Identifying postbreeding molting sites and factors influencing molting chronology for gadwall (*Mareca strepera*) and mallards (*Anas platyrhynchos*) nesting in the Suisun Marsh of California.

By

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Dedication

I would like to dedicate this thesis to my parents, Dan and Sheri Kohl. They have supported me through my whole life financially and emotionally, always providing me with encouragement and sound advice. My father introduced me to the waterfowl world through hunting, and I would have never had the passion for this profession if it weren’t for him dragging me out of bed in the morning to take me out to the blind. Without their support I would never be the man I am today.

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Thesis Abstract

I monitored postbreeding movements of hen gadwall (*Mareca strepera*) and hen mallards (*Anas platyrhynchos*) nesting in the Suisun Marsh of California to determine wing molt chronology and molt site selection during 2015-2018. GPS-GSM backpacks were attached to hen gadwall and mallards nesting on Grizzly Island State Wildlife Area and private duck clubs within the Suisun Marsh. Birds affixed with transmitters were tracked remotely after the breeding season. I was able to acquire molting chronology information for 49 gadwall and 77 mallards as well as determine molting locations for 52 gadwall and 111 mallards. On average, gadwall that left Suisun to molt elsewhere, departed on August 1st (CI ± 4.48) while mallards departed on July 25th (± 5.05). Gadwall mean migration distance from Suisun to molt site was 344 km (± 46.84), while mallards traveled on average 155 km (± 34.29). Greater than 55% of the marked gadwall hens molted within two primary watershed basins; the Lower Klamath (27 %) and Upper Klamath Basin (31%) in northeastern California and southern Oregon, respectively. Mallards were much more spread out across California and Oregon with 88% of the marked hens molting within 6 basins. These basins included the Suisun Marsh (31%), Sacramento-San Joaquin Delta (10%), Butte Basin (12%), Colusa Basin (12%), Lower Klamath Basin (11%), and the Upper Klamath Basin (12%). Molt start date for gadwall ranged from July 10th – Sept 23rd with a mean start date of August 26th (± 4.60). Molt start date for mallards ranged from June 16th – October 8th with a mean start date of August 25th (± 4.11). Gadwall had a mean molting activity duration of 34.44 days (± 3.01) and mallards had a duration of 40.53 days (± 2.96). Gadwall and mallards used primarily permanent marsh (90.38% and 63.06%, respectively) to undergo molt. Gadwall and mallards appear to exhibit molt site fidelity, especially to permanent wetlands. Conservation and active management of these high-use

molting areas utilized by California breeding hen gadwall and mallards can improve postbreeding survival and improve California breeding waterfowl populations.

Using nesting data collected during the breeding season as well as data gleaned from postbreeding movements, I also analyzed how reproduction could potentially affect postbreeding ecology, specifically the synchronous wing molt. Using linear multiple regression models, I modeled the effects of year, nest initiation date, nest end date, nest success, age (SY vs ASY), and body condition on three response variables. These response variables included molt migration distance, molting activity duration, and molt start date. Molt migration distance was analyzed as both a response variable as well as an explanatory variable in predicting molt start date and molting activity duration. Molt start date was likewise included in candidate models to estimate molting activity duration. The top performing model for molt migration distance for hen gadwall was the null model, suggesting the explanatory variables analyzed were not good predictors of molt migration distance. However, nest initiation date was a strong predictor for molt migration distance for hen mallards. Model-averaged estimates indicated molt migration distance was reduced by 3.056 km (SE = 1.251) for every day later a hen mallard initiated a nest during the spring. The top model when analyzing molting activity duration in gadwall, included molt migration distance as the explanatory variable. Yet, this model competed with the null model suggesting limited statistical support for migration distance predicting molting activity duration in gadwall. An additive model that included molt start date and nest success as the variables was the top performing model in estimating molting activity duration in mallards. Model estimates indicated molting activity duration decreased 0.5 days (SE = 0.10) for every day later a mallard started to molt and decreased by 7.9 days (SE = 3.56) if a hen mallard had a successful nest. There was not a strong relationship between molt start date and any of the parameters analyzed for gadwall with the null model being the top performing model. However, annual variation (year) was a good predictor in determining molt start date in mallards. Mean MSD for mallards varied by more than 3 weeks amongst years, with the earliest occurring in 2016 on August 21st (SE = 3.22), followed by 2018 on August 22nd (SE = 6.21), then 2017 on September 8th (SE = 6.52), and the latest occurring in 2015 on September 11th (SE = 9.22). Further research needs to be conducted to gain a better understanding of how annual variation, in conjunction with cross-seasonal effects influences, not only the wing molt but other waterfowl life history events, as these interactions may have large scale implications in waterfowl population dynamics.

Chapter 1

Identifying postbreeding molting sites for gadwall (*Mareca strepera*) and mallards (*Anas platyrhynchos*) nesting in the Suisun Marsh of California

Abstract

I monitored postbreeding movements of hen gadwall (*Mareca strepera*) and hen mallards (*Anas platyrhynchos*) nesting in the Suisun Marsh of California to determine wing molt chronology and molt site selection during 2015-2018. GPS-GSM backpacks were attached to hen gadwall and mallards nesting on Grizzly Island State Wildlife Area and private duck clubs within the Suisun Marsh. Birds affixed with transmitters were tracked remotely after the breeding season. I was able to acquire molting chronology information for 49 gadwall and 77 mallards as well as determine molting locations for 52 gadwall and 111 mallards. On average, gadwall that left Suisun to molt elsewhere, departed on August 1st (CI ± 4.48) while mallards departed on July 25th (± 5.05). Gadwall mean migration distance from the Suisun Marsh to molt site was 345 km (± 46.84), while mallards traveled on average 155 km (± 34.29). Fifty-eight percent of marked gadwall hens molted within two primary watershed basins; the Lower Klamath (27 %) and Upper Klamath Basin (31%) in northeastern California and southern Oregon, respectively. Mallards were much more spread out across California and Oregon with 88% of the marked hens molting within 6 basins. These basins included the Suisun Marsh (31%), Sacramento-San Joaquin Delta (10%), Butte Basin (12%), Colusa Basin (12%), Lower Klamath Basin (11%), and the Upper Klamath Basin (12%). Molt start date for gadwall ranged from July 10th – Sept 23rd with a mean start date of August 26th (± 4.60). Molt start date for mallards ranged from June 16th – October 8th with a mean start date of August 25th (± 4.11). Gadwall had a mean molting activity duration of 34.44 days (± 3.01) and mallards had a duration of 40.53 days (± 2.96). Gadwall and mallards used primarily permanent marsh (90.38% and

63.06%, respectively) to undergo molt. Gadwall and mallards appear to exhibit molt site fidelity, especially to permanent wetlands. Conservation and active management of these high-use molting areas utilized by California breeding hen gadwall and mallards can improve postbreeding survival and improve California breeding waterfowl populations.

Introduction

The structure of a bird's flight feathers plays a vital role in thermoregulation, flight dynamics, protection, communication, and breeding (Stettenheim 1976). The maintenance of these feathers on an annual basis ensures that these functions are sustained and that a bird maintains the ability to survive and reproduce. The periodic replacement of these feathers is called "molt" (Holmgren and Hedenström 1995, Murphy 1996). The avian family, *Anatidae*, containing the ducks, geese, and swans, is 1 of 11 families of birds where feathers of the wing tracts or remiges (including the primaries, secondaries, and wing coverts) are replaced synchronously in the late summer or early autumn, a process that renders the bird temporarily flightless (Hohman *et al.* 1992, Pyle 2005). *Anatinae*, the sub-family of *Anatidae*, which encompasses the "true ducks" (Batt 1992), undergo two molts each year once they have reached adulthood, the definitive prealternate (adult pre-breeding) and the definitive prebasic (adult post-breeding) molt (Pyle 2005). The definitive prebasic molt (hereafter referred as "wing molt') encompasses both a body molt and the previously described wing molt. Waterfowl rely on their flight capabilities to exploit food reserves, escape predators, and migrate. However, during the wing molt these capabilities are lost and birds must depend on the nutrition and protection provided by the wetland they have selected on which to spend the duration of the flightless period (Ringelman 1990).

Gadwall (*Mareca strepera*) and mallards (*Anas platyrhynchos*) are the two most common species of breeding ducks within California (CDFW 2018) and comprise a large portion of the California hunter harvest during the waterfowl season annually (Olson 2018). In addition, harvest of several dabbling duck species within the Pacific Flyway states relies extensively on within-state production (De Sobrino *et al.* 2017). Sensitivity analysis by Oldenburger (2008) showed that mallard population growth rates in California were limited by adult female survival during the non-breeding season. Further, Fleskes *et al.* (2017) showed that mortality during the molt period was very high, especially in NE California where a large portion of the statewide breeding population travels to undergo wing molt (Mauser 1991, Yarris *et al.* 1994, Fleskes *et al*. 2010).

Many of the studies conducted on molting gadwall and mallards have focused on captive birds (Boyd 1961, Oring 1968, Balat 1970, Pehrsson 1987), banding recaptures (Timmermann and Lebret 1951, Owen and King 1979, Panek and Majewski 1990, Gehrold 2014), observations of large congregations of molting ducks (Oring 1969), or the use of VHF radio telemetry (Gilmer *et al.* 1977, Yarris *et al.* 1994, Fleskes *et al.* 2010) to estimate molt chronology and duration. Studies of wild birds mostly focused on hens that molted relatively short distances from their nesting area (Gilmer *et al.* 1977, Mauser 1991). However, some California breeding waterfowl disperse from the breeding grounds to regions great distances away to perform their wing molt (Yarris *et al.* 1994, Fleskes *et al.* 2010). This pre-molt shift to areas away from the breeding ground is known as a “molt migration” (Salomonsen 1968, Jehl 1990). Yarris *et al.* (1994) and Fleskes *et al.* (2010), used VHF radiotelemetry backpacks to track mallard hens throughout the postbreeding season and provided new and informative data highlighting key molting areas within the Pacific Flyway. However, temporal and spatial data acquired by these studies was very coarse and VHF studies are labor intensive, yielding few daily locations, and requiring triangulation to estimate locations which is imprecise.

Due to the advancement of Global Positioning System – Global System for Mobile communications technology (hereafter GPS-GSM), researchers now have the ability to track waterfowl remotely and acquire very accurate locations of an individual at frequent intervals (Kays *et al.* 2015). The goal of my study was to employ new GPS-GSM transmitter technology to track more precisely the movement of gadwall and mallards throughout their annual cycle. Specifically, I focus here on postbreeding movements and molt site selection of birds breeding in the Suisun Marsh during 2015-2018. In doing so, I develop a more refined estimate of molt chronology, molt migration distance, and molt duration of breeding gadwall and mallards. These data will help to better understand the postbreeding ecology of waterfowl in California and, importantly, identify key pathways of molt migration and molt site selection that will be vital for wetland conservation planning.

Study Area

My work focused on birds breeding on the Grizzly Island Wildlife Area (WA), located within the Suisun Marsh CA (38º 40’N, 121º 97’ W). The Suisun Marsh is a large brackish estuary at the downstream end of the Sacramento-San Joaquin Delta (Fig. 1). Grizzly Island WA contains approximately 2,000 ha of seasonal wetlands and 1,600 ha of grassland uplands (Fig. 2). The majority of the hens affixed with GPS-GSM transmitters were captured in the 800 ha upland complex within the WA which is managed as breeding grounds for waterfowl (Fig. 2). A few hens were captured shortly after the nesting season during summer banding efforts (June - August) on private duck clubs adjacent to the WA. Postbreeding movements and molt sites were located in watershed basins across California, Oregon, and Nevada.

Methods

Duck Capture and Transmitter Attachment

I caught hens during the spring and summer (April 1st-August 2nd) of 2015-2018. Ducks were trapped on nests using dipnets as well as funnel traps placed over the nest (Dietz 1994). During the summer months (June-August) baited funnel traps in wetlands adjacent to the WA were utilized to capture hens which were assumed to be Suisun Marsh breeders. Nest searches were conducted using methodology described in Klett *et al.* (1986) and Mclandress *et al.* (1996). Hens were trapped on the nest after 8 days of incubation. The incubation stage of eggs was determined using candling (Weller 1956). Once captured, birds were sexed and then aged using wing feather characteristics and plumage (Krapu *et al.* 1979, Carney 1992). Morphological measurements (mass, flattened wing chord length, short tarsus length, and exposed culmen length; Dzubin and Cooch 1992) were collected for each hen that was affixed with a transmitter. Three types of transmitters were used during the study. The initial transmitter deployed was the Ecotone Saker L series (n = 143), which weighed approximately 17 grams and was placed on hens between 2015-2018. The second transmitter type, the Ecotone Crex series (n = 8), weighed 14 grams and was affixed to hens during the 2017 and 2018 field seasons. The final transmitter utilized was the Ornitela Ornitrack-15 (n = 45), which weighed 15 grams and was used during the 2018 field season. All transmitters were attached to the birds using an adjustable body harness (Dwyer 1992) made of high-grade automotive elastic (Conrad-Jarvis, Corp.). All transmitters were solar powered GPS-GSM trackers that utilized 2G/3G cellular networks to transmit GPS locational data.

Data Collection

I was only interested in the time frame in which wing molt could occur for gadwall (Oring 1968, Oring 1969, Gehrold 2014) and mallards (Yarris *et al.* 1994, Fox *et al.* 2013), so I restricted the dataset to a 153-day period from June 15th to November 15th (hereafter "molt period") for each year. The movement data for each individual bird included a GPS location and associated timestamp.

Although GPS trackers can record precise estimates of animal locations at frequent intervals, GPS fix success can be influenced by a number of environmental factors and usually is incomplete (Nielsen *et al.* 2009). In my study, the frequency of GPS locational data for each bird varied greatly with some individuals having multiple locations every day throughout the molt period, while others had weeks of missing data. I created a frequency table to determine the frequency of days that each bird had at least one location recorded. Any bird that exhibited a zero (no locations recorded throughout the molt period) in the frequency table was removed from the analysis. Birds were also removed with the bottom 15% of frequency data (days with at least one bird location during molt period) from analysis. To ensure that data frequency did not significantly change "molting activity duration" (see Molt Determination methods for definition) calculations, I separated the remaining birds into quartiles for frequency data as well as for maximum gaps in data records (longest consecutive gap between locations) during the molt period. I placed birds into data resolution categories based on where they fell in the quartiles for each data resolution attribute (frequency of data and data gaps). High-resolution birds comprised the 75th (139 days) and 50th percentile (118 days) of frequency data during the molt period (153 total days) and had no data gaps larger than 13.79 hours. Medium-resolution birds comprised the 75th, 50th, and 25th (81 days) percentiles in frequency data and had no data gaps larger than 3.15

days. Low-resolution birds contained the 75th, 50th, and 25th percentiles in frequency data and had data gaps no larger than 13.62 days. Finally, bad-resolution birds were birds that were in the 50th and 25th percentiles but had data gaps greater than 13.62 days. Any bird that was considered to have bad-resolution data or did not fit in the other data resolution categories was excluded from the molting activity duration analysis but could still be used to determine molt location through visual inspection of locations and distance between relocations (subsequent bird locations in a time-series).

The GPS-interval ranged from a location every 15 minutes to every 6 hours depending on the battery level of the transmitter. To standardize the time, tracks were linearly re-discretized at 6-hour intervals using the function ‘redisltraj’ in the R package ‘adehabitatLT’ (Calenge *et al.* 2009). This allowed me to analyze total distance moved between relocations and a moving average of distance across a time-series for each bird. It also allowed me to investigate interspecific and intraspecific relationships of the wing molt. The re-discretized function produced a “regular” time-series (no data gaps) for each bird through the molt period which gave me the ability to segment the time-series using the procedure described below.

Molt Determination

Gadwall and mallards are flightless during their wing molt (Hohman *et al.* 1992) so I used distance moved between relocations (step-lengths) as well as a 2-day moving average of distance between relocations to determine the wing molt. I assumed that once a bird became flightless it would be restricted to a wetland or other water body that would limit their space use within the landscape. For my analyses, I describe the time interval of molting activity as the “molting activity duration” (hereafter MAD). This includes flightless periods following feather drop/regrowth as well as periods preceding and subsequent to the flightless period where birds exhibit similar movement patterns. Due to the inability of the remote sensing techniques available to me (described below) to discriminate periods of highly localized movement that results from behavioral aspects of space use instead of actual morphological limitations, I will refer to molting as both the period when the bird is incapable of flight due to feather growth and the period when the bird chooses not to fly due to concurrent behavior patterns. To determine the correct spatial scale cut-off in MAD, I used methods described in Beatty (2014, 2015). Using high-resolution data birds (*n* = 26: gadwall = 12, mallard = 14), I calculated the natural log of distance moved (km) between relocations (GPS locations every 6 hours) to obtain an empirical distribution of step-lengths. The 'density' function in R was used to fit and visualize a Gaussian fixed kernel density estimate to the step-lengths (distance between subsequent GPS relocations) for each species. Since I was only concerned with movements at a localized spatial scale, I narrowed the plots to focus on distances between 0 and 5 km. I identified the approximate breakpoint between within-wetland movements and localized movements (Beatty 2015) to be ~ 500 m for both gadwall (Fig. 3) and mallards (Fig. 4).

After testing ten stationary GPS transmitters over six days (1740 total locations), I found that only 2% of locations resulted in an error over 500 m and only 0.2% of locations resulted in an error over 1000 m. To be conservative with movement estimates and to allow GPS error to be assimilated within the step-lengths I chose 1000 m as the cut-off to determine MAD (Fig. 3 and 4) for each species, while the 2-day moving average cutoff was set at 500 m, with some exceptions described below.

