



RESEARCH ARTICLE

Effects of breeding and molt activity on songbird site fidelity

Luiza Figueira,^{1,2} Pedro Martins,^{1,2} C. John Ralph,^{1,3} Jaime L. Stephens,^{1,4} John D. Alexander,¹ and Jared D. Wolfe^{1,4,*}

¹ Klamath Bird Observatory, Ashland, Oregon, USA

² Observatório de Aves da Mantiqueira, Resende, RJ, Brazil

³ USDA Forest Service, Pacific Southwest Research Station, Arcata, California, USA

⁴ College of Forest Resources and Environmental Science, Michigan Technological University, Houghton, Michigan, USA

* Corresponding author: jdwolfe@mtu.edu

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ABSTRACT

The prebasic molt is a perilous period for songbirds, characterized by heightened energetic demands and vulnerability to predators. Given these vulnerabilities, songbirds are under selective pressure to locate and use quality habitat during the prebasic molt, potentially resulting in site fidelity between years. In this study, we aimed to determine how differences in breeding and molting activity affected site fidelity for a diversity of species at the landscape scale. To accomplish our objective, we used 31 yr of banding data from northern California and southern Oregon for 16 species of songbirds with Cormack-Jolly-Seber analyses and weighted linear regression models to assess the effects of molting and breeding activity on the probability of a species returning to a site in subsequent years. Despite substantial variation in site use for breeding and/or molting, each study species had at least some locations that were used for both breeding and molting. Captured breeding birds ($n = 18,574$) were much more common than molting birds ($n = 7,622$). Breeding activity was positively correlated with higher site fidelity for 10 of the 16 species, while we found little evidence of a relationship between molting activity and site fidelity. Only the Dark-eyed Junco (*Junco hyemalis*) showed increased site fidelity with increased presence of molt activity. It is likely that a shifting mosaic of food resources during the post-breeding period drives dynamic movements of songbirds in search of the necessary resources to successfully complete their annual molt.

Keywords: conservation, full-life-cycle, migration, post-breeding, prebasic molt, songbird

LAY SUMMARY

- Birds rely on a myriad of food resources and habitats to reproduce and successfully complete their annual molt.
- We used long-term capture data to assess how 16 species of songbirds varied their use of different habitats during the breeding and molting seasons in northern California and southern Oregon.
- Additionally, we determined how breeding and molting activities influenced the chance of an individual returning to a site year after year.
- While breeding increased an individual's chance of using the same site between years, we found little evidence that molt affected an individual's propensity to return to a site.
- Unlike breeding territories, birds appear less likely to return to the same area to molt year after year. This flexibility is likely necessary to locate dispersed and unpredictable food resources during the molting season.

Efeitos das atividades de reprodução e muda na fidelidade ao sítio por aves passeriformes

RESUMO

O período em que uma ave está realizando sua muda pré-básica é um caracterizado por uma alta demanda energética e maior vulnerabilidade a predadores, sendo assim um período de alto risco para a ave em muda. Dadas as vulnerabilidades do período de muda, aves, em especial passeriformes, estão sob pressão seletiva ao escolher local e habitat onde vão realizar a troca de suas penas, potencialmente resultando em uma fidelidade ao sítio entre anos. Neste estudo visamos identificar como as atividades de reprodução versus muda pré-básica, que acontece após o período reprodutivo para migrantes neotropicais, afetam a fidelidade ao sítio em uma escala da paisagem. Para isso, nós usamos 31 anos de dados de anilhamento de aves incluindo 16 espécies de passeriformes neste estudo. Usamos modelos Cormack-Jolly-Seber e regressão linear ponderada para identificar possíveis efeitos das atividades de muda e reprodução na probabilidade de indivíduos de cada espécie retornarem em anos seguintes para o mesmo sítio em que realizaram a respectiva atividade, incluindo região do norte da Califórnia ao sul do Oregon, nos Estados Unidos da América. Apesar de variação substancial

na relação espacial entre reprodução e muda dentre e entre espécies, nenhuma das espécies estudadas mostrou total separação de sítios reprodutivos versus sítios de muda. A captura de aves em condição reprodutiva foi muito maior (18,574) do que captura de aves durante muda pré-básicas (7,622). A atividade reprodutiva foi positivamente relacionada com maior fidelidade ao sítio para 10 dentre as 16 espécies estudadas, mas encontramos pouca evidência para qualquer efeito de atividade de muda na fidelidade ao sítio. Apenas *Junco hyemalis* teve uma fidelidade ao sítio aumentada junto de maior atividade de muda. Possivelmente um dinâmico mosaico de recursos alimentares durante o período pós-reprodutivo direciona a dinâmica de movimentos de passarinhos à procura dos recursos necessários para completar seu ciclo anual com sucesso.

