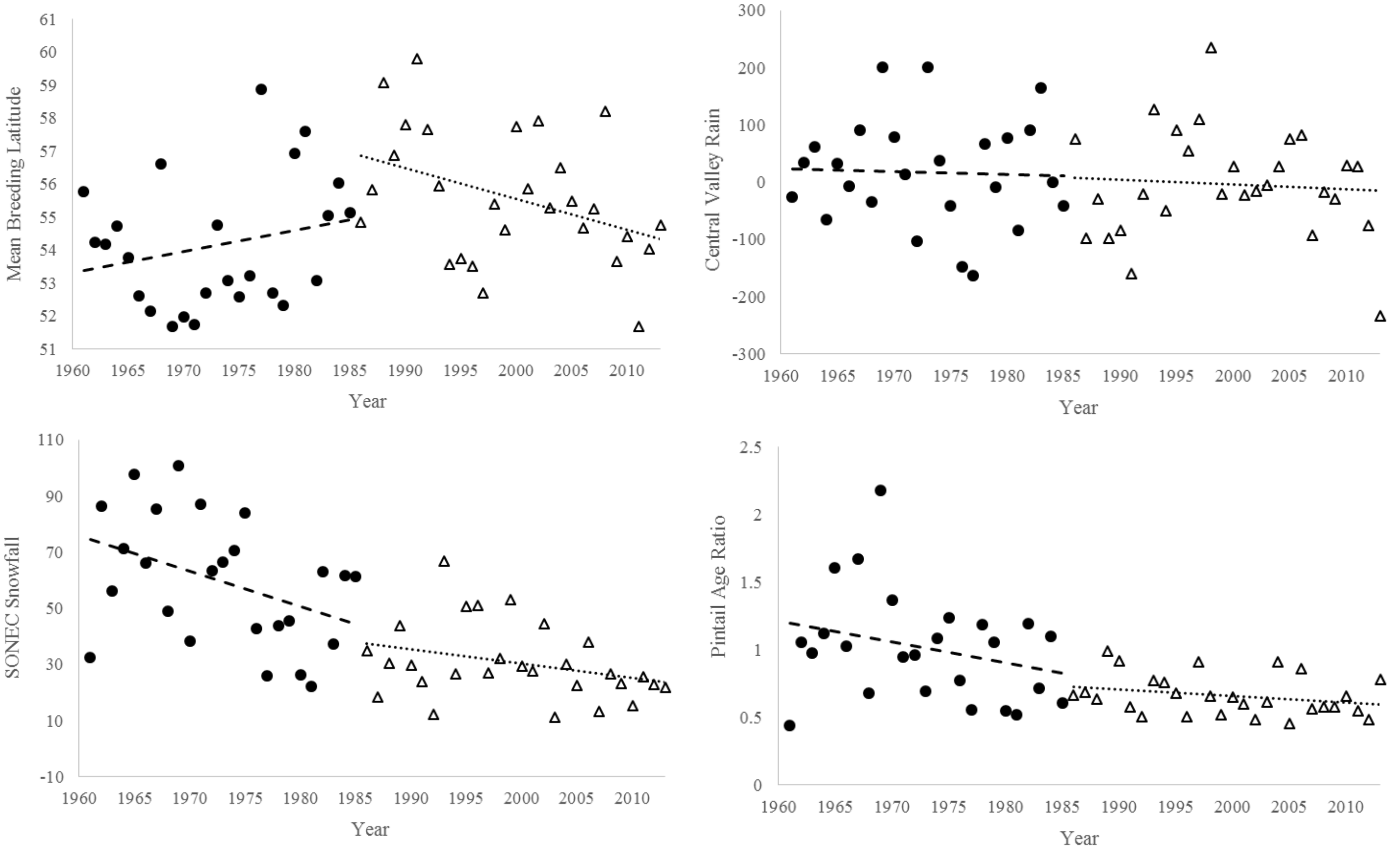

Figure 3. The relationship between pintail productivity and habitat condition indicators in winter, spring staging, and breeding seasons, split into early and late series years.