I determined MAD for each bird by using a segmentation algorithm which utilized step-lengths as well as the moving average of the step-lengths. I segmented birds' paths using the 'segmentation' function in the 'segclust2d' package (bivariate Segmentation/Clustering Methods and Tools) in the R statistical computing program (Patin *et al.* 2008). Given a time-series with total length *n*, which in this case is the molt period (June 15th-Novemeber 15th), there are *K* stationary phases or segments (Fig. 3). These segments are defined by a sequence of consecutive random variables sharing the same distribution, particularly the same mean and variance. Once these parameters change, a new segment starts. The bivariate inputs used to determine segmentation along the time-series were step-lengths between relocations and a moving average of step-lengths between relocations (every 6 hours) over two days (8 relocations). I used a combination of these inputs to minimize false change-points (change in means and variance) in the time-series caused by GPS error, in turn causing false segments to be determined by the function. The high and medium-resolution data birds were over-segmented (K = 20) to ensure that the start and end of molt activity was captured. Due to the large data gaps in the low-resolution data, the 'redisltraj' function produced identical values for the step-lengths which the segmentation function treated as a stationary phase (identical mean and variance) or segment, therefore K was limited to 6. The segmentation function produces a plot of the moving average distance (8 locations) and step-lengths between relocations (every 6 hours) across the time-series (molt period) for each bird with each determined segment color coded (Fig. 5).

I considered segments "molting activity" if they were longer than 20 days with a moving average distance mean below 500 m for the entirety of each segment. The 20-day minimum was based on other studies of molting gadwall and mallards that determined birds to have a minimum flightless period of 22-33 days (Boyd 1961, Oring 1968, Balat 1970, Owen and King 1979, Klint 1982, Pehrsson 1987, Panek and Majewski 1990). Since both the high and medium-resolution data birds were over-segmented, I would concatenate segments if they were adjacent to each other and the mean of the moving average for the segments were below 500 m. To ensure that

GPS errors were not excluding segments from the entirety of the molt duration, I included segments if the mean moving average was under 500 m for the entire segment and, based on the previously mentioned error testing, only 2% of relocations within the segment had step-lengths greater than 1000 m (500 m movement between relocations plus a 500 m error threshold), with two relocations with step-lengths > 1000 m being the minimum limit for each segment. If the time-series had more than one segment or segments that fit the criteria, then the segment(s) with the lower mean moving average was selected.

Once all start and end dates for the MAD were specified for individuals through the segmentation process, I visually truthed the MAD by inspecting the GPS data points and corrected if needed. For example, due to long distance flights (Suisun to the Klamath Basin) that some birds perform to reach their molting area, the moving average sometimes did not reflect the actual start of molting activity (a few days delayed, due to the averaging of the large flight). Thus, the molt start date would be corrected with the visual observation of that bird arriving to the wetland where they molted. Low-resolution birds also had to be visually truthed more than the high and medium-resolution birds since these data could not be over-segmented ($K = 6$ instead of 20) due to large data gaps and low frequency data.

Suisun Departure and Molt Location Determination

For birds that left the Suisun Marsh to perform a molt migration (Salomonsen 1968), I used the last location that the bird was within the Suisun Basin based on the description of the watershed basins of California within the Central Valley Joint Venture 2006 Implementation Plan (CVJV 2006; Fig. 1). I determined molt location from the GPS location taken from the determined start date of the MAD. I also assessed molt locations for bad-resolution birds and birds that did not fit into any data quality criteria due to infrequent GPS locations and/or large data gaps. I determined molt location of these birds through visual inspection of their movements during the molt period. If a bird began to show molting activity (< 500 m 2-day moving average of step-lengths) for more than six days (> 24 locations) but the bird then died, or the transmitter failed, I still included that site as a molt location. Molt locations were specified to watershed sub-basins (CVJV 2006, OHJV 2005). Distance traveled to molt site or "molt migration distance" was calculated from the coordinates from the last location within the Suisun Basin to the first location of the determined molt start date and time.

Wetland Classification

I classified all wetland habitats used by birds in the study to molt using a similar system presented by Stewart and Kantrud (1971), which was based on hydrology (i.e., seasonal flood duration). Wetlands that were flooded less than 10 months during a water year (i.e., October 1st-September 30th) were considered seasonal marshes. Wetlands flooded from 10-18 months during a water year were considered semi-permanent marshes. All wetlands that were flooded more than 18 months were considered permanent wetlands. I determined hydrology of each molting location using a combination of historical satellite imagery provided by DigitalGlobe Inc., Landsat, and Planet Labs Inc.

Statistical Analysis

I used R 3.5.2 (R Development Core Team 2018) to perform all statistical analyses. I calculated the mean for Suisun Basin departure date (hereafter SDD), molt migration distance (hereafter MMD), molt start date (hereafter MSD), and MAD for the annual as well as the complete study dataset (2015-2018) for both species with 95% confidence intervals. To test for significant differences (*P-value* < 0.05) between species for each response variable, I used a one-way ANOVA as implemented in the ANOVA package in R. I also used a one-way ANOVA to determine annual differences within species for each response variable. Since the lower limit for MAD was set at 20 days, the interquartile range for MAD was calculated for each species to establish the upper limit of MAD to remove any potential outliers which could skew calculations.

Results

Suisun Basin Departure and Molt Migration Distance

I report molting information for both gadwall (*n* = 49) and mallards (*n* = 77). The mean departure date for gadwall that left the Suisun basin to undergo the wing molt elsewhere was August 1st (CI ± 4.48 days), whereas mallard hens departed earlier, July 25th (± 5.05 days; Table 1). There were no statistically detectable differences within or between species in annual SDD (Table 8). Annual MMD did not change significantly ($P = 0.217$) for hen gadwall, yet, it did vary significantly for hen mallards ($P = 0.026$). Female gadwall exhibited the largest mean MMD with birds traveling 344.6 km (± 46.8 km) while mallard hens traveled 155.2 km (± 34.3 km) to reach their molting areas (Table 2). Mean MMD differed significantly among species ($P < 0.001$; Table 8). The farthest a bird (hen gadwall) traveled to molt was to Summer Lake, Oregon, 540 km from the Suisun Marsh.

Molt Site Selection

I was able to determine molt sites or locations for 163 birds, 111 mallards and 52 gadwall (Table 6). Mallards utilized a wide array of basins within California, Oregon, and Nevada to undergo wing molt, although there were six main basins that were utilized by 10% (11 or more individuals) or more of the birds (Tables 6 and 7). Both the Butte and Colusa Basin in the northern Sacramento Valley (hereafter NSV), located on the west and east side of the Sacramento River, respectively, had 13 (12%) birds molt within their boundaries, mostly focused on seasonal wetlands in private duck clubs within the Butte Sink region and federal wildlife refuge property (Fig. 7; Table 10 and 11). The delta region of California (southern Sacramento Valley or SSV), which is the confluence of the Sacramento and San Joaquin River systems, had 10% (*n* = 11) of use by molting mallards that exploited seasonal marshes on duck clubs near Liberty Island that were flooded in late August (Fig. 8; Table 11). Twenty-five mallards traveled north from the Suisun Marsh to the southern Oregon and northeastern California (SONEC) region (Fig. 6). Twelve (11%) of these birds traveled to the Lower Klamath Basin (hereafter LKB), located on the eastern California and Oregon border. These birds primarily used permanent marshes on Lower Klamath National Wildlife Refuge (NWR) and Tulelake NWR (Fig. 6; Table 11). The Upper Klamath Lake Basin (hereafter UKB), also in the SONEC region, was also utilized by mallards with 13 hens (12%) making use of permanent wetlands adjacent to Agency Lake/Upper Klamath Lake; this area comprises BLM (Wood River Wetland), FWS (Upper Klamath NWR), and The Nature Conservancy (Williamson River Delta) properties (Fig. 6). The Suisun Marsh Basin (hereafter SM) had the highest percentage of molting mallards with 31% (*n* = 34) of the birds electing to stay within the SM to undergo wing molt. These birds also primarily used permanent wetlands, mainly on private duck clubs (Fig. 9; Table 11).

Gadwall, in contrast to mallards, were attracted to mainly two basins during the study to perform their wing molt, the LKB and UKB (Fig. 6; Tables 6 and 7). These two basins encompassed 57% (*n* = 30) of the total sample size (*n* = 52) that molt locations were determined for, while the next highest use was the SM and northeast California region with 6% (*n* = 3) of marked gadwall molting in each basin. Gadwall utilizing the LKB and UKB, used similar areas as the mallards, with the majority of birds molting in permanent wetlands on Wood River Wetland (*n* = 10), Williamson River Delta (*n* = 4), and Tulelake NWR (*n* = 12) (Fig. 6; Table 11).

The annual use of each basin varied among species and years (Tables 6 and 7). Gadwall consistently molted in the Klamath Basin annually, with molt locations occurring in both the LKB and UKB (Table 7). Mallards molted within both of those regions also throughout the study, however, the number of birds utilizing these regions fluctuated greatly each year (Table 6). Annual use of the SM by molting mallards was consistent, while gadwall only used the SM during the first two years of the study. Mallards also molted within the NSV (American, Butte, and Colusa Basins) during 2016-2018, yet, during 2015, only a small percentage of mallard molt locations occurred in the NSV. Gadwall molting within the NSV was inconsistent (Table 6), although, these proportions were based on small sample sizes (only 4 individuals molted in the NSV during 2015-18).

Wetland Types Utilized

Hens of both species overwhelmingly opted for permanent wetlands (72% of total birds) to undergo wing molt (Table 9), with 63% of mallards (*n* = 70) and 90% of gadwall (*n* = 47) selecting permanent marshes. Seventeen percent of mallards molted in seasonal wetlands that were flooded in early to mid-August to provide habitat for winter migrating waterfowl; mallards used semi-permanent marshes approximately 10% of the time. Gadwall minimally used seasonal and semi-permanent marshes, 4% (*n* = 2) and 6% (*n* = 4) of birds molted in these wetland types, respectively. Ownership for molting wetlands was dominated by private party (*n* = 69, 42%) and federally owned refuge lands (*n* = 60, 37%); these two entities also managed most of the permanent marsh used by birds during the study (Table 10).

Molt Start and Molting Activity Duration

Neither gadwall nor mallards displayed intraspecific annual differences in MSD (Table 8). When comparing MSD, gadwall and mallards only varied by a day, with a mean start date for gadwall of August 26th (n = 52, ± 4.60 days) and August 25th (n = 111, ± 4.11 days) for mallards (Table 3). Gadwall hens exhibited molting activity as early as July 10th and as late as October 28th, while a few female mallards exhibited molting activity by June 16th and one mallard displayed molting activity until November 15th (Table 4). This was the end of the designated “molt period”, and so this hen may have continued to display molting activity, although it was most likely flighted by November 15th since it had been on the wetland for 38+ days.

When comparing data resolution (high, medium, and low) MAD did not vary for either gadwall (P = 0.17) or mallards (P = 0.879) so all data were combined to estimate MAD for each species. MAD did not vary annually for either gadwall or mallards (P = 0.557; P = 0.204, respectively; Table 8), with mean MAD for gadwall of 34.4 days (n = 34, ± 3.01 days) and mean MAD for mallards of 40.5 days (n = 59, ± 2.96 days; Table 5). Gadwall MAD ranged from as short as 20 days to a maximum of 52 days, while mallards ranged from a minimum of 23 days to a maximum of 69.8 days. Birds were most likely flighted before these maximum ranges of MAD, but they were still utilizing a small area (wetland) and not deviating from “molting activity,” thus it was hard to determine when these birds regained flight ability. There were significant differences between species in MAD (P = 0.008).

Molt Site Fidelity

Given transmitter failure and impacts from cell network providers transitioning from 2G to 3G cell networks, many of the transmitters did not function across multiple molting seasons. I had data for more than 1 year for only 13 of a possible 163 individuals, and no birds with more than 2 years of data (Table 12). Of the gadwall (n = 2) and mallards (n = 11) that had more than 1 molt season of data, results were varied with only 1 gadwall returning to the same basin to molt while 6 mallards returned to the same basin and 5 molted in other basins the following year. Five of the 7 hens (71%) that did return to the same watershed basin, molted in permanent wetlands the preceding year, and 4 of the 6 birds (67%) that changed basins molted in temporary wetlands (i.e., semi-permanent, seasonal, or irrigated agriculture) the year prior (Table 12).

Discussion

Molt Migration and Departure

Localized winter and spring precipitation in the Suisun Marsh (SM) can increase nesting density, average clutch size of waterfowl, and improve re-nesting success (Greenwood *et al.* 1995, Mclandress *et al.* 1996). Increased snow runoff through the Sacramento-San Joaquin River Delta System can also allow wetland managers to provide summer water as well as improve water quality within wetlands by decreasing salinity concentrations (Miller *et al.* 1975, Rollins 1981). Nesting and brood rearing conditions changed greatly each year between 2015-2018, with 2015 being a below average water year for precipitation in the SM and record low Sierra snowpack (5% of average; CADWR 2015) yet, during the 2017 water year, SM experienced above average precipitation and the Sierra snowpack was 159% of normal (CADWR 2017). Although these factors influence both egg, nest, and brood success, the variability that occurred did not seem to influence when ducks departed from SM since neither species exhibited significant intra or interspecies annual change.

The years of 2015 and 2016 were an extension of a four-year drought that occurred within California (CADWR 2015; CADWR 2016) and, consequently, summer water and permanent wetlands, which are highly preferred by both species (Table 9; Ringelman 1990), were most likely scarce in the Sacramento Valley (NSV and SSV). The lack of suitable habitat during these years may have caused gadwall to fly further north to utilize the LKB and UKB wetlands in a higher proportion. The LKB and UKB historically have been altered less by land use practices (i.e., agriculture and flood control) and permanent wetlands were affected less severely when compared to California Central Valley marshes (Akins 1970). The significant annual change ($P = 0.026$) in MMD for mallards may have been caused by the fluctuations of available molting habitat throughout SM, Sacramento Valley, and Klamath Basin (LKB and UKB). A high percentage of mallards used the SM during the first year of the study which limited the mean MMD; however, the following year MMD increased considerably as more birds utilized seasonal marshes in the Sacramento Valley and flew further north as habitat conditions improved in the Klamath Basin (NOAA 2018). During 2017-18, MMD for mallards trended downward as molting habitat conditions likely improved; more water was available to flood wetlands in SM, SSV, and NSV due to increased summer water availability (DWR 2017).

The significant interspecific difference ($P < 0.001$) in mean MMD between gadwall and mallards may be an indication that mallards have the ability to exploit other types of wetlands to undergo molt beyond permanent marshes. This behavioral plasticity in the selection of wetland type for molting enables mallards to make greater use of the landscape (Zhang *et al.* 2006) present in the Sacramento Valley, San Joaquin Valley, and Delta. Mallards also used the SM consistently more during the study than gadwall (Table 6 and 7), contributing to a lower mean MMD.

Molt Chronology

The range of the MADs observed in this study for both gadwall and mallard hens were consistent with previous research. Oring (1968) observed tertial feathers in adult female gadwall being acquired as early as the 5th of August and as late as early October. Furthermore, Oring (1969) reported that 43% (6 of 14) of his captive nonbreeders were flightless by August 5th. Palmer (1976) stated that, at Lower Souris Refuge in North Dakota, early female gadwall flightless dates were August 2nd and 5th, with the peak in late August to early September. Although a few individuals in our study became flightless prior to August 5th (*n* = 5, 11.9%), the majority of female gadwall were flightless in August and September (*n* = 48, 92.3%). Chabreck (1966) recorded 2-3 dozen flightless female gadwall in Louisiana in October, with 2 being flightless until November 15th. Chabreck concluded that these hens migrated southward to their wintering grounds to undergo their wing molt after successfully rearing late broods. Oring (1969) also stated that successful breeding female gadwall do not shed their remiges until 6 weeks after their nests hatched.

Nesting information from the birds captured in our study yield an estimated mean nest initiation date (Klett *et al.* 1986) of May 11th (*n* = 62, ± 4.09 days), similar to the median date (May 7th) found in Szalay (2003) for gadwall nesting in the San Joaquin Valley of California. Accounting for a 26-day incubation period (Oring 1969) for a successful nest plus six weeks of brood care, females should shed their remiges approximately mid to late July, yet the majority of hens in our study became flightless more than a month later. Oring's (1969) research was conducted on captive birds and his estimates were based on birds molting in the general area where they nested. Almost all of the gadwall hens 94% (*n* = 49) in our study departed SM and flew to other regions to undergo wing molt (Table 6). Nest initiation for gadwall was also much later in Oring (1969) compared to our study (May 11th ± 4.09 days), with a mean nest initiation of May 26th for wild nests and May 28th for captive nests. It has been suggested that successful gadwall breeders may undergo their wing molt in the general area where they nested and become flightless while tending their preflight young (Chabreck 1966, Palmer 1976). A few of the birds that molted in SM may have done so, but many of the gadwall instead dispersed and left SM after the breeding season, whether they brought off a successful nest or not. Gadwall may be seeking more suitable habitat conditions to undergo the wing molt which are not present in the breeding marshes within SM (Gilmer *at al.* 1977).

Our results are also consistent with previous research on the molt chronology of hen mallards. Mallard hens caught at Abberton Reservoir, Essex, England exhibited an analogous molt chronology with a majority of flightless hens being observed between August 1st and September 1st, and a few females molting as early as June 11th and as late as September 30th (Boyd 1961). Gilmer *et al.* (1977) monitored 27 hens using radio telemetry in North-Central Minnesota and found the earliest hen became flightless on July 15th, 15 females shed flight feathers after September 1st, and 5 hens had not yet begun to molt when observations ceased on September 10th. Gilmer *et al.* (1977) also reported that 2 hen mallards remained with their young into the flightless period, which, although rare, had also been observed in other studies (Raitasuo 1964, Salmonsen 1968). This may have been the case with the 2 hens in our study that started molting activity in mid to late June and stayed within the Suisun Basin to molt. With over 30% (*n* = 34) of mallards (Table 7) in our study staying within the Suisun Basin to molt, hens staying with their brood until they become flightless may not be uncommon with this breeding population.