Palavras-chave: ciclo-de-vida, habitat, passeriforme, pós-reprodução, migração, muda pré-básica

INTRODUCTION

Identifying how variation in an individual's fitness across different phases of the annual cycle (breeding, molt, and migration) affects broader patterns of population growth has long been a focus of ornithological research. Variation in fitness appears dynamic, where an individual's experience in one phase of the annual cycle can interact or carry over to affect fitness in another phase, thereby complicating efforts to disentangle the relative influence of breeding, molt, and migration on observed changes in bird abundance (Hostetler et al. 2015, Marra et al. 2015). To date, the majority of studies focused on linking phases of the annual cycle to broader measures of population growth have been limited to breeding and, to a lesser extent, overwintering (Marra et al. 2015). Interestingly, several of these studies have converged on similar conclusions: those events experienced outside the breeding period disproportionately influence population growth (Sillett and Holmes 2002, Faaborg et al. 2010, Rockwell et al. 2017, Rushing et al. 2017).

Research focused on the prebasic molt periods are uncommon. This may be in part due to logistical difficulties of conducting such studies. For example, mark-recapture studies of molting songbirds are challenging because birds become less active during molt (Vega Rivera et al. 1998) and at the same time less constrained by territoriality. Further, in some instances, individuals undergo molt-migration (e.g., Leu and Thompson 2002, Pyle et al. 2009, Wiegardt et al. 2017, Tonra and Reudink 2018). Ultimately, intensive and long-term bird capture efforts during the post-breeding period are necessary to assess molting bird populations; unfortunately, rigorous studies and bird monitoring efforts focused on birds undergoing the prebasic molt remain limited.

Songbirds accomplish the prebasic molt in a multitude of ways. Birds that replace feathers following the breeding season may molt on their summer grounds, as is the case in nonmigratory species and a few migrants. Alternately, they may migrate prior to molt and undergo the prebasic molt on their wintering grounds or molt along their migratory routes, which is the case for 30–46% of Neotropical migrants (Leu and Thompson 2002, Pyle et al. 2018). Many songbird species in western North America are known as

“molt-migrants,” a term that has been commonly used to describe birds that leave their summer grounds and make a partial migration to molt in monsoonal regions of northern Mexico and the southwestern United States prior to continuing migration farther south (Rohwer et al. 2007, Pyle et al. 2009). In a recent review on molt-migration, Tonra and Reudink (2018) detailed the diversity of movements birds make to molt and suggest that molt-migration applies to any “temporal overlap in molt and migration life history stages.” Regardless of the diversity of molt-migration strategies, among the many species that molt prior to fall migration, we remain uncertain what proportion of a given species' population regularly moves out of breeding territories to molt. For example, Vega Rivera et al. (1999) examined Wood Thrush (*Hylocichla mustelina*) post-breeding movements and behavior and found that while some individuals lingered at breeding territories to undergo molt, others moved to nearby or distant sites to molt. Swainson's Thrush (*Catharus ustulatus*), a long-distance Neotropical migrant known to molt on its summer grounds (Pyle 1997), was also documented undergoing the prebasic molt during fall migration at sites outside the species' breeding range (Cherry 1985). More recently, Pyle et al. (2018) found that the chances of individual birds molting on their breeding territories varies temporally and spatially across a species' range. Thus, the myriad of ways birds accomplished their prebasic molt appears variable between species and individuals and might reflect a continuum rather than categorical classification.