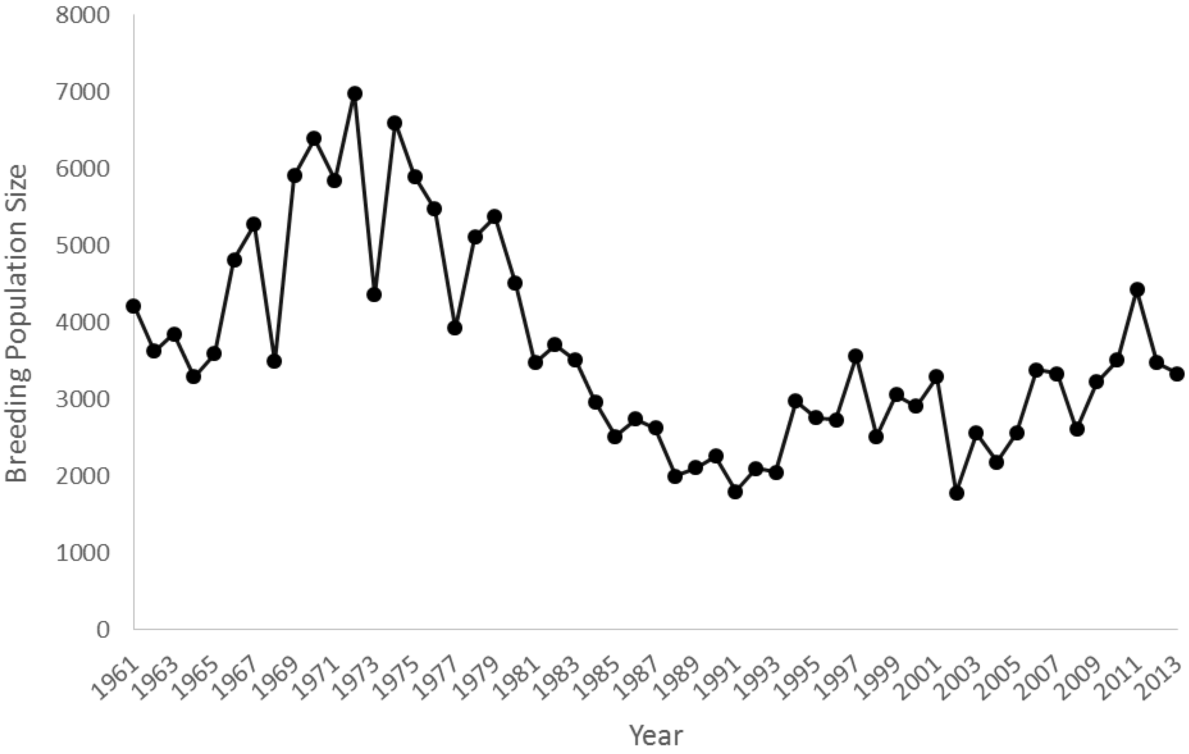

Figure 4. Breeding population size estimates for Northern pintails in the traditional survey area, 1961 – 2013.

DISCUSSION

Examinations of cross-seasonal effects in migratory birds have increased dramatically in the last several years, largely driven by an increase in available technology and understanding of migratory connectivity and timing (Cohen et al. 2017). While the importance of the non-breeding season in waterfowl has been examined in many species, the role of staging and migration habitats influence on subsequent productivity have not been evaluated closely for dabbling ducks. We found strong evidence that habitat conditions during spring staging in SONEC was an important predictor of subsequent pintail productivity. Our results provide insight into the relative influence of habitat conditions on the dynamics of Pacific Flyway pintail.

Our results support the spring condition hypothesis put forth by Anteau and Afton (2004) to explain the decline in continental Lesser scaup populations, that states reduced body condition of females during spring migration can be a driving factor bird’s subsequent reproductive success. A decline in the availability or quality of spring staging habitat may cause a reduction in female pintail body condition during spring migration, and subsequent condition of females upon arrival on the breeding grounds, impacting reproductive success. While the mechanism causing lower productivity for pintail is not known, like mallard, pintail rely in part on stored endogenous energy for breeding, and mallards in better body condition have higher nesting propensity, initiate nests days earlier, and have larger clutch sizes than those in poor body condition (Devries et al. 2008). Additionally, female mallards in better body condition had a higher re-nesting rate, and the effect of condition on re-nesting rates was especially heightened when nests were destroyed in mid-incubation or later (Arnold et al. 2010). Our results indicate the need for additional research on the role migration habitats may have on pintail population size, especially given the continental populations decline and persistent low numbers.

Habitat conditions in spring were more influential on pintail productivity than wetland conditions in winter or wetland conditions on the breeding grounds. If pintail rely on endogenous energy for breeding then it is intuitive that habitats during spring migration can be more important than winter as migration regions like SONEC are closer in space and time to breeding areas than winter areas like California's Central Valley. Additionally, pintail spend considerable time in SONEC, averaging 21 days and ranging from just a few days to 95 days and most pintails using SONEC subsequently migrate directly to breeding sites in Alaska or the Prairie Pothole region (Miller et al. 2005). In contrast, Central Flyway pintail average only a few days on spring staging areas in the Rainwater Basin area of Nebraska. Snowpack in the Pacific Northwest has decreased around 10 percent in the last 100 years (Mote et al. 2005) and our calculations of total snowfall in SONEC indicate that mean total snowfall declined by 48% between the early years and the later years of this study, which may have implications for the capacity of pintail populations to respond to habitat management elsewhere in the annual cycle.