Molt Site Selection

Gadwall nesting within the SM appear to have a strong affinity to permanent wetlands in the Klamath Basin (Table 7) when selecting a wing molt site. A more detailed GIS mapping effort that documents the distribution of all available potential molting habitat would be needed to better assess gadwall molt site selection. However, the two wetlands that were chosen by the majority of gadwall females, Wood River Wetland BLM property in the UKB and Sump 1B on Tule Lake NWR in the LKB, are long standing permanent wetlands. The restoration of Wood River Wetlands in 1995 by the Bureau of Land Management (BLM) allowed for winter flood water to inundate the South Unit of the wetland during the spring and early summer, leading to persistent water even in late summer (Carpenter *et al.* 2009). Water levels in Sump 1B have been maintained year-round since 2014 to provide more molting habitat for migrating waterfowl (Bureau of Reclamation 2015). These wetlands not only provided reliable water during the late summer months prior to and throughout the study period, but they also provided large stands of emergent and submergent vegetation, providing concealment from predators and disturbances (Ringelman 1990). Permanent, large, and unfragmented wetlands have been shown to improve survival in molting waterfowl (Fleskes *et al.* 2010). Assuming Suisun Marsh breeders show similar philopatry to their breeding and molting grounds as seen in other waterfowl studies (Batt 1992), increased survivorship of birds using these wetlands would increase the proportion of these hens present during the spring to be caught and affixed with a transmitter.

Breeding mallards in California have been previously shown to utilize the Klamath Basin and Sacramento Valley to undergo wing molt during the late summer (Yarris *et al*. 1994, Fleskes *et al*. 2010). Yarris *et al*. (1994) found 60% (*n* = 12) of their sample of mallards that nested in the Suisun Marsh molted in the Klamath Basin, with 6 hens molting at Upper Klamath Lake and 3 molting at Tule Lake NWR. Fleskes *et al.* (2010) also found that 80% of 81 molting hen mallards marked in the Klamath Basin wintered in the Central Valley of California, particularly the NSV with some of these individuals moving into the SM during the late-winter. Mallards in our study primarily used the same wetlands as gadwall in both the UKB (Wood River Wetland) and LKB (Sump 1B), suggesting similarities in molting wetland preference of the two species. Use of the Sacramento Valley by mallards in our study was similar to Yarris *et al.* (1994). I found that 27% (*n* = 30) of birds molted in the Sacramento Valley (American, Butte, and Colusa Basins) compared to 20% (*n* = 5) in Yarris *at al.* (1994). One conspicuous difference between the two studies is the proportion of use within the SM by hen mallards with over 30% (*n* = 34) of the hens in this study using the SM, while Yarris *et al.* (1994) only reported 10% (*n* = 2) used the SM. This may be due to annual variation in breeding conditions, water availability, or marsh management within the SM; conditions in the 1987 field season may have been less favorable. The SM historically was comprised of managed marsh with an emphasis on habitat for wintering waterfowl; thus, many wetlands may have been drained shortly after the breeding season to leach saline soils and promote the growth of wetland waterfowl food (Rollins 1981). Currently, some of the historic managed wetlands on private duck clubs are in the process of being restored to tidal marsh due to the implementation of The Suisun Marsh Habitat Management Preservation, and Restoration Plan in 2014 (Suisun Marsh Habitat Management, Preservation, and Restoration Plan 2013). Since these marsh levees have been breached recently, they are presently functioning as early successional tidal marshes and are subtidal. Although not ideal in promoting winter waterfowl food due to the potential for water high in salinity to permeate the substrate (Miller 1975, Rollins 1981), the wetlands are flooded year-round most years providing late summer molting habitat. The presence of this late summer water may offer enough suitable habitat to entice Suisun breeding mallards to molt there. Analogous to gadwall, mallards preferred permanent wetlands to spend their MAD (Table 8), although unexpectedly, hens were able to exploit seasonal marshes as well. These seasonal wetlands likely provided highly abundant food resources, both in moist-soil plant seeds as well as protein-rich invertebrates (Frederickson 1988) that are needed to meet the nutrient requirements to undergo a successful molt (Young and Boag 1982, Heitmeyer 1988). Semi-permanent wetlands may have reduced invertebrate loads compared to seasonal marshes (Frederickson 1988) and due to their infrequent flood scheme, they may not provide the annual stability of permanent wetlands. Consequently, semi-permanent wetlands are selected at a lower rate than permanent and seasonal wetlands by postbreeding gadwall and mallards.

Molting Activity Duration

Average molting activity duration in this study for both female gadwall and mallards was consistent with published research for the two species, although our estimates may have been lengthened due to the inability to determine when the birds lost and regained the ability of flight. Oring (1968) reported that captive gadwall completely renewed their wings in 35-40 days but were able to fly by day 25. Timmermann and Lebret (1951) indicated that a Dutch park mallard may be able to fly again after 23-24 days, prior to the complete renewal of their primaries. In another captive mallard study, Boyd (1961) estimated the flightless period to be 24-26 days for English mallards. Panek and Majewski (1990) estimated the flightless period to be 22-29 days in wild drake mallards by capturing and recapturing wild birds during the wing molt in Poland and assessing the rate of remex growth in males. They estimated that drakes would be able to attain flight when their remiges had reached 75-83% of final length. Balat (1970) and Owen and King (1979), two studies using wild stock to evaluate the flightless period of mallards, estimated longer flightless periods of 29-33 and 33-36 days, respectively. The findings from Balat (1970) and Owen and King (1979) seem to be more closely aligned to the mean molting activity duration of hen mallards in our study. Pehrsson (1987) suggested that domesticated and urbanized birds have shorter flightless periods than wild-strain birds. The results of my study seem to concur with that statement; although I observed birds flighted on the lower end of the estimated flightless period, the mean molt duration for both gadwall and mallards was 7-10 days longer than previously published. These longer molt durations of wild-strain birds may be due to reduced food availability and nutrient limitation within the environment, specifically protein (Heitmeyer 1988). Reduced food availability has been shown to delay prebasic molt in both mallards (Heitmeyer 1987) and northern pintail (Miller 1986), and nutrient restrictions have also been demonstrated to extend the molt duration in mallards (Richardson and Kaminski 1992) as well as in White-crowned sparrows (Murphy *et al.* 1988).

Molt Site Fidelity

Waterfowl species have been shown to exhibit a high rate of philopatry to wintering, breeding, and postbreeding (i.e., molting sites) areas during their lifetime (Hohman *et al.* 1992, Robertson and Cooke 1999). Postbreeding use areas, specifically molting sites, have not been studied as extensively as wintering and breeding areas, and the research that has been conducted has primarily used band returns to develop an estimate of fidelity. These studies have shown that waterfowl do tend to return to the same region annually to undergo the wing molt (Hohman *et al.* 1992, Bowman and Brown 1992, Bollinger and Derksen 1996, Flint *et al.* 2000, Phillips *et al.* 2006, Gehrold 2014), although estimates of the rate of return can differ greatly between species.

Bowman and Brown (1992) found that 52% of black ducks (*Anas rubripes*) return to the same pond in which they molted the previous year in northern Labrador. Gehrold (2014) reported return rates of 59% and 54% the following year for molting male and female gadwall, respectively, at Ismaning reservoir near Munich, Germany. In contrast, Bollinger and Derksen (1996) studying molting black brant (*Branta bernicla*) on the North Slope of Alaska observed a fidelity rate of > 90% and Flint *et al.* (2000) reported fidelity rates of > 95% for molt locations of Stellar's eiders (*Polysticta stelleri*) along the Alaskan Peninsula. Molt site fidelity rates may be higher within species that select areas with lower environmental variability, such as marine environments which tend to be more predictable and stable compared to freshwater habitats (Robertson and Cooke 1999). Although the sample size of both gadwall and mallards within our study with two years of data was small (gadwall = 2, mallards = 11), the rate of molt site fidelity (gadwall = 50%, mallard = 55%) was similar to that found in Gehrold (2014) and Bowman and Brown (1992). The habitat predictability and stability relationship proposed by Robertson and Cooke (1999) appears to hold true not only for interspecies selection for molt sites but also for intraspecies, as 71% (5 of 7) of the individuals that returned to the same watershed basin, utilized permanent wetlands the previous year.

Management Implications

The historic wetlands in the Central Valley and Klamath Basin of Califonia have been drastically altered and reduced over the last century as agriculture operations acquired much of the available fertile soils across the landscape (Gilmer *et al.* 1982, OWJV 2001, Dahl 2011, Garone 2011). The majority of wetlands that are still present within the valley are managed to minimize crop depredation by maximizing food for wintering and migrating waterfowl. To do this, managers draw down wetlands in late spring to promote moist-soil plant growth (Gilmer *et* *al.* 1982). Consequently, stable emergent summer wetlands (i.e., reliable summer water available annually) are rare. A compounding factor is that water availability is low and water demands are extremely high during late summer when birds are undergoing the wing molt (Garone 2011). The wetlands that are present during the late summer are located primarily on private duck clubs and public lands managed for wildlife (Gilmer *et al.* 1982). For example, the birds in this study used predominantly federal and private lands during wing molt (Table 10). Mosquito abatement can be a further constraint in allocating summer water to waterfowl for both private and public wildlife managers. Escalating abatement costs can significantly impact the yearly operating budget for a wildlife area or duck club, diminishing the funds for other projects such as wetland restoration or improvement (Gray Lodge WA Water Management Plan 2011).

In this study, I identified the significant use of permanent wetlands by gadwall and mallards nesting in California for their molting sites. I suggest that providing a greater extent of these habitats in California will likely reduce the frequency and distance of molt migration behavior. Increased permanent wetlands would also benefit cinnamon teal (*Spatula cyanoptera*), as they are also an important component of the breeding duck community in California (CDFW 2018). Important waterfowl regions in the Pacific Flyway must be protected and maintain stable desirable habitat through the acquisition of appropriate water rights and proper wetland management to ensure increased survival of molting waterfowl (see also Ringelman 1990, Fleskes *et al*. 2010). Although private landowners can be encouraged with possible incentives to provide summer water, it will fall primarily on federal and state wildlife areas to provide this function as water costs are high and management of these types of wetlands are expensive (CVJV 2006).

An important management objective will be to revisit and revise the management strategies that many wetland managers within California have adopted. California is unique when compared to other states, because it not only provides vital habitat to migrating waterfowl but also is a key breeding area for the species mentioned. Many managers place little emphasis on the breeding and postbreeding (i.e., wing molt) aspect of California resident waterfowl, with the focus instead on maximizing food values in wetlands to support winter waterfowl populations. I recommend that California wetland managers revise this strategy to consider the entire annual cycle of waterfowl so that appropriate habitat can be provided for all important annual stages (i.e., wintering, breeding, molting). Additionally, the behavioral plasticity in molting mallards that I observed in this study suggests that innovative and novel wetland management strategies might be adopted such as flooding seasonal marshes in mid to late August to provide molting habitat without reducing the ability to produce winter food for migrating waterfowl. Taking this approach, we can continue to strive to meet the population objectives set forth in the U.S. Fish and Wildlife North American Waterfowl Management Plan (USFWS 2012) as well as making a concerted effort to improve our state waterfowl breeding population goals (CVJV 2006).

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Figures – Chapter 1

Figure 1. Suisun Marsh, California with Grizzly Island Wildlife Area (WA) highlighted.

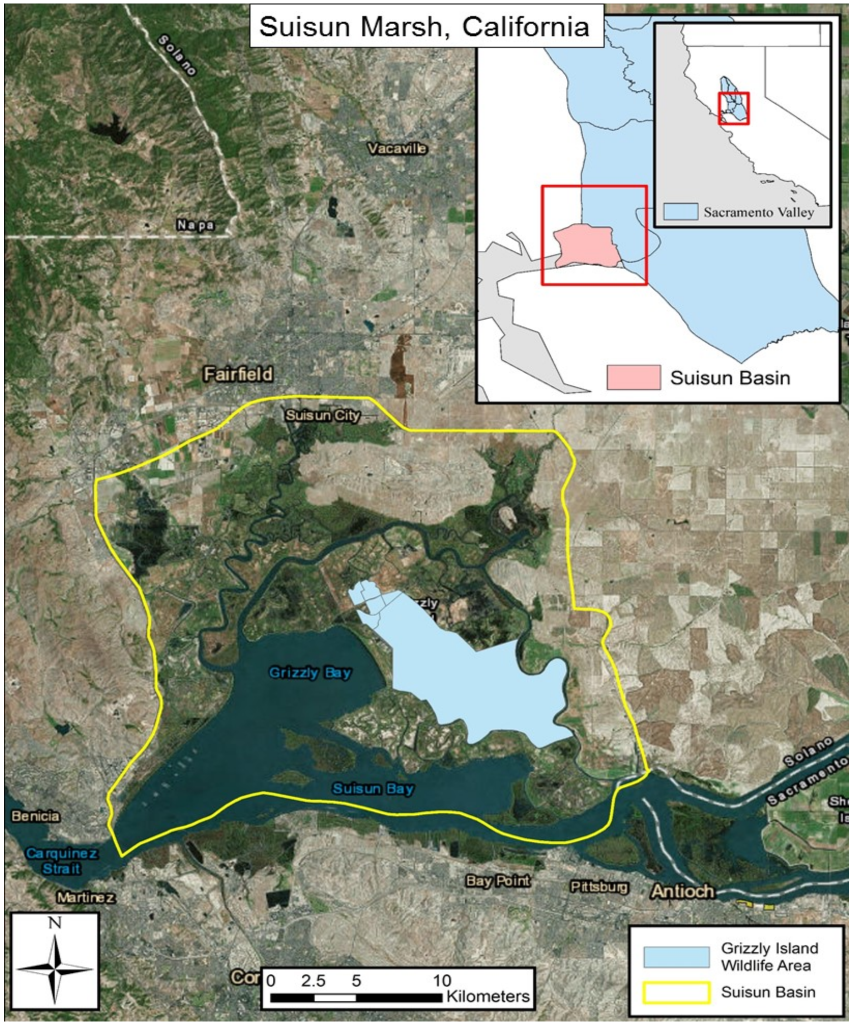


Figure 2. Grizzly Island Wildlife Area (WA) with uplands fields highlighted where nesting hen gadwall and mallards were monitored and captured during 2015-2018. Ducks that were not captured on nest were caught on duck clubs adjacent to the WA during summer banding efforts during June-August.

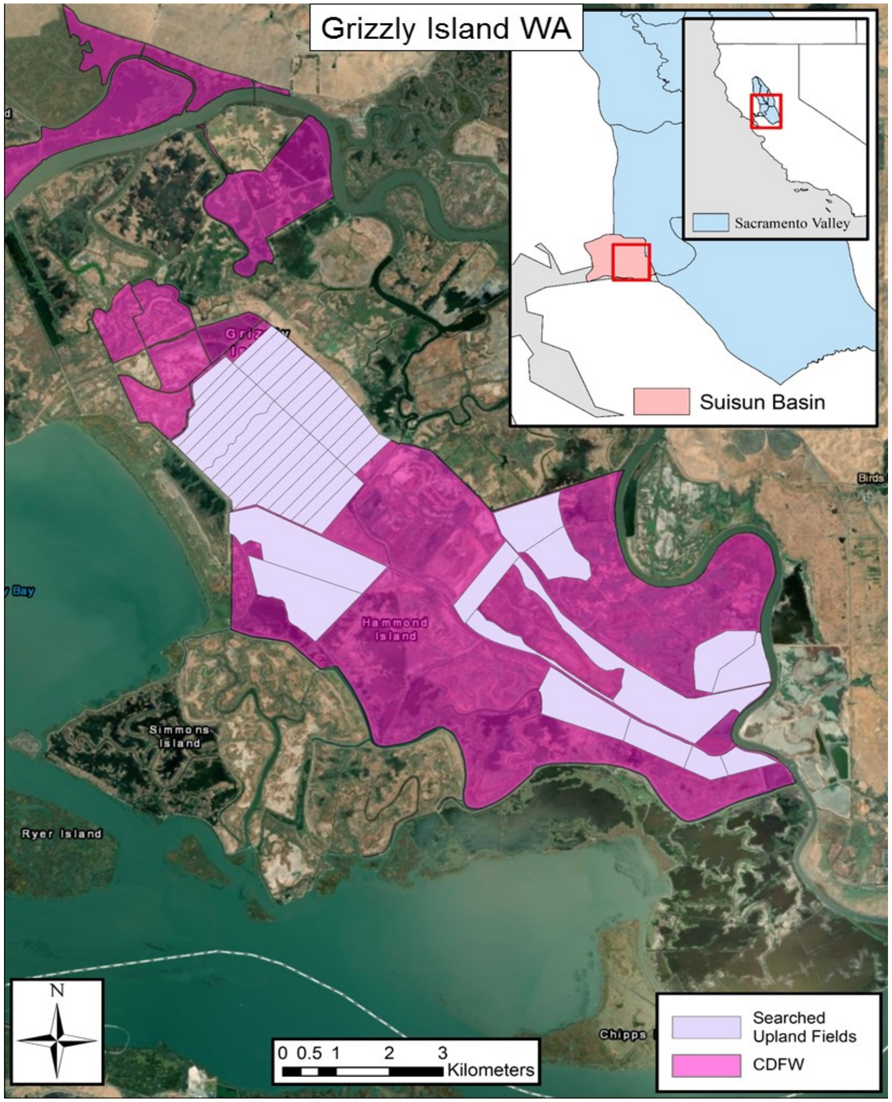


Figure 3. Distribution of gadwall (*n* = 12) step-lengths (distance between relocations) in molt period during 2015-2018. Dotted line represents 500 m cut-off for within wetland movements, red line represents determined 1000 m cut-off for “molting activity” determination.