Bird movements are thought to be largely based on food availability (e.g., Moore et al. 1995, Pyle et al. 2009, Gow and Stutchbury 2013, Hsiung et al. 2018), but can also be driven by predators (Ydenberg et al. 2007, Pomeroy and Lindstrom 2006) and climatic conditions (Jenni and Schaub 2003, Marra et al. 2005, Hsiung et al. 2018). Both proximate drivers (such as age and sex, body condition, and timing of breeding) and ultimate drivers (such as environmental variables) play a role in determining the timing and route of migration and, subsequently, the timing and location of the prebasic molt. Differences in molt patterns between hatching-year and adult birds also influence the timing of fall migration between age classes (Carlisle et al. 2005), whereby adults of most songbird species undergo a more extensive molt (the usually complete prebasic molt)

during the post-breeding period than their hatching-year counterparts (the preformative molt, most commonly partial but possibly incomplete or complete). Additionally, variation in the cessation of breeding activity will influence timing of molt, where individuals that successfully fledge young late in the breeding season have been found to undergo a late prebasic molt (Stutchbury et al. 2011).

The return to a specific site by a bird between years, known as site fidelity, is well documented at both breeding and wintering sites (Ralph and Mewaldt 1976, Greenwood 1980, Warkentin and Hernandez 1996, Wunderle and Latta 2000, Markovets and Yosef 2005, Newton 2008). Site fidelity is also common at migratory stopover sites among waterfowl and shorebird species (e.g., Newton 2008, Taylor and Bishop 2014) and, more recently, has been reported, albeit rarely, for some songbirds as well (Marshall et al. 2005, Somershoe et al. 2009, Vogt et al. 2012, Barboutis et al. 2014, Wright et al. 2018; see Catry et al. 2004 for a counterpoint). The nearly ubiquitous nature of breeding site fidelity across avian taxa reflects the benefits associated with previous knowledge of a particular location, likely improving territory acquisition, foraging efficiency, potential breeding partners, and predator avoidance (Greenwood and Harvey 1982). It remains unknown if some of these factors—like foraging efficiency and predator avoidance—influence the interannual site fidelity of songbirds during their prebasic molt.

In this study, we examined how molt spatially overlaps with breeding activity across 16 songbird species in northern California and southern Oregon, and how the use of a site for molting may affect site fidelity. Our specific goals were to (1) identify and describe how different species vary their use of breeding and post-breeding sites to molt, and (2) determine if molt activity at a given site is positively associated with the return of individuals to that specific site between years. To accomplish our objectives, we used 31 yr of bird capture data in a series of mark–recapture analyses. Our study represents the first attempt, to our knowledge, to assess the influence of molt on site fidelity among songbirds in the western United States.

METHODS

We used capture–mark–recapture data from 50 banding sites across the Klamath-Siskiyou Bioregion of northern California and southern Oregon (Alexander et al. 2004, Alexander 2011; Figure 1, Appendix Table 3). Each site had at least 9 daily capture efforts between May and October in the years included in the study. Capture efforts were usually scheduled once every 7–10 days, with nets opened for 5–6 hr (weather allowing) starting 15 min before sunrise, following Ralph et al. (1993) and Stephens et al. (2010).

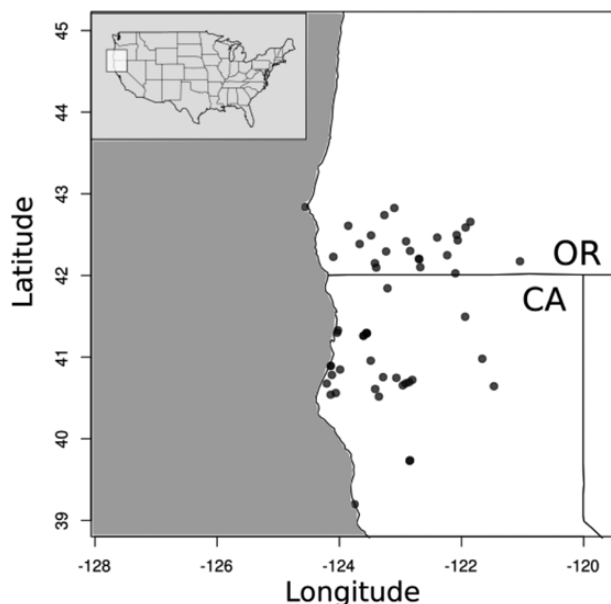


FIGURE 1. Filled circles mark 50 unique constant-effort mist-netting banding sites from the Klamath Bird Monitoring Network in Oregon and California where data used in this study were collected.