Overflight of the Prairie Pothole Region is well known for pintail when prairie wetland conditions are poor, and such overflights are associated with a decline in productivity; however, the mechanisms of a 2.4˚ latitude overflight of the prairies (about 150 miles) by breeding pintail is poorly understood (Runge and Boomer 2005). It may be that more northern latitudes are less productive than more southern breeding strata, or that there is a shorter period between arrival and egg-laying in more northern breeding areas (Austin et al. 1998, Afton and Anderson 2001).

Given our results showing a relationship between SONEC habitat and productivity, it is equally plausible more northern breeding is associated with greater endogenous energy expenditure during migration and subsequently less energy available for reproduction. The later explanation could be exacerbated by poor habitat conditions in SONEC causing birds to initiate flights to breeding grounds with lower body reserves. Additional work is needed to distinguish among these ideas.

Overall, cross-seasonal influences declined for both winter and spring from early to late time periods. The amount and variation in Central Valley rainfall has not changed appreciably with time (Fig. 3), so changes in rainfall patterns are not responsible for the eroded relationship between winter rains and pintail productivity. The weaker relationship may occur for a variety of reasons, including smaller pintail population size, habitat restoration activities, and changing agricultural practices in the Central Valley. Pintail may be buffered from variation in annual rainfall by increased management and habitat restoration, including an increase in refuge acreage, providing water to managed lands during drought years, and an increase and flooding of rice acres. Since 1990, the California Central Valley Joint Venture has protected, restored, or enhanced over 56,778 acres of wetlands in the Central Valley. In 1992 rice field burning was banned, and by 2002-2003 over 70% of rice acreage was winter flooded, around 354,633 acres, greatly benefiting wintering waterfowl (CVJV 2006). The impact of rainfall in winter only had an effect at high population levels, so the smaller population of pintails since the 1980's may have reduced the habitat acreage needed to adequately support wintering pintails. Taken together, the reduction of a signal compared to the Heitmeyer & Raveling (1988) original work is consistent with the hypothesis that habitat conditions during winter in the California Central Valley are adequate met to meet the habitat needs of the current pintail population size. Consistent with this explanation, the mean body mass of pintails wintering in the California Central Valley has increased 4.3% between the 1979-1993 and 2006-2008 time periods (Fleskes et al. 2016) and winter survival of pintails after the close of hunting season, during late winter when resource availability is comparatively low is very high (Rice et al. 2010).

Reasons for the loss of a cross-seasonal influence for SONEC during the latter timer period are less clear. Compared to California's Central Valley, little is known about the history of habitat conditions in SONEC and the specific influence of changes in snowfall totals on wetland habitat are unknown as is any understanding of changes in grazing, cropping, or irrigation practices in the region since 1961. Clearly, the decline in total snow may have reduced the quantity or quality of SONEC habitats for migrating pintail and more work is needed to evaluate patterns in habitat change over time in SONEC.

Finally, unlike measures of wetland habitat availability during winter or breeding, trends in SONEC snowfall during 1961-2013 correlate with trends in pintail age ratios (Fig. 3) and trends in pintail age ratios generally track long term patterns in pintail population size. This suggests that habitat conditions during spring migration may have explanatory power for understanding trends in continental pintail population size. Our measure of spring habitat conditions, like our indices of wetland habitat conditions during breeding and winter seasons, is indirect and may benefit from a finer scale measure of on the ground conditions that birds are experiencing. Given the high variability of both the population metrics of pintail and weather indices, a linear relationship may not be the appropriate measure of long term pattern in population abundance of a migratory bird like the pintail. The continental pintail population declined dramatically around the year 1980 (Hestbeck 1995), coincidental with a decline in SONEC snowfall, and it does not appear to be a consistent downward trend, but instead more akin to a state shift with the pintail population fluctuating around a new, lower mean value after a steady decline from around 1980 to 1992 (Figure 4). Recent analyses of annual survival of pintail have indicated that survival is relatively high in comparison to other dabbling ducks, and that reduced harvest limits do not appear to have a significant impact on the continental population (Bartzen and Dufour 2017). In addition these analyses indicate that reduced survival did not coincide with the population decline, even when analyzed solely in those regions where the population decline was most pronounced. This indicates that managers should consider other mechanisms that may be limiting the pintail population. Despite the decline in signal in the later years in our results, SONEC should be a focus area for pintail conservation and research.

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