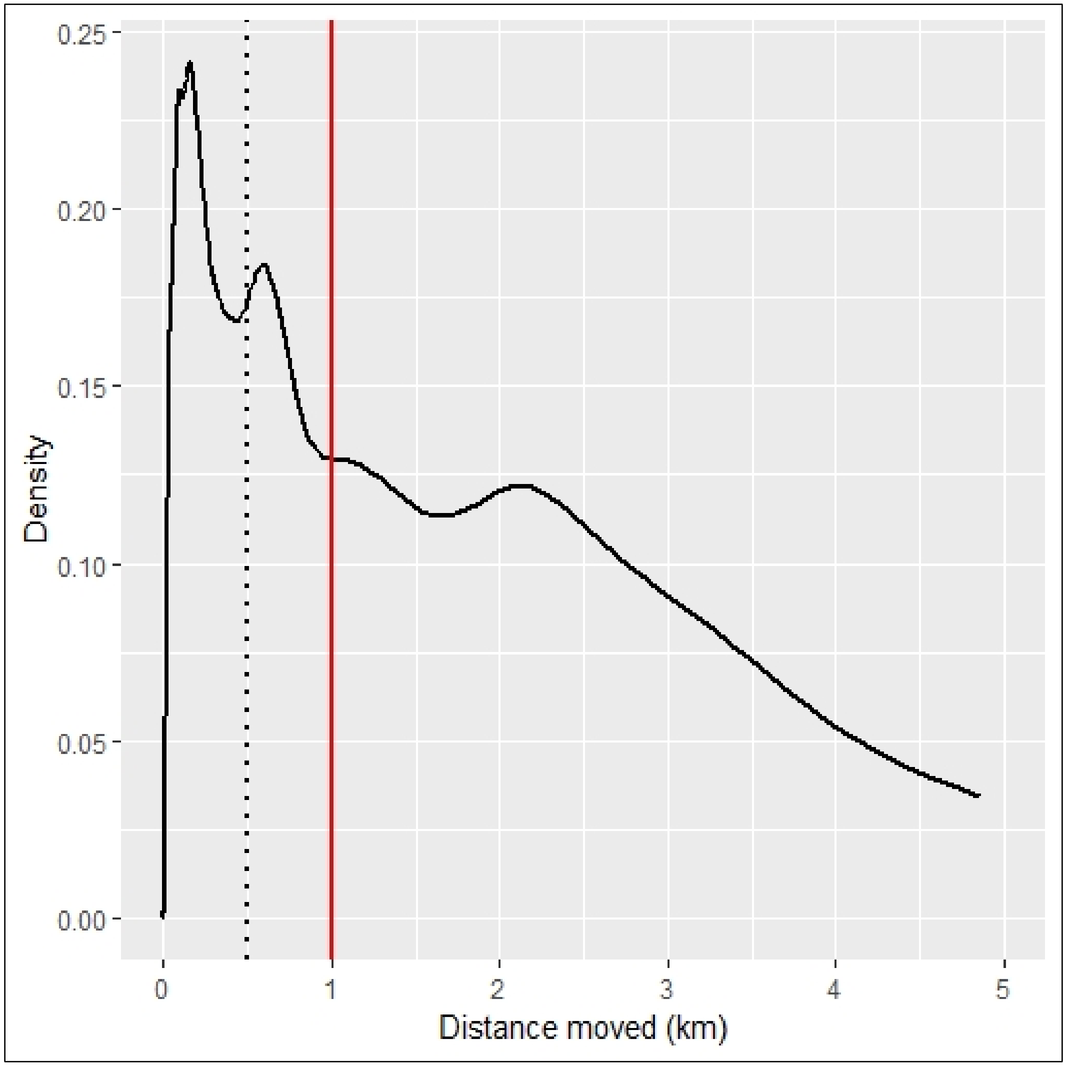


Figure 4. Distribution of mallard (*n* = 14) step-lengths (distance between relocations) during molt period during 2015-2018. Dotted line represents 500 m cut-off for within wetland movements, red line represents determined 1000 m cut-off for “molting activity” determination.

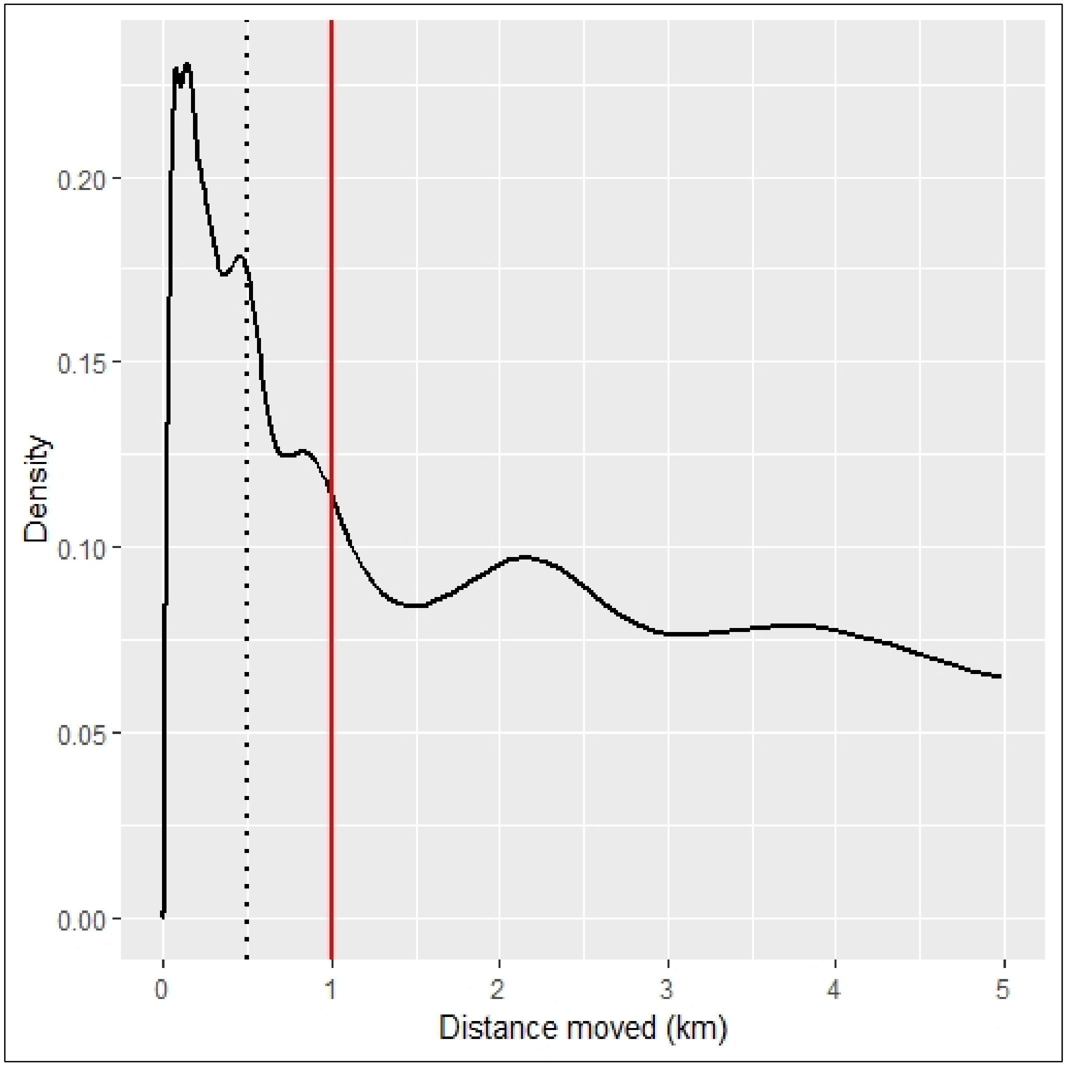


Figure 5. Segmentation (*K* = 20) of a mallard hen during the 2016 molting period. Displayed is distance between relocations (dist) on a 6-hour GPS interval and 2-day moving average (m.av) with the determined molting activity duration (8/28 – 10/5/16) highlighted.

Figure 6. Determined postbreeding molting locations of Suisun Marsh breeding gadwall (*n* = 30) and mallards (*n* = 25) in the Klamath Basin (Upper and Lower Klamath Basins) in California and Oregon during 2015-2018.

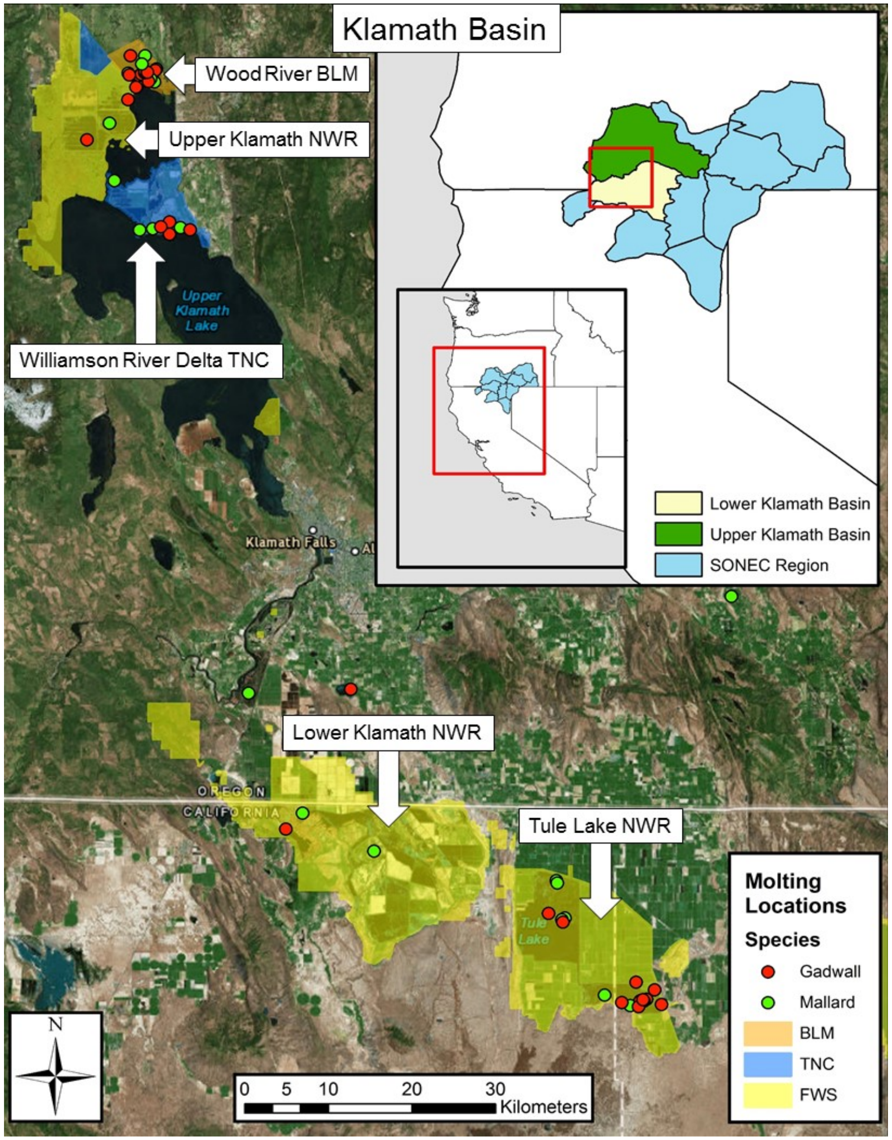


Figure 7. Determined postbreeding molting locations of Suisun Marsh breeding gadwall (n = 4) and mallards (n = 30) in the Northern Sacramento Valley (American, Butte, Colusa, and Sutter Basins) during 2015-2018.

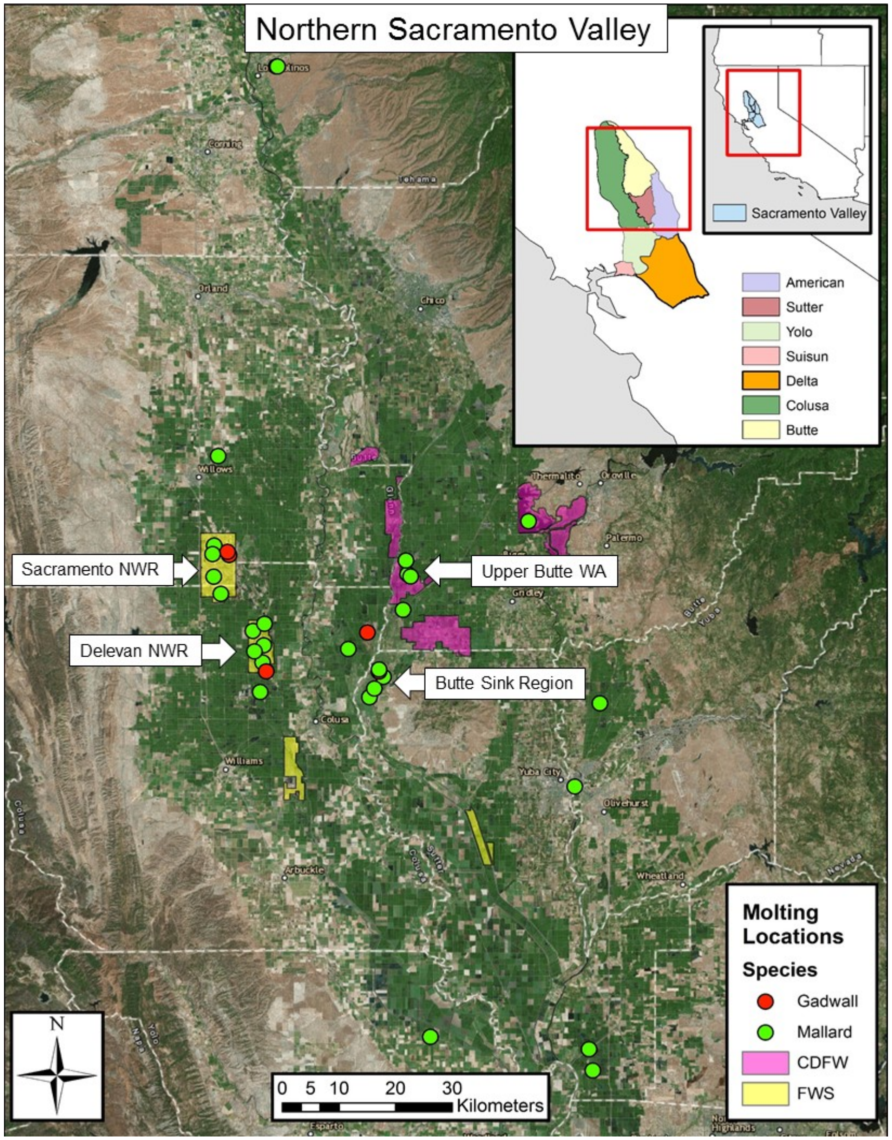


Figure 8. Determined postbreeding molting locations of Suisun Marsh breeding gadwall (*n* = 3) and mallards (*n* = 46) in the Southern Sacramento Valley (Delta, Suisun, and Yolo Basins) during 2015-2018.