Each banding site had 8–15 mist nets that were 3 m tall and 12 m in length, with 36-mm mesh. Each net was at a fixed location with minor adjustments or occasional changes of net location between years. Sites were operated from 1982 to 2013, with each site operated between 3 and 31 yr.

For each captured individual we assessed age class, development of cloacal protuberance and brood patch, and symmetrical remigial molt following Ralph et al. (1993) and Pyle (1997). We only used capture data of adult (after-hatching year) individuals in this analysis. We examined 16 songbird species that met 3 basic criteria: occurred at 5 or more of our banding sites, captured at least 50 adult individuals at each site, and had individuals captured undergoing prebasic molt (Table 1).

Site Use for Breeding and Molting

For our first objective (i.e. identify and describe how different species vary their use of breeding and post-breeding sites for molting), we classified captured individuals into one of four classes for each banding site (Table 1): (1) *breeder*, if the individual was captured at least once with a vascularized or wrinkled brood patch or a medium to large cloacal protuberance; (2) *molter*, if it was captured at least once with symmetric molt in the remiges; (3) *both*, if it was captured both as a breeder and as a molter; and (4) *unclassified*, if it was never captured while breeding or molting. We then calculated the percentages of each activity class for each banding site and each species. Our classification combined all years of data rather than assessing variation in local activity by year because we lacked the number of

TABLE 1. List of study species with (1) common name; (2) scientific name; (3) migratory name; (4) total number of banding sites where each species had at least 50 adult individuals captured; (5) total number of adult individuals (AHY) of each species included in this study; (6) percentage of adult individuals classified as breeders (i.e. individuals captured at least once in breeding condition, but never with molt); (7) percentage of adult molters (i.e. individuals captured at least once undergoing prebasic molt, but never in breeding condition); (8) percentage of adult both (i.e. individuals that were captured both during breeding and molting at the same location); and (9) percentage of adults unclassified (i.e. individuals never captured either breeding or molting). Banding sites were located in southern Oregon and northern California, and data were collected from 1982 to 2013, between May and October.

Common name	Scientific name	Migratory guild	Total sites	Total individuals AHY	% Breeder	% Molter	% Both (breeder and molter)	% Unclassified
Swainson's Thrush	<i>Catharus ustulatus</i>	Long-distance Neotropical migrant	24	4,276	38	6	4	52
American Robin	<i>Turdus migratorius</i>	Resident or short-distance migrant	13	1,851	55	10	7	28
Wrentit	<i>Chamaea fasciata</i>	Resident	6	668	46	12	22	20
Orange-crowned Warbler	<i>Oreothlypis celata</i>	Short- to long-distance migrant	18	2,425	11	19	2	68
Nashville Warbler	<i>Oreothlypis ruficapilla</i>	Long-distance Neotropical migrant	9	914	48	23	4	25
Yellow Warbler	<i>Setophaga petechia</i>	Long-distance Neotropical migrant	15	3,168	25	5	6	64
Yellow-rumped Warbler	<i>Setophaga coronata</i>	Short- to long-distance migrant	14	2,550	37	19	3	41
Hermit Warbler	<i>Setophaga occidentalis</i>	Resident, short-distance to long-distance migrant	7	689	42	24	8	26
MacGillivray's Warbler	<i>Geothlypis tolmiei</i>	Long-distance Neotropical migrant	22	2,941	47	8	8	37
Wilson's Warbler	<i>Wilsonia pusilla</i>	Long-distance Neotropical migrant	28	3,823	19	6	3	72
Yellow-breasted Chat	<i>Icteria virens</i>	Long-distance Neotropical migrant	11	1,365	51	11	6	32
Spotted Towhee	<i>Pipilo maculatus</i>	Resident or short-distance migrant	17	1,883	34	13	8	45
Song Sparrow	<i>Melospiza melodia</i>	Resident or short-distance migrant	36	5,946	54	7	9	30
White-crowned Sparrow	<i>Zonotrichia leucophrys</i>	Resident, short-distance to long-distance migrant	12	1,160	7	5	2	86
Dark-eyed Junco	<i>Junco hyemalis</i>	Resident or short-distance migrant	20	4,017	27	23	13	37
Purple Finch	<i>Haemorhous purpureus</i>	Resident or short-distance migrant	15	4,911	47	11	5	37

captures necessary to classify annual variation in bird activity at a given site.