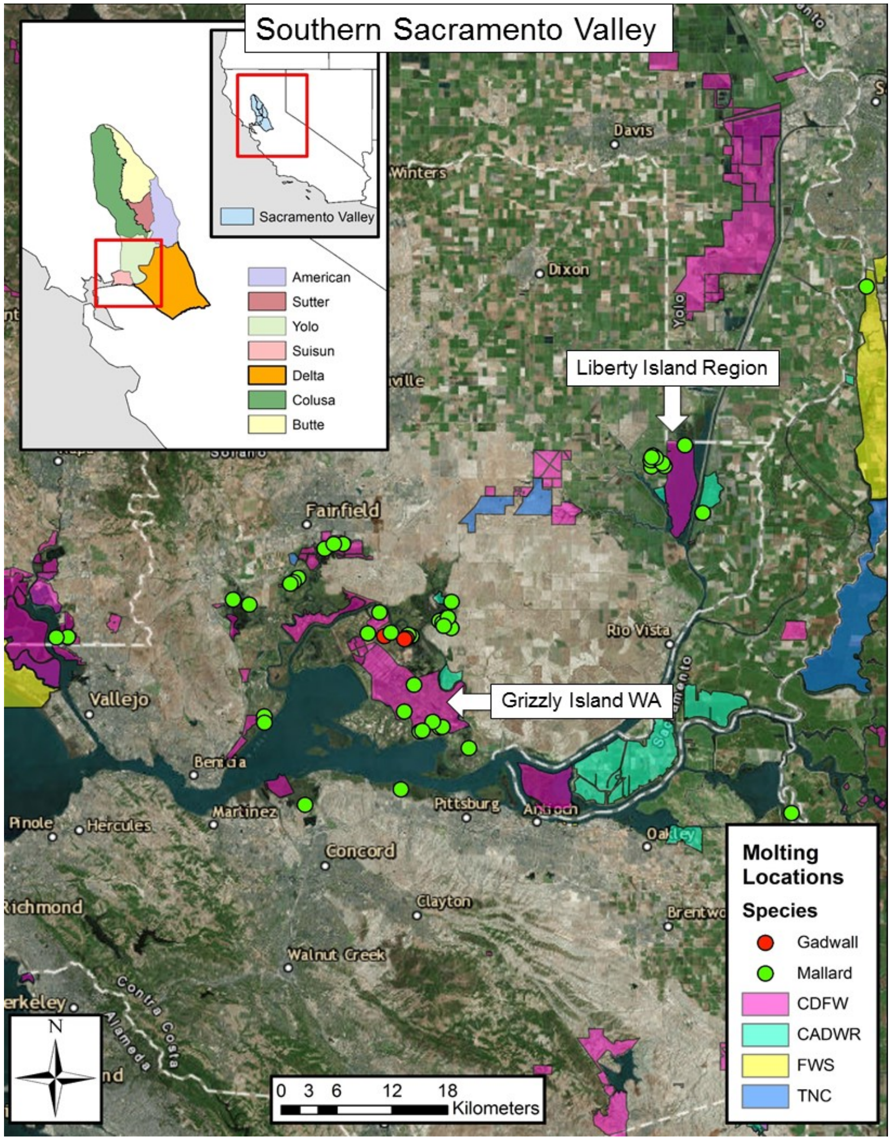
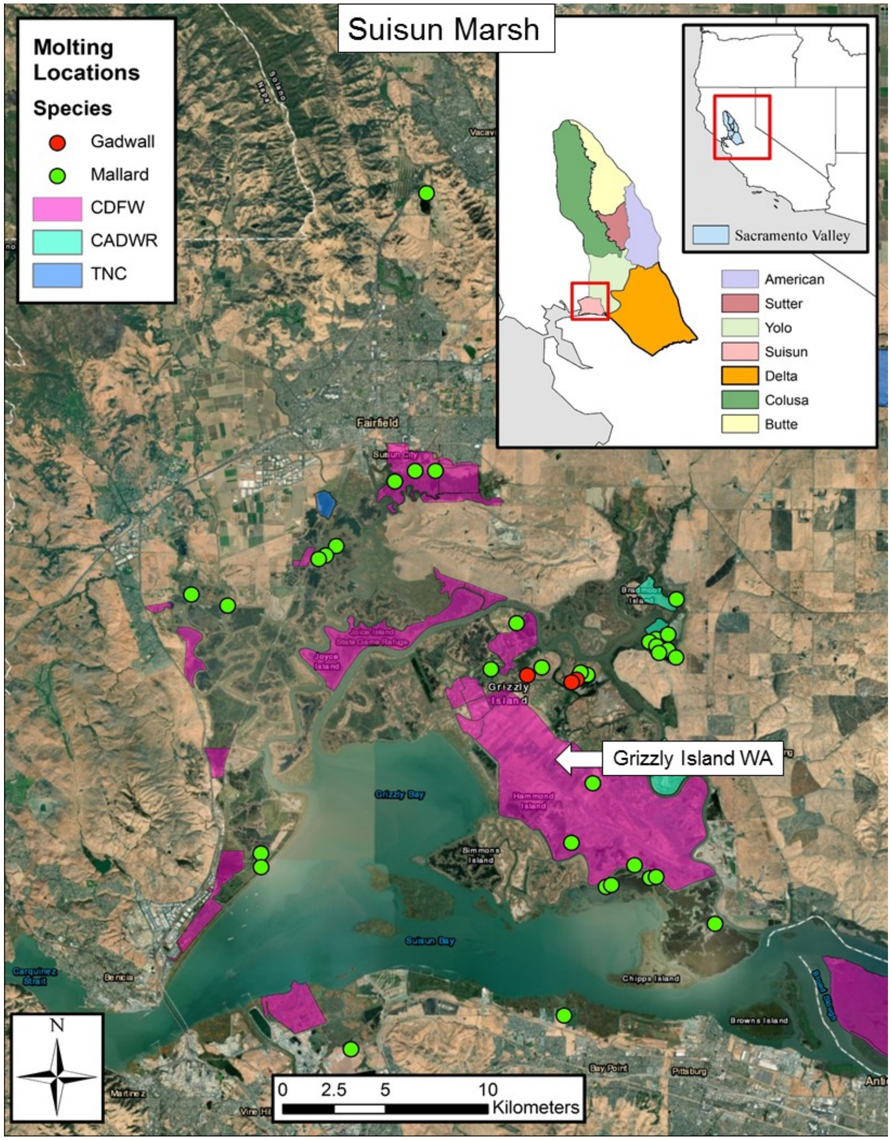


Figure 9. Determined postbreeding molting locations of Suisun Marsh breeding gadwall (*n* = 3) and mallards (*n* = 34) in the Suisun Marsh during 2015-2018.



Tables – Chapter 1

Table 1. Annual mean Julian/calendar date of Suisun Marsh breeding gadwall and mallards that departed the Suisun Marsh (SDD) to perform a postbreeding molt migration during 2015-2018.

	Gadwall						Mallards					
Year	n	Julian Date	Calender Date	SD	SE	CI	n	Julian Date	Calender Date	SD	SE	CI
2015	10	213	Aug. 1	9.37	2.96	6.71	8	221	Aug. 8	21.25	7.51	17.76
2016	22	216	Aug. 4	18.62	3.97	8.25	35	203	July 22	21.43	3.62	7.36
2017	4	214	Aug. 1	8.02	4.01	12.76	21	211	July 30	19.08	4.16	8.68
2018	13	207	July 26	15.12	4.19	9.14	13	201	July 20	26.91	7.46	16.26
Total	49	213	Aug. 1	15.61	2.23	4.48	77	207	July 25	22.25	2.54	5.05

Table 2. Annual mean molt migration distance (km; MMD) of Suisun Marsh breeding gadwall and mallards during 2015-2018. Birds that stayed within the Suisun Marsh to molt were given a value of 0 km as molt migration distance.

	Gadwall					Mallards				
Year	n	Mean Distance (km)	SD	SE	CI	n	Mean Distance (km)	SD	SE	CI
2015	11	389.03	170.76	51.49	114.72	17	116.25	182.72	44.32	93.95
2016	24	363.72	167.80	34.25	70.86	43	220.23	198.34	30.25	61.04
2017	4	379.92	170.11	85.06	270.68	30	121.78	158.70	28.97	59.26
2018	13	260.89	155.73	43.19	94.10	21	101.36	147.66	32.22	67.22
Total	52	344.61	168.24	23.33	46.84	111	155.21	182.28	17.30	34.29

Table 3. Annual mean Julian/calendar postbreeding molt start date (MSD) for Suisun Marsh breeding gadwall and mallards during 2015-2018.

	Gadwall						Mallards					
Year	n	Julian Date	Calender Date	SD	SE	CI	n	Julian Date	Calender Date	SD	SE	CI
2015	11	236	Aug. 24	20.13	6.07	13.52	17	246	Sept. 3	21.12	5.12	10.86
2016	24	240	Aug. 28	15.66	3.20	6.61	43	233	Aug. 21	16.96	2.59	5.22
2017	4	229	Aug. 17	3.70	1.85	5.88	30	239	Aug. 27	18.96	3.46	7.08
2018	14	238	Aug. 26	17.67	4.90	10.68	22	233	Aug. 21	31.85	6.95	14.50
Total	52	238	Aug. 26	16.53	2.29	4.60	111	237	Aug. 25	21.87	2.08	4.11

Table 4. Range and mean of molt start (MSD) and end dates for Suisun Marsh breeding gadwall (*n* = 52) and mallards (*n* = 111) during 2015-2018.

		Min.	1st Qtr	Median	Mean	3rd Qtr	Max.
Gadwall	Start	July 10	Aug. 17	Aug. 27	Aug. 26	Sept. 5	Sept. 23
	End	Aug. 15	Sep. 23	Oct. 1	Sept. 30	Oct. 11	Oct. 28
Mallards	Start	June 16	Aug. 15	Aug. 26	Aug. 25	Sept. 11	Oct. 8
	End	Aug. 19	Sept. 21	Oct. 7	Oct. 5	Oct. 18	Nov. 15

Table 5. Range and mean of molting activity duration (MAD) for Suisun Marsh breeding gadwall and mallards during 2015-2018.

	Min.	1st Qtr	Median	Mean	3rd Qtr	Max.
Gadwall	20.00	28.88	33.12	34.44	39.56	52.00
Mallards	23.00	32.38	38.25	40.53	48.50	69.75

	n	Mean Duration (days)	SD	SE	CI
Gadwall	34	34.44	8.62	1.48	3.01
Mallards	59	40.53	11.34	1.48	2.96

Table 6. Annual number of Suisun Marsh breeding gadwall and mallards migrating to each watershed basin to molt in California, Oregon, and Nevada during 2015-2018.

	Gadwall				Gadwall Total	Mallard				Mallard Total	Total
Basins	2015	2016	2017	2018		2015	2016	2017	2018		
American	-	-	-	-	0	-	2	1	1	4	4
Butte	1	-	1	-	2	-	6	3	4	13	15
Colusa	-	-	-	2	2	1	6	4	2	13	15
Coastal Range	-	1	-	-	1	-	1	-	-	1	2
Delta	-	-	-	-	0	1	2	6	2	11	11
Lower Klamath	3	8	1	2	14	2	6	4	-	12	26
Modoc Plateau	-	-	-	-	0	-	2	-	-	2	2
Pyramid Lake, NV	-	-	-	2	2	-	-	-	-	0	2
North Coast	-	1	-	1	2	-	-	-	-	0	2
North SF Bay	-	-	-	-	0	1	-	1	-	2	2
North Sierra	-	2	-	-	2	-	-	-	-	0	2
Northeast California	-	1	-	2	3	-	-	-	-	0	3
San Joaquin	-	-	-	1	1	1	1	1	1	4	5
Shasta Valley	1	-	-	1	2	1	-	-	-	1	3
Southern California	-	-	-	1	1	-	-	-	-	0	1
Suisun	1	2	-	-	3	9	8	9	8	34	37
Summer Lake, OR	1	-	-	-	1	-	-	-	-	0	1
Upper Klamath, OR	4	9	2	1	16	1	9	1	2	13	29
Yolo	-	-	-	-	0	-	-	-	1	1	1
Total	11	24	4	13	52	17	43	30	21	111	163

Table 7. Annual proportion of sample size of Suisun Marsh breeding gadwall (*n* = 52) and mallards (*n* = 163) molting in each watershed basin during 2015-2018.

	Gadwall				Gadwall Total	Mallard				Mallard Total	Total
Basins	2015	2016	2017	2018		2015	2016	2017	2018		
American	-	-	-	-	0.0%	-	4.7%	3.3%	4.8%	3.6%	2.5%
Butte	9.1%	-	25.0%	-	3.8%	-	14.0%	10.0%	19.0%	11.7%	9.2%
Colusa	-	-	-	15.4%	3.8%	5.9%	14.0%	13.3%	9.5%	11.7%	9.2%
Coastal Range	-	4.2%	-	-	1.9%	-	2.3%	-	-	0.9%	1.2%
Delta	-	-	-	-	0.0%	5.9%	4.7%	20.0%	9.5%	9.9%	6.7%
Lower Klamath	27.3%	33.3%	25.0%	15.4%	26.9%	11.8%	14.0%	13.3%	-	10.8%	16.0%
Modoc Plateau	-	-	-	-	0.0%	-	4.7%	-	-	1.8%	1.2%
Pyramid Lake, NV	-	-	-	15.4%	3.8%	-	-	-	-	0.0%	1.2%
North Coast	-	4.2%	-	7.7%	3.8%	-	-	-	-	0.0%	1.2%
North SF Bay	-	-	-	-	0.0%	5.9%	-	3.3%	-	1.8%	1.2%
North Sierra	-	8.3%	-	-	3.8%	-	-	-	-	0.0%	1.2%
Northeast California	-	4.2%	-	15.4%	5.8%	-	-	-	-	0.0%	1.8%
San Joaquin	-	-	-	7.7%	1.9%	5.9%	2.3%	3.3%	4.8%	3.6%	3.1%
Shasta Valley	9.1%	-	-	7.7%	3.8%	5.9%	-	-	-	0.9%	1.8%
Southern California	-	-	-	7.7%	1.9%	-	-	-	-	0.0%	0.6%
Suisun	9.1%	8.3%	-	-	5.8%	52.9%	18.6%	30.0%	38.1%	30.6%	22.7%
Summer Lake, OR	9.1%	-	-	-	1.9%	-	-	-	-	0.0%	0.6%
Upper Klamath, OR	36.4%	37.5%	50.0%	7.7%	30.8%	5.9%	20.9%	3.3%	9.5%	11.7%	17.8%
Yolo	-	-	-	-	0.0%	-	-	-	4.8%	0.9%	0.6%

Table 8. ANOVA results comparing Suisun departure date (SDD), mean molt migraton distance (MMD), molt start date (MSD), and molting activity duration (MAD), annually and between species for Suisun Marsh breeding gadwall (*n* = 52) and mallards (*n* = 163) during 2015-2018.

	Suisun Departure			Migration Distance			Molt Start			Molt Duration		
	Between Years			Between Years			Between Years			Between Years		
	Df	F-value	P-value	Df	F-value	P-value	Df	F-value	P-value	Df	F-value	P-value
Gadwall	3	1.406	0.253	3	1.538	0.217	3	0.545	0.654	3	0.704	0.557
Mallards	3	2.009	0.120	3	3.213	0.026	3	1.906	0.133	3	1.581	0.204
	Between Species			Between Species			Between Species			Between Species		
	Df	F-value	P-value	Df	F-value	P-value	Df	F-value	P-value	Df	F-value	P-value
	1	2.886	0.0918	1	40.11	<.0001	1	0.286	0.594	1	7.343	0.008

Table 9. Molting wetland types utilized (total number and percentage) by Suisun Marsh breeding gadwall and mallards each year during 2015-2018.

	Gadwall				Gadwall Total	Mallard				Mallard Total	Total
Wetland Type	2015	2016	2017	2018		2015	2016	2017	2018		
Irrigated Ag	-	-	-	-	0	-	1	-	-	1	1
Permanent	9	24	3	11	47	12	26	18	14	7-	117
Seasonal	1	-	1	-	2	1	1-	1-	5	26	28
Semi-Permanent	1	-	-	2	3	4	6	2	2	14	17
Total	11	24	4	13	52	17	43	30	21	111	163

	Gadwall				Gadwall Total	Mallard				Mallard Total	Total
Wetland Type	2015	2016	2017	2018		2015	2016	2017	2018		
Irrigated Ag	-	-	-	-	0.00%	-	2.33%	-	-	0.90%	0.61%
Permanent	81.82%	100.00%	75.00%	84.62%	90.38%	70.59%	60.47%	60.00%	66.67%	63.06%	71.78%
Seasonal	9.09%	-	25.00%	-	3.85%	5.88%	23.26%	33.33%	23.81%	23.42%	17.18%
Semi-Permanent	9.09%	-	-	15.38%	5.77%	23.53%	13.95%	6.67%	9.52%	12.61%	10.43%

Table 10. Entities that operate each type of molting wetland that were utilized by Suisun Marsh breeding gadwall and mallards during 2015-2018.

Ownership	Irrigated Ag	Permanent	Seasonal	Semi-Permanent	Total
City	0	5	0	0	5
County	0	1	0	0	1
Federal	0	47	8	5	60
NGO	0	13	0	0	13
Private	1	38	20	10	69
State	0	13	0	2	15

Table 11. Total number of molting wetland types that were utilized by Suisun Marsh breeding gadwall (*n* = 52) and mallards (*n* = 111) in each basin during 2015-2018.

Basins	Irrigated Ag	Permanent	Seasonal	Semi-Permanent	Total
American	-	3	1	-	4
Butte	-	3	10	2	15
Colusa	-	1	10	4	15
Coastal Range	-	2	-	-	2
Delta	-	2	7	2	11
Lower Klamath	-	25	-	1	26
Modoc Plateau	1	1	-	-	2
Pyramid Lake, NV	-	2	-	-	2
North Coast	-	2	-	-	2
North SF Bay	-	2	-	-	2
North Sierra	-	2	-	-	2
Northeast California	-	3	-	-	3
San Joaquin	-	5	-	-	5
Shasta Valley	-	3	-	-	3
Southern California	-	1	-	-	1
Suisun	-	29	-	8	37
Summer Lake, OR	-	1	-	-	1
Upper Klamath, OR	-	29	-	-	29
Yolo	-	1	-	-	1
Total	1	117	28	17	163

Table 12. Watershed basins and wetland type (P = Permanent, S = Seasonal, SP = Semi-permanent, IA = Irrigated agriculture) utilized to undergo molt by Suisun Marsh breeding gadwall (*n* = 2) and mallards (*n* = 11) with two years of molting data during 2015-2018.

	Gadwall				Mallards																					
	WATE 26.1		BIRD 70.1		BIRD 09.1		BIRD 22.1		BIRD 33.1		BIRD 44.1		SAKR 08.1		SAKR 12.1		SAKR 16.1		SAKR 20.1		WATE 11.1		WATE 13.2		WATE 15.1	
Basins	2015	2016	2016	2017	2016	2017	2016	2017	2016	2017	2016	2017	2017	2018	2017	2018	2017	2018	2017	2018	2015	2016	2016	2017	2015	2016
Butte									X				X										X	X		
Colusa							X	X										X								
Coastal Range																										X
Delta																	X									
Lower Klamath	X		X	X	X	X				X		X														
Modoc Plateau											X															
San Joaquin																										
Suisun															X	X			X	X					X	
Upper Klamath, OR		X												X							X	X				
Wetland Type	P	P	P	P	P	P	S	P	S	P	IA	P	S	P	P	P	S	S	SP	SP	P	P	P	P	P	P

Chapter 2

Identifying factors influencing the ecology of the simultaneous wing molt in gadwall (*Mareca strepera*) and mallards (*Anas platyrhynchos*) nesting in the Suisun Marsh of California

Abstract

Using GPS-GSM backpacks, I tracked and monitored hen gadwall (*Mareca stepera*) and hen mallards (*Anas platyrhynchos*) nesting in the Suisun Marsh of California during 2015-2018. Using nesting data collected during the breeding season as well as data gleaned from postbreeding movements, I analyzed how reproduction could potentially affect postbreeding ecology, specifically the synchronous wing molt. Using linear multiple regression models, I modeled the effects of year, nest initiation date, nest end date, nest success, age (SY vs ASY), and body condition on three response variables. These response variables included molt migration distance, molting activity duration, and molt start date. Molt migration distance was analyzed as both a response variable as well as an explanatory variable in predicting molt start date and molting activity duration. Molt start date was likewise included in candidate models to estimate molting activity duration. The top performing model for molt migration distance for hen gadwall was the null model, suggesting the explanatory variables analyzed were not good predictors of molt migration distance. However, nest initiation date was a strong predictor for molt migration distance for hen mallards. Model-averaged estimates indicated molt migration distance was reduced by 3.056 km (SE = 1.251) for every day later a hen mallard initiated a nest during the spring. The top model when analyzing molting activity duration in gadwall, included molt migration distance as the explanatory variable. Yet, this model competed with the null model suggesting limited statistical support for migration distance predicting molting activity duration in gadwall. An additive model that included molt start date and nest success as the variables was the top performing model in estimating molting activity duration in mallards.

Model estimates indicated molting activity duration decreased 0.5 days (SE = 0.10) for every day later a mallard started to molt and decreased by 7.9 days (SE = 3.56) if a hen mallard had a successful nest. Once again, there was not a strong relationship between molt start date and any of the parameters analyzed for gadwall with the null model being the top performing model. However, annual variation (year) was the top model in determining molt start date in mallards. Predicted mean molt start date for mallards varied by more than 3 weeks amongst years, with the earliest occurring in 2016 on August 21st (SE = 3.22), followed by 2018 on August 22nd (SE = 6.21), then 2017 on September 8th (SE = 6.52), and the latest occurring in 2015 on September 11th (SE = 9.22). Further research needs to be conducted to gain a better understanding of how annual variation in conjunction with cross-seasonal effects influences, not only the wing molt but other waterfowl life history events, as these interactions may have large scale implications in waterfowl population dynamics.

Introduction

The breeding season and synchronous wing molt (hereafter referred to as "wing molt" or "molt") are subsequent life-history events and important parts of the waterfowl annual cycle (Batt 1992, Hohman *et al*. 1992). Endogenous reserves (i.e., lipids and protein) are the most important factors in determining the degree of success (i.e., fecundity, survival) a bird will have during the breeding and molting periods (Gloutney and Clark 1991, Richardson and Kaminski 1992, Hohman *et al*. 1992). The measurement of these nutrient reserves or nutritional state has been defined as an animal's "body condition" (Jakob *et al*. 1996). Poor body condition prior to the breeding season can lead to hens having delayed nest initiation, smaller clutches, and a lower rate of breeding success (Pattenden and Boag 1989, Devries et al. 2008). Similar harmful consequences can occur when birds begin the wing molt with a reduced body condition, which can result in a delayed molt, longer molt duration, and lower quality grown feathers (Pehrsson 1987, Richardson and Kaminski 1992). Furthermore, temporal constraints in late summer due to devoted time to nest and brood care have been shown to cause some Artic-breeding birds to increase the rate of their wing molt in late summer, leading to lower quality feathers being grown (Dietz *et al.* 2013). Cross-seasonal effects have been analyzed linking winter body condition and reproductive success in waterfowl (Barboza and Jorde 2002, Devries *et al.* 2008) as well as connecting these effects to the potential changes at a population level (Davies and Cooke 1983, Alisauskas 2002). However, research is lacking in understanding the more proximate consequences of reproductive investment on postbreeding life history ecology (i.e., wing molt, molt survival) in waterfowl.

Gadwall (*Mareca stepera*) and mallards (*Anas platyrhynchos*) are the two most common breeding ducks in California (CDFW 2018) and comprise a large portion of the annual waterfowl harvest (Olson 2018). These two species utilize many regions in California and Oregon to undergo their annual wing molt during the late summer (refer to chapter 1; Yarris *et al.* 1994, Fleskes *et al.* 2010). Demographic models have suggested that California mallard populations are highly sensitive to adult female survival during the non-breeding season (Oldenburger 2008). Furthermore, high mortality has been associated with the wing molt due to the inability of birds to escape predators and disease (Fleskes *et al.* 2010, Fleskes *et al.* 2017).

Through the advancement of GPS-GSM (Global Positioning System – Global System for Mobile communications) technology, researchers now have the ability to remotely track and monitor waterfowl with fine spatiotemporal detail throughout the annual cycle (i.e., breeding, molting, overwintering). Analyzing movements within and among these life history periods would provide a better understanding of what areas are critical for each period, how seasonal factors (i.e., precipitation) may influence movement, and how each period may influence another (i.e., cross-seasonal effects). The goal of my study is to utilize this new GPS-GSM technology to track hen gadwall and mallards from the breeding grounds located in the Suisun Marsh of California to their selected molting locations during 2015-2018. Using nesting information gathered for marked birds (i.e., nest initiation, nest fate) as well as data gleaned from postbreeding movements (i.e., molt migration distance) and molt site selection, I assess potential relationships and trade-offs that exist between the breeding season and the wing molt. Better understanding of these interactions can help in guiding future management and conservation decisions as well as develop more refined demographic models for California breeding waterfowl.

Methods

Study Area, Duck Capture and Transmitter Attachment, Data Collection, and Molt Activity Determination

Please refer to chapter 1 for detailed description of methods.

Data Analysis

I examined the relationships of three response variables to assess the impact of nesting demographics on molt migration distance (hereafter MMD), molt start date (hereafter MSD), and molting activity duration (see chapter 1 for definition; hereafter MAD) using linear multiple regression models (Burnham and Anderson 2002). I was also interested in how these factors varied among years (2015-2018; hereafter YEAR), nest start date (hereafter NSD), nest success (hatched: yes or no; hereafter NS), nest end date (hereafter NED), age (second-year vs after second-year; hereafter AGE), and a scaled index of body condition from the end of nesting (hereafter SBCIe). I analyzed MMD as both a response variable as well as an explanatory variable in predicting MSD and MAD. MSD was likewise included in candidate models to estimate MAD. I estimated effects and indicated variable importance across a candidate set of models using information-theoretic approaches including estimation of relative model importance and model averaging (Burnham and Anderson 2002).

We located duck nests by searching individual upland fields every 3 weeks following standard nest-searching techniques modified from Mclandress *et al.* (1996). We determined NS for each individual nest during the field season through weekly nest visits using methods laid out in Klett *et al.* (1986). We established NSD by determining incubation stage by candling eggs (Weller 1956) on the first nest visit and estimated by back-dating from the age (incubation stage plus clutch size) when we found the nest; assuming that ducks laid 1 egg/day. We determined NED through a few methods depending on the status of the nest during the weekly visit. If the nest was hatching during the visit, then nest end date was recorded as the day of the visit. If the nest hatched prior to the next nest visit, then the nest end date was calculated based on the last recorded incubation stage. If the nest was depredated by a predator, then the nest end date was placed at the median date between the last and current nest visit. Lastly, if the nest was abandoned then the nest end date was placed at the previous nest visit date.

To determine SBCIe, I first calculated a body condition index for each duck by calculating the ratio of body mass at capture by wing length (Ringelman and Szymczak 1985). Next, I natural log-transformed these values to rescale them relative to mean value for each species to create a normally distributed body condition index centered on zero. Since duck body condition is known to decline during incubation (Gatti 1983, Afton and Paulus 1992), mass-at-capture may represent an imprecise estimate of body condition. I conducted a linear regression between scaled body condition index and nest age at capture to create an equation to predict body condition index at nest termination for each hen. The relationship between scaled body condition index and nest age was significant ($y = 0.040 + -0.003X$, $R^2 = 0.07$, P-value = 0.002).

I also assessed SBCIe throughout the breeding season for both species by using a linear regression between SBCIe and NSD. This relationship was not significant ($y = -0.10 + 0.001X$, $R^2 = 0.02$, $P = 0.07$), indicating additional endogenous cycles/temporal variation did not need to be included for precise projections of body condition.

I conducted all statistical analyses using R statistical software (R Core Team 2016). Due to different molting ecology (i.e., MMD, MAD, molt site selection; refer to chapter 1), I analyzed gadwall and mallards separately. For each species, I developed a suite of candidate models based on *a priori* hypotheses. After running my analysis, I conducted model selection for each of the three response variables using the package ‘ModelInference’ (Herzog 2018). I conducted correlations between nesting parameters to guard against multicollinearity which can lead to problems in interpreting predictor variables (Mansfield and Helms 1982). I found that NSD and NED were highly correlated ($R^2 = 0.79$, $P < 0.001$). Therefore, I modeled them separately with a complete model set with each of the response variables and chose the parameter that performed the best to retain in the candidate model sets. I modeled MMD using YEAR, NSD, NS, AGE, and SBCIe (model set, $n = 40$). I modeled MAD using YEAR, NED, NS, MMD, MSD, AGE, and SBCIe ($n = 160$). Lastly, I modeled MSD using YEAR, NED, NS, MMD, AGE, and SBCIe ($n = 80$). I only included variables as additive effects except for YEAR which occurred both additively and as an interaction with SBCIe (YEAR*SBCIe) in each model set. This interaction was added to account for annual variation that may occur in body condition due to climatic patterns and habitat conditions (Owen and Cook 1977). I fit linear regression models using the ‘lm’ function in the package ‘stats’. I used Akaike’s information criterion with second order correction for small sample sizes (AIC_c) to rank models. Only models with ΔAICc less than 2.0 of the top performing model were retained. Variable importance was determined using the ‘estimateVariableImportance’ function in package ‘ModelInference’ which calculated variable importance and conditional parameter estimates with associated standard errors across all models for each response variable. I ranked variables using the parameter likelihood value (Burnham and Anderson 2002) and determined significance based on their associated *P*-values (< 0.05) within each variable summary. I used conditional model average coefficients for significant variables to predict effects on explanatory variables and present results with 95% confidence intervals.

Results

The number of available samples for each analysis varied because of differences in the capacity to acquire data for each response variable, resulting from gaps in relocation acquisition and ambiguous nesting information. For both MMD and MSD, telemetry and breeding records were sufficient to identify migration patterns for 47 female gadwall and 66 female mallards. The MAD analysis was limited to 36 female gadwall and 41 female mallards due to my inability to identify MAD for all individuals resulting from intermittent relocation collection. The MAD model set for mallards was limited to years 2016-2018 because I was not able to identify parameters to calculate MAD for birds in 2015.

Molt Migration Distance

The top performing model for MMD for hen gadwall was the null suggesting the variables considered were not effective predictors of MMD (Table 1). NSD performed similarly to the null with a ΔAICc of 0.150 and nearly the same AIC weight ($w_i = 0.11$). The NSD parameter also showed some evidence in determining MMD in hen gadwall with a parameter likelihood of 0.515 but it was not significant ($P = 0.147$; Table 1).

For female mallards, 3 highly inter-related models were nearly equivalent at estimating MMD (ΔAICc < 2.0). NSD was included in all 3 of the models, reflected by a high parameter likelihood value (0.850), and was significant in determining MMD ($P = 0.007$; Table 2). Model-averaged estimates indicated MMD was reduced by 3.056 km (SE = 1.251) for each day increase of NSD (Fig. 1). Models that included AGE and NSD (ΔAICc = 0.751) as well as NS and NSD (ΔAICc = 0.964) as covariates performed similarly to NSD (Table 2). Although the model AGE and NSD ranked higher than NSD and NS, the AGE parameter did not have a significant effect on MMD ($P = 0.450$) suggesting it did not add much to the model, while NS showed some evidence ($P = 0.074$) in determining MMD. Estimates indicated mallards increased their MMD by 59.98 km (SE = 49.35) when producing a successful nest compared to birds that were unsuccessful that initiated a nest on the same date (Fig. 2).

Molting Activity Duration

MAD for female gadwall was best estimated with MMD as a sole covariate, but this model competed with the null model which was ranked second among candidate models (Table 3). Although there was only limited statistical support from model-averaged estimates (-1.8 days per 100 km traveled to molt, SE = 1.0; Fig. 3), there was some evidence of MMD predicting MAD (parameter likelihood = 0.611, $P = 0.067$).

The top model to predict MAD in female mallards included both MSD and NS (Table 4). MSD and NS had parameter likelihood values of 1.0 and 0.788, respectively, and MSD was significant in predicting MAD ($P < 0.001$). The second-best performing model included NS, MMD, and MSD (ΔAICc = 0.336) as covariates. However, MMD had a much lower parameter likelihood value compared to NS and MSD and was not significant ($P = 0.917$) in determining MAD. Model estimates indicated MAD decreased by 0.5 days (SE = 0.10) for every day later a bird started molt and decreased by 7.9 days (SE = 3.56) if a bird yielded a successful nest (Fig. 4).

Molt Start Date

The top performing model when examining MSD for hen gadwall was the null model suggesting no relationship between the parameters analyzed and MSD (Table 5). This is reflected in the variable importance table as all variables displayed a parameter likelihood value of less than 0.50 and were not significant in predicting MSD.

Annual variation (YEAR) was the only factor affecting female mallard MSD in the top model (Table 6). YEAR had a parameter likelihood value of 0.554 and was significant ($P = 0.035$) in determining MSD. Model estimated mean MSD varied by more than 3 weeks amongst years, with the earliest occurring in 2016 on August 21st (SE = 3.22), followed by 2018 on August 22nd (SE = 6.21), then 2017 on September 8th (SE = 6.52), and the latest occurring in 2015 on September 11th (SE = 9.22, Fig. 5). MSD and NED was the next best performing model (ΔAICc = 0.980) and NED was determined to be a significant variable ($P = 0.049$) in MSD predictions. Model estimates indicated for every 10-day increment increase of NED for mallards, MSD was delayed by 2.2 days (SE = 1.65; Fig. 6).

Discussion

Molt Migration Distance

Although MMD is a continuous variable it can also indicate specific regions within California and Oregon that were utilized by female gadwall and mallards. The main regions that were laid out in chapter 1 were as follows (ascending order from closest to furthest from breeding grounds based on MMD traveled by transmitter birds): Suisun Marsh (hereafter SM; MMD = 0 km), South Sacramento Valley (hereafter SSV; $\bar{x}$ = 29.87 km, SE = 1.91), North Sacramento Valley (hereafter NSV; $\bar{x}$ = 124.8 km, SE = 6.62), Lower Klamath Basin (hereafter LKB; $\bar{x}$ = 420.77 km, SE = 2.31), and Upper Klamath Basin (hereafter UKB; $\bar{x}$ = 491.08 km, SE = 1.74).

Throughout the study 57% of the hen gadwall I marked used the LKB and UKB regions to undergo wing molt (refer to chapter 1). Thus, it is reasonable that the variables analyzed in this study were not effective at explaining the small variation present in MMD (Fig. 1).

Mallards within this study who initiated nests earlier tended to migrate farther to undergo their wing molt, however, successful nesters migrated farther than failed nesters, initiating nesting on the same date (Fig. 2). Hens with earlier NSD may have had higher brood survival (Dzuz and Clark 1998), allowing them to produce a flighted brood with ample time to seek out more suitable molting habitat away from SM. Further analysis could evaluate if marked hens with unsuccessful nests early in spring re-nested later in the breeding season (Arnold *et al.* 2010), extending their stay on the breeding grounds and potentially limiting their opportunity to seek molting habitat away from SM. Hens that initiated nests later in the spring may not have had the time to seek more desirable molting habitat, forcing them to stay within or in closer proximity to SM. A conclusion that can be surmised is that hen mallards, when given the opportunity (i.e., produce a successful brood early in the breeding season), prefer to travel away from the SM to regions such as the LKB or UKB to molt. This may be due to deteriorating habitat conditions in the late summer months in the SM, as salinity levels begin to increase in wetlands (Miller *et al.* 1975, Rollins 1981, Garone 2011) or wetlands become scarcer as managers begin to draw marshes down to perform maintenance or attempt to grow duck food for the arrival of migrating ducks in the coming fall (Gilmer *et al.* 1982). Waterfowl may have an affinity to LKB and UKB regions due to the wetlands present in the Klamath Basin being less severely affected by agriculture and urbanization than other regions within the Sacramento Valley (Akins 1970). These wetlands may also be more reliable from year to year and less vulnerable to vast changes in habitat conditions such as drought (Akins 1970) which may promote molt site fidelity (Robertson and Cooke 1999). The increased survival for molting waterfowl in these areas may be a function of these static conditions (Fleskes *et al.* 2010).

Molting Activity Duration

Although not significant, it is noteworthy that MAD was less in gadwall with larger MMD values, which are birds primarily using the LKB and UKB regions (Fig. 1 and 3). I expected that the flightless duration was not actually affected, however, the few birds that chose to molt in SM or NSV (lower MMD values) had more time to exploit their selected molting wetlands to forage and increase their nutrient reserves before and after the flightless period, therefore increasing their MAD. Wetlands located in the LKB and UKB regions, although preferred (refer to chapter 1, Fleskes *et al.* 2010), may not provide a large food source such as invertebrates and moist-soil plants due to their long hydroperiod (Ringelman 1990, Corti *et al.* 2013) and less intense management. Therefore, birds must explore other marshes shortly after gaining flight to replenish their depleted nutrient reserves. Another compounding factor may be the fact that the hunting season in the Klamath region also begins in late September, a month earlier then the Sacramento Valley, which may force birds to displace from their molting wetlands due to disturbance from hunters.

As with gadwall, the flightless period within MAD for mallards may not have been directly affected by the increasing MSD (Fig. 4). Birds with later MSD were most likely successful breeders or re-nesters, which predisposed them to stay within SM into early summer leaving little time to explore and assess wetlands. These birds may have been faced with less than ideal habitat conditions, as food sources become depleted and water quality and availability begins to diminish in late summer (Miller *at al.* 1975, Rollins 1981). These declining condtions may compel birds to shorten their MAD as much as possible so more desirable habitats could be found and exploited.

Molt Start Date

The variables analyzed were not good predictors of MSD for hen gadwall, which is not unexpected as gadwall mean nest initiation for the study was 10 days later than mallards (gadwall: $\bar{x}$ = 130. 89, SE = 2.04; mallards: $\bar{x}$ = 120.9, SE = 2.37). Further, most gadwall traveled to the Klamath Basin to molt (Fig. 1), leaving a smaller window (molting period) to undergo molt and less variation within MSD when compared to hen mallards.

During 2015, most marked hen mallards stayed within SM (53%) or departed much later than in subsequent years (refer to chapter 1). This may have occurred due to trapping efforts being delayed, causing a large portion (87.5%) of mallards being caught later in the breeding season in late May and June. These late nesters would have an increased chance of staying within SM (Fig. 2) as well as delaying their MSD (Fig. 6). During 2016 – 2018 trapping effort was more consistent across the spring, with most mallards being caught on nest between late April - June. Although 2015 had disproportionate trapping effort across the breeding season, there may have been contributing factors leading to the difference in MSD. 2015 was the extension of a four-year drought (2011-2015; CADWR 2015) and birds that departed SM may have had difficulty locating desirable molting habitat, leading to a delayed MSD. 2017 showed a similar MSD as 2015, however conditions were vastly different as fall/winter precipitation and snowpack were at record high levels leading to the late onset of spring temperatures (CADWR 2017). Nest initiation for waterfowl has been correlated with temperatures in late April and May (Hammond and Douglas 1984) which was demonstrated in 2017, as mean nest initiation for mallards affixed with transmitters occurred 23 days later ($\bar{x}$ =143.3, SE = 7.98) than the study mean ($\bar{x}$ = 120.9, SE = 2.37). This delay in nest initiation caused an increase of NED for the 2017 mallards and may have contributed in delaying MSD (Fig. 6). 2016 and 2018 had analogous fall/winter precipitation and snowpack with just below average totals (CADWR 2018). Habitat conditions were presumably similar during these two years for both breeding and molting leading to comparable MSD.

Conclusion and Cross -Seasonal Effects

There have been many studies analyzing the cross-seasonal effects on waterfowl from one critical life-history event to the next, especially in regard to winter habitat and body condition affecting reproductive success the following breeding season (refer to Sedinger and Alisauaskas 2014). This study provides evidence of how the breeding season may potentially impact the subsequent important annual event of the synchronous wing molt. Costs of reproduction, such as temporal constraints due to nest incubation and brood care, seems to impede the ability for mallards to fly great distances to exploit preferred habitat in the Klamath Basin as well as limits the time available for birds to seek desirable molting habitat. Although it is yet to be determined if the actual flightless period is affected, the duration that both gadwall and mallards utilize wetlands before and after the molt appears to be affected by how far a bird must travel (or region utilized) to find suitable molting habitat as well as how late a bird nests into the breeding season. These effects caused by reproduction need to be further researched to determine how they may change pre and post molting body condition, survivorship of molting birds, and degree of molt success (i.e., quality of feathers produced; Pehrsson 1987). Lower quality birds post-molt can lead to lower winter body condition which can affect winter survival and mate selection, along with affecting breeding propensity, nest initiation date, and clutch size the following nesting season (Heitmeyer 1995, Devries *et al.* 2008). These cross-seasonal effects need to be better understood as they may have large scale implications in waterfowl population dynamics.

Management Implications

Through this research I have demonstrated that gadwall and mallards nesting in the SM, when certain conditions are met (i.e., early nest initiation), prefer to depart from SM and molt in other regions; particularly the Klamath Basin. Greater molt migration distances can lead to lower body condition prior to the wing molt as more nutrient reserves are depleted (Bairlein 1990). This may lead to delayed molt and longer molt durations (Richardson and Kaminski 1992) increasing risk to predation and disease. Many successful breeding hens are confined to the breeding grounds to raise a brood until late July, leaving little opportunity to find preferred molting habitat in Klamath. Thus, these females must molt in potentially less desirable wetlands that are in close proximity to the SM.

Summer molting wetlands need to be more readily available across the landscape, especially within SM to provide late breeders with quality molting habitat that can maximize hen survival during this vulnerable period. By increasing the survival of successful breeding hens through the molt I would expect an increase in the rate of returning older birds (ASY females) to SM to breed each spring (Doty and Lee 1974, Lokemoen *et al.* 1990). Older nesting birds have been shown to have a greater breeding propensity, earlier nest initiation, larger clutch sizes, better body condition, and higher rates of re-nesting (Coulter and Miller 1968, Krapu and Doty 1979, Arnold *et al.* 2010). The breeding season in coordination with other life cycle components, the wing molt being a particularly critical one, plays an integral role in population dynamics of waterfowl and through the improvement of many of the factors mentioned, not only SM but California, can vastly increase regional breeding waterfowl populations.

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Figures – Chapter 2

Figure 1. Predicted postbreeding **Molt Migration Distance (MMD)** (km) based on **Nest Start Date (NSD)** (Julian date) for female mallards (*n* = 66) nesting in the Suisun Marsh of California during 2015-2018 using conditional model-averaged coefficients. Gadwall (*n* = 47) mean MMD displayed showing majority of hens traveling to the Klamath Basin.

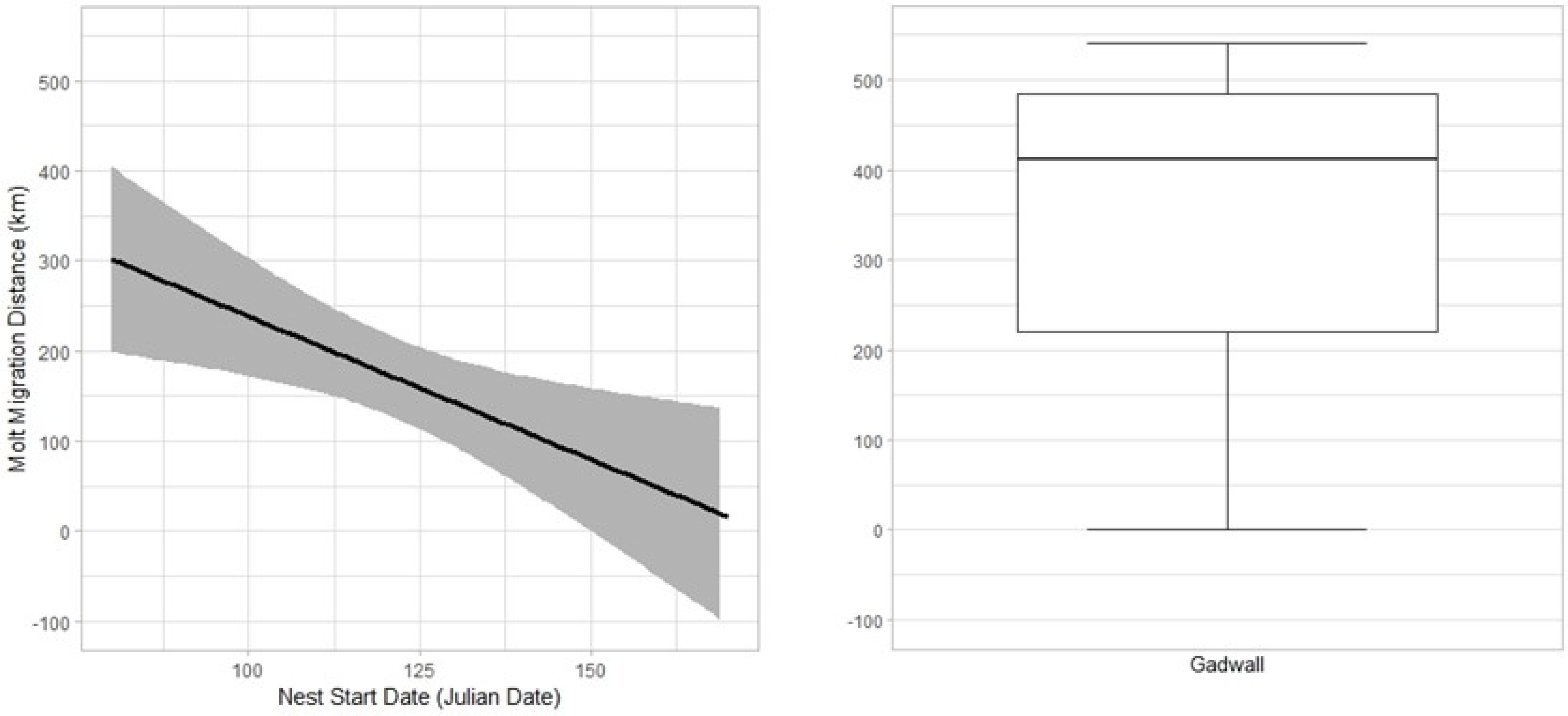


Figure 2. Predicted postbreeding **Molt Migration Distance (MMD)** (km) based on **Nest Start Date (NED)** (Julian Date) and **Nest Success (NS)** for female mallards (n = 66) nesting in the Suisun Marsh of California during 2015-2018 using conditional model-averaged coefficients.

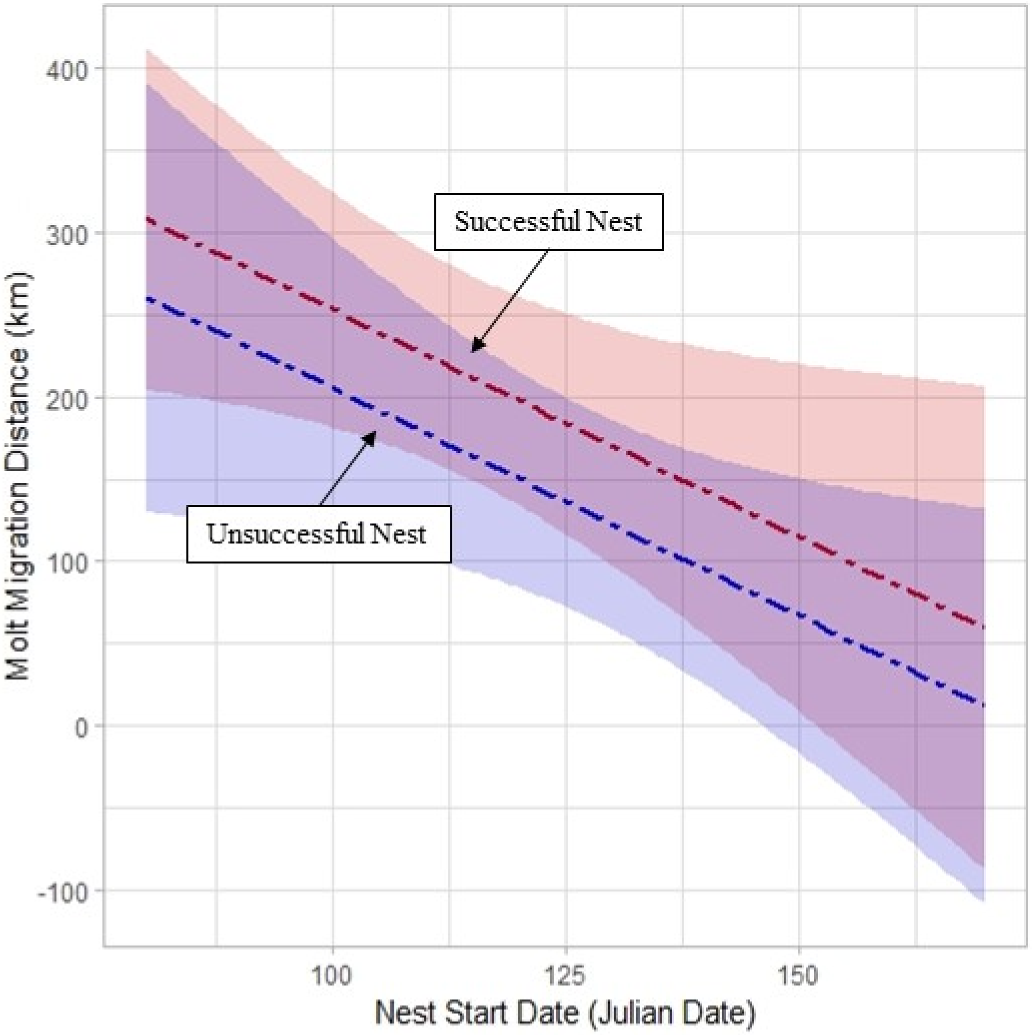


Figure 3. Predicted postbreeding **Molting Activity Duration (MAD)** (days) based on **Molt Migration Distance (MSD)** (km) of female gadwall (*n* = 36) nesting in the Suisun Marsh of California during 2015-2018 using conditional model-averaged coefficients.

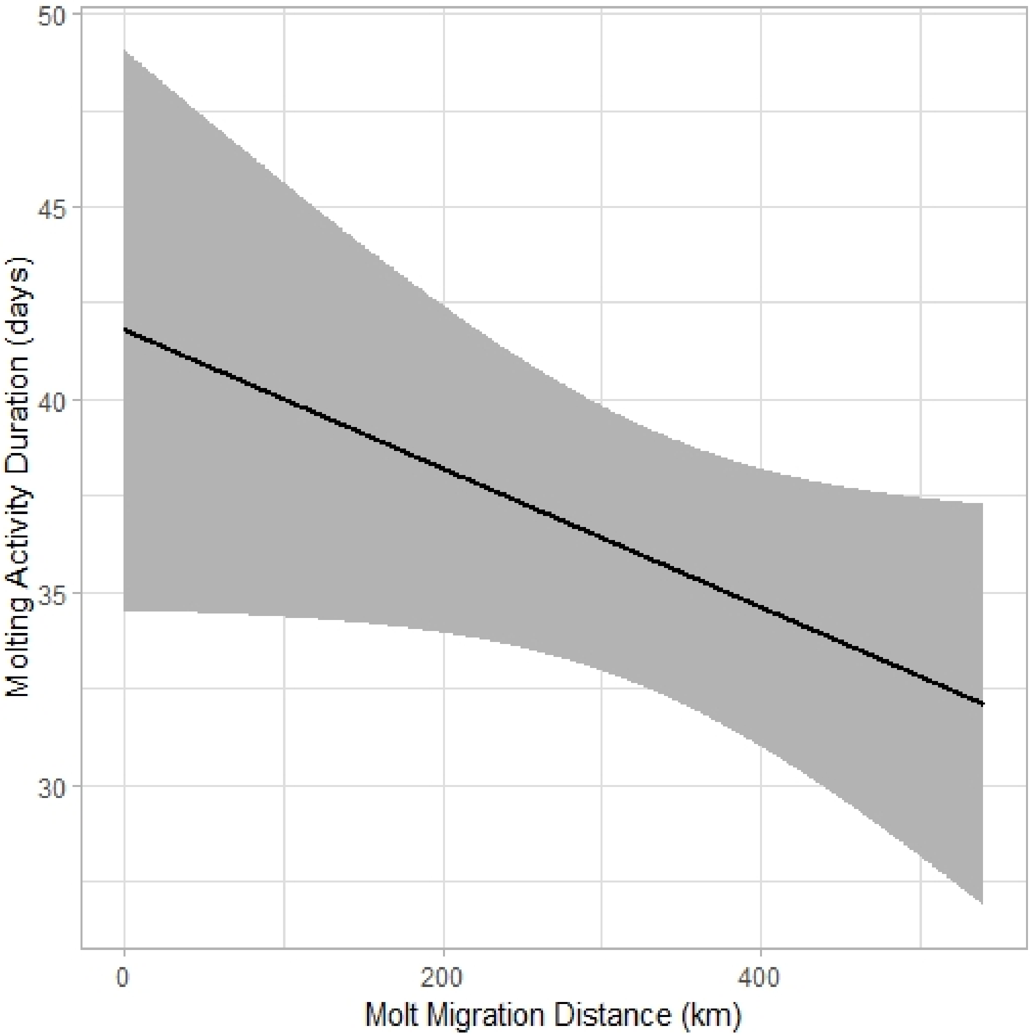
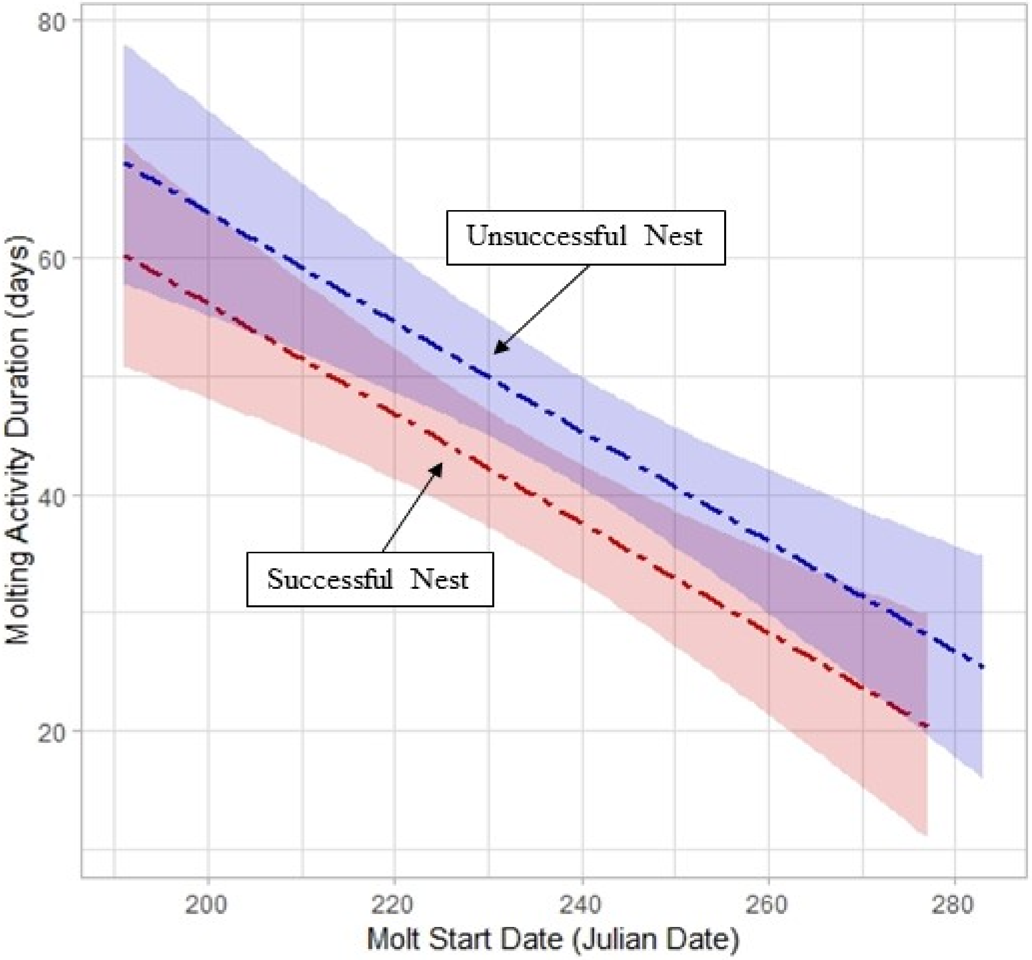


Figure 4. Predicted postbreeding **Molting Activity Duration[a] (MAD)** (days) based on **Molt Start Date (MSD)** (Julian date) and **Nest Success (NS)** for female mallards (*n* = 41) nesting in the Suisun Marsh of California during 2015-2018 using conditional model-averaged coefficients.



[a] Molting Activity Duration (MAD) minimum estimate was set at 20 days based on methods described in chapter 1.

Figure 5. Predicted postbreeding **Molt Start Date (MSD)** (Julian date) based on **Year** (**YEAR**) for female mallards (*n* = 66) nesting in the Suisun Marsh of California during 2015-2018 using conditional model-averaged coefficients.

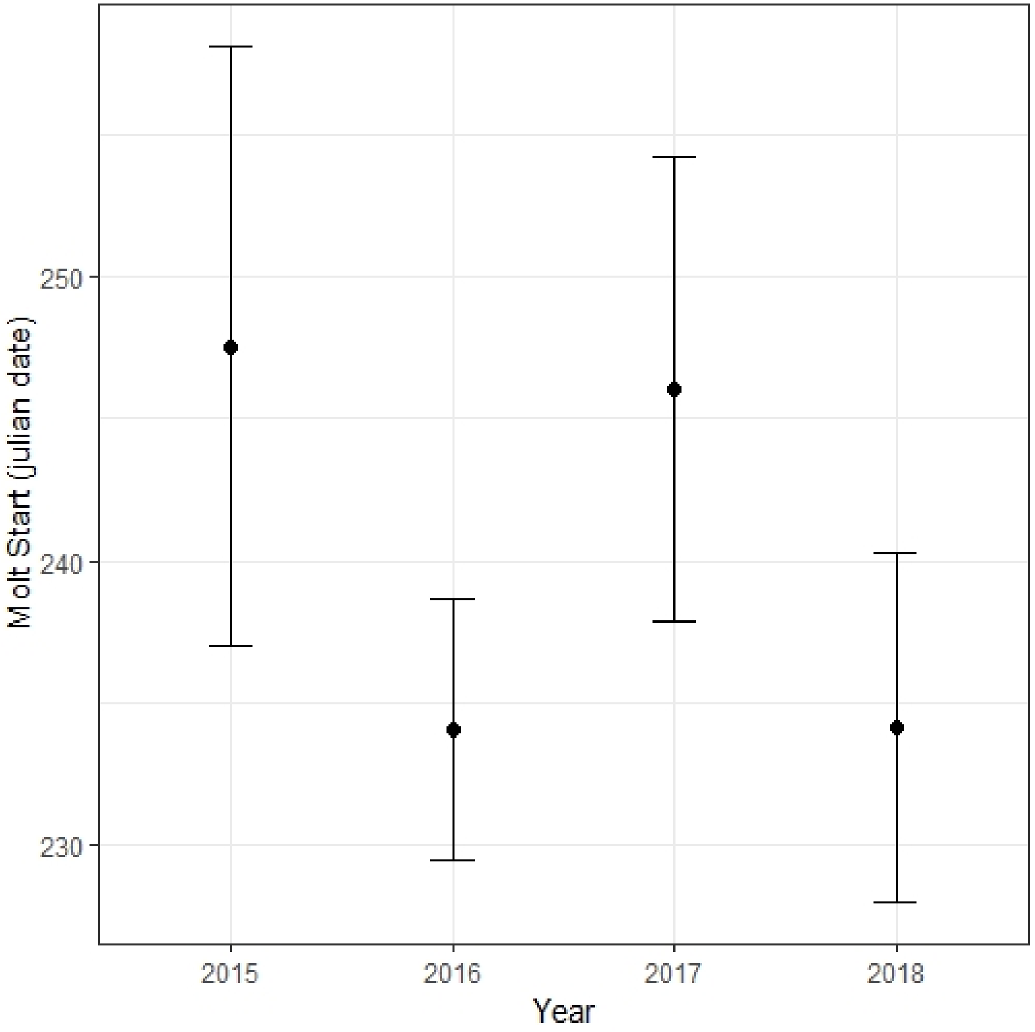
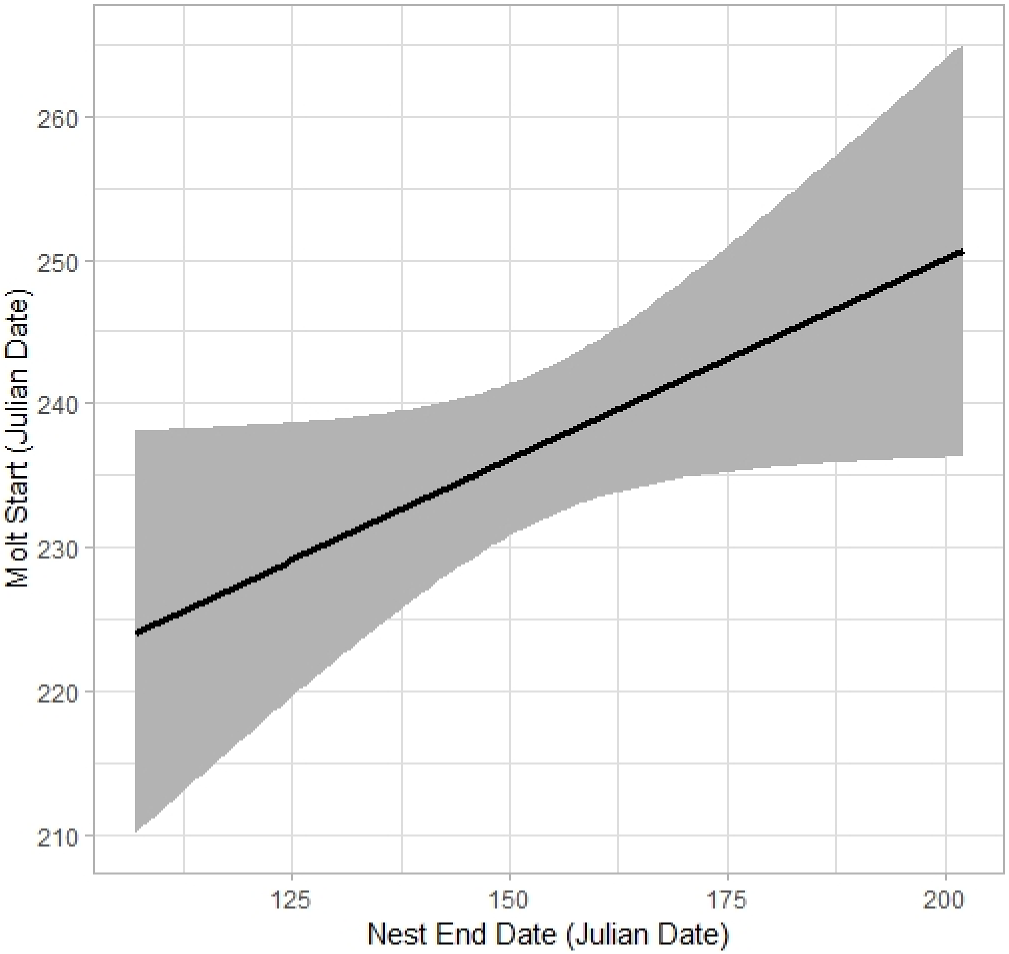


Figure 6. Predicted postbreeding **Molt Start Date (MSD)** (Julian date) based on **Nest End Date** (**NED**) for female mallards (*n* = 66) nesting in the Suisun Marsh of California during 2015-2018 using conditional model-averaged coefficients.



Tables – Chapter 2

Table 1. Model selection results for **Molt Migration Distance (MMD)** for female gadwall (*n* = 47) nesting in the Suisun Marsh of California during 2015-2018 based on combinations of fixed factors for **AGE**, **YEAR**, and **Nest Success (NS)** as well as continuous factors of **Nest Start Date (NSD),** and **Scaled BCI at Nest End (SBCIe)**. Only models with ΔAICc < 2.0 presented.

No.	Model	K	-2 LogLH	AIC	ΔAIC	w_i
40	Null	2	617.58	621.85	0	0.12
5	NSD	3	615.45	622.00	0.15	0.11
4	AGE	3	615.77	622.33	0.471	0.09
14	YEAR + NSD	6	608.45	622.55	0.698	0.08
15	AGE + NSD	4	614.09	623.04	1.187	0.07
2	SBCIe	3	617.06	623.62	1.769	0.05

K number of parameters; -2 log likelihood; Akaike's information criterion (AICc); difference in AICc relative to the lowest AICc (ΔAICc), Akaike weight (*wi*).

Variable Importance

Variable	PL	R^2	DF	F	*P*
NSD	0.515	0.024	46	2.178	0.147
AGE	0.369	0.019	46	1.922	0.172
YEAR	0.276	-0.011	45	0.498	0.484
SBCIe	0.256	0.012	44	1.198	0.322
NS	0.252	-0.018	46	0.156	0.695
SBCIe*YEAR	0.001	-0.050	39	0.687	0.682

Parameter likelihood (PL); P-value; Adjusted R^2, Degrees of freedom (DF); F-statistic (F).

Table 2. Model selection results for **Molt Migration Distance (MMD)** for female mallards (*n* = 66) nesting in the Suisun Marsh of California during 2015- 2018 based on combinations of fixed factors for **AGE**, **YEAR**, and **Nest Success (NS)** as well as continuous factors of **Nest Start Date (NSD),** and **Scaled BCI at Nest End (SBCIe)**. Only models with ΔAICc < 2.0 presented.

No.	Model	K	-2 LogLH	AIC	ΔAIC	w_i
5	NSD	3	873.00	879.39	0	0.22
15	AGE + NSD	4	871.48	880.14	0.751	0.15
9	NS + NSD	4	871.98	880.64	1.251	0.12

K number of parameters; -2 log likelihood; Akaike's information criterion (AICc); difference in AICc relative to the lowest AICc (ΔAICc), Akaike weight (*wi*).

Variable Importance

Variable	PL	R^2	DF	F	*P*
NSD	0.850	0.093	65	7.752	0.007
NS	0.392	0.034	65	3.295	0.074
AGE	0.380	-0.006	65	0.577	0.450
SBCIe	0.256	-0.008	64	0.482	0.490
YEAR	0.163	0.055	63	2.285	0.087
SBCIe*YEAR	0.002	0.011	58	1.104	0.373

Parameter likelihood (PL); P-value; Adjusted R^2, Degrees of freedom (DF); F-statistic (F).

Table 3. Model selection results for **Molting Activity Duration (MAD)** for female gadwall (*n* = 36) nesting in the Suisun Marsh of California during 2015-2018 based on combinations of fixed factors for **AGE**, **YEAR**, and **Nest** Success (NS) as well as continuous factors of **Nest End Date (NED)**, **Scaled BCI at Nest End (SBCIe), Molt Migration Distance (MMD),** and **Molt Start Date (MSD)**. Only models with ΔAICc < 2.0 presented.

No.	Model	K	-2 LogLH	AIC	ΔAIC	w_i
6	MMD	3	267.29	274.04	0	0.20
160	Null	2	270.97	275.34	1.301	0.10
21	SCBCIe + MMD	4	266.69	275.98	1.94	0.07
12	NED + MMD	4	266.69	275.98	1.946	0.06

K number of parameters; -2 log likelihood; Akaike's information criterion (AICc); difference in AICc relative to the lowest AICc (ΔAICc), Akaike weight (*wi*).

Variable Importance

Variable	PL	R^2	DF	F	*P*
MMD	0.611	0.067	35	3.584	0.067
SBCIe	0.271	-0.005	34	0.823	0.371
MSD	0.255	-0.007	35	0.767	0.387
NED	0.237	-0.025	34	0.154	0.697
NS	0.223	-0.027	35	0.059	0.810
AGE	0.218	-0.029	35	<0.001	0.996
YEAR	0.033	-0.021	33	0.748	0.531
SBCIe*YEAR	0.002	0.036	28	1.185	0.343

Parameter likelihood (PL); P-value; Adjusted R^2, Degrees of freedom (DF); F-statistic (F).

Table 4. Model selection results for **Molting Activity Duration (MAD)** for female mallards (*n* = 41) nesting in the Suisun Marsh of California during 2016-2018 (no data for 2015) based on combinations of fixed factors for **AGE**, **YEAR**, and **Nest** Success (NS) as well as continuous factors of **Nest End Date (NED)**, **Scaled BCI at Nest End (SBCIe), Molt Migration Distance (MMD),** and **Molt Start Date (MSD)**. Only models with ΔAICc < 2.0 presented.

No.	Model	K	-2 LogLH	AIC	ΔAIC	w_i
18	NS + MSD	4	304.63	313.74	0	0.19
53	NS + MSD + MMD	5	302.37	314.08	0.336	0.16
33	NED + NS + MSD	5	304.01	315.72	1.976	0.07

K number of parameters; -2 log likelihood; Akaike's information criterion (AICc); difference in AICc relative to the lowest AICc (ΔAICc), Akaike weight (*w*i).

Variable Importance

Variable	PL	R^2	DF	F	*P*
MSD	1.000	0.318	40	20.090	<0.001
NS	0.788	0.014	40	1.570	0.218
MMD	0.488	-0.025	40	0.011	0.917
NED	0.249	-0.023	40	0.077	0.783
AGE	0.217	-0.023	40	0.060	0.808
SBCIe	0.215	-0.016	40	0.344	0.561
YEAR	0.063	0.015	38	1.202	0.322
SBCIe*YEAR	0.001	-0.022	35	0.850	0.540

Parameter likelihood (PL); P-value; Adjusted R^2, Degrees of freedom (DF); F-statistic (F).

Table 5. Model selection results for **Molt Start Date (MSD)** for female gadwall ($n = 47$) nesting in the Suisun Marsh of California during 2015-2018 based on combinations of fixed factors for **AGE**, **YEAR**, and **Nest Success (NS)** as well as continuous factors of **Nest End Date (NED)**, **Scaled BCI at Nest End (SBCIe),** and **Molt Migration Distance (MMD)**. Only models with ΔAICc < 2.0 presented.

No.	Model	K	-2 LogLH	AIC	ΔAIC	w_i
80	Null	2	397.49	401.76	0	0.17
3	SBCIe	3	395.56	402.11	0.354	0.14

K number of parameters; -2 log likelihood; Akaike's information criterion (AICc); difference in AICc relative to the lowest AICc (ΔAICc), Akaike weight (*w*i).

Variable Importance

Variable	PL	R^2	DF	F	*P*
SBCIe	0.424	0.019	45	1.887	0.176
MMD	0.246	-0.016	46	0.244	0.624
NED	0.244	-0.017	45	0.240	0.627
NS	0.235	-0.021	46	0.051	0.822
AGE	0.230	-0.022	46	0.001	0.979
YEAR	0.049	-0.025	44	0.624	0.603
SBCIe*YEAR	0.001	-0.005	39	0.969	0.467

Parameter likelihood (PL); P-value; Adjusted R^2, Degrees of freedom (DF); F-statistic (F).

Table 6. Model selection results for **Molt Start Date (MSD)** for female mallards ($n = 66$) nesting in the Suisun Marsh of California during 2015-2018 based on combinations of fixed factors for **AGE**, **YEAR**, and **Nest Success (NS)** as well as continuous factors of **Nest End Date (NED)**, **Nest Start Date (NSD)**, **Scaled BCI at Nest End (SBCIe),** and **Molt Migration Distance (MMD)**. Only models with ΔAICc < 2.0 presented.

No.	Model	K	-2 LogLH	AIC	ΔAIC	w_i
4	YEAR	5	582.07	593.07	0	0.14
1	NED	3	587.66	594.05	0.98	0.09
10	NED + YEAR	6	581.25	594.67	1.603	0.06

K number of parameters; -2 log likelihood; Akaike's information criterion (AICc); difference in AICc relative to the lowest AICc (ΔAICc), Akaike weight (*w*i).

Variable Importance

Variable	PL	R^2	DF	F	*P*
YEAR	0.608	0.086	63	3.057	0.035
NED	0.449	0.045	64	4.037	0.049
SBCIe	0.252	-0.016	64	0.004	0.948
MMD	0.242	-0.004	65	0.706	0.404
NS	0.234	-0.009	65	0.403	0.528
AGE	0.231	-0.015	65	0.004	0.949
SBCIe*YEAR	0.004	0.048	58	1.472	0.195

Parameter likelihood (PL); P-value; Adjusted R^2, Degrees of freedom (DF); F-statistic (F).