Site Fidelity

Site fidelity is a challenging parameter to estimate when based on capture–mark–recapture data because it is confounded by biological (whether or not a bird survives) and methodological (if the bird is recaptured) processes. That is, the chance of an individual bird being recaptured between years at a given site is a result of (1) the probability of the individual surviving between years, plus (2) the probability of the individual returning to that specific site (site fidelity), and (3) the probability that it will actually be recaptured during a banding effort.

We used recapture probability as a proxy for site fidelity, and for this we assume that survival and recapture probability are constant traits for each species across sites. However, we acknowledge that survival may vary within a species even at a regional scale depending on the general habitat quality of a specific site (Donovan et al. 1995, Wolfe et al. 2014). As such, we used survival estimates from geographically broad models (DeSante et al. 2015) that include all Bird Conservation Regions (BCR). Variability of these geographically broad survival estimates (i.e. standard deviation) is typically larger than survival estimates from spatially restricted models (i.e. models that include a single BCR) since our geographically broad estimates account for variation in survival rates of a species throughout its range. Recapture probability is also a parameter that may vary in space and time within species, even using standardized sampling methods. Thus, our models represent an oversimplification of survival and recapture probability that, nonetheless, provide useful insights into patterns of site fidelity associated with molt activity.

To estimate recapture probability, referred to here as site fidelity, we used a Cormack–Jolly–Seber (CJS) model in a Bayesian framework where we estimated parameters for each species. Each species' model provided 2 parameters: survival and fidelity. Survival was fixed as constant and informed with a strong prior. We used the distribution (mean and standard deviation) of estimated survival from the *Vital Rates of North American Landbirds* project, developed by the Institute of Bird Populations (DeSante et al. 2015). More specifically, we used their model-averaged estimated parameters of apparent survival from their transient CJS models. As a result of this informed prior, our model assumed greater certainty around the prior survival distribution, leaving the variation in our capture–mark–recapture data to be explained by the difference in estimated fidelity. Fidelity was estimated independently for each banding site with no year (time) effect due to data limitations. Importantly, we did not aim to derive final estimates of fidelity for each site and species. Our goal was to use

recapture probability to identify relative variation in site fidelity between stations.

We used our estimated parameter of site fidelity for each species and site to fit 4 different weighted linear models (outlined below) to test if the increased proportion of local molters or both (therefore indicating local molt activity by breeders) was positively correlated with estimated site fidelity. Given that our response variable (site fidelity) was an estimated parameter, we used a weighted linear regression to mitigate the violation of an important assumption associated with linear regression: constant variance in the residuals (heteroscedasticity). Our weighted regression accounts for this violation by giving greater weight to those response variables with lower associated uncertainty, and less weight to the response variables with higher uncertainty, when estimating the regression slope (β).

To assess associations between site fidelity and molting/breeding activity, we created 4 weighted linear regression models: *Breeders fidelity* estimated the relationship between the local proportion of *breeders* and site fidelity (Eq. 1); *Molters fidelity* estimated the relationship between the local proportion of *molters* and site fidelity (Eq. 2); *Activity fidelity* estimated the relationship between overall local activity (the combined proportion of *breeders*, *molters*, and *both*) and site fidelity (Eq. 3); and *Interaction fidelity* estimated the relationship between the additive effects of *breeders* and *molters* on site fidelity (Eq. 4).

$$\mu_j = \alpha + \beta \times \text{breed}_j \quad (1)$$

$$\mu_j = \alpha + \beta \times \text{molt}_j \quad (2)$$

$$\mu_j = \alpha + \beta \times (\text{molt}_j + \text{breed}_j + \text{both}_j) \quad (3)$$

$$\mu_j = \alpha + \beta_1 \times \text{molt}_j + \beta_1 \times \text{breed}_j \quad (4)$$

where α is the intercept and β is the slope of the correlation of activity and site fidelity; *breed* is the proportion of “breeders” at site j ; *molt* is the proportion of “molters” at site j ; and *both* is the proportion of “both” at site j . The estimated correlation of activity and site fidelity is then given by median estimated β and its 95% credible interval. We compared results from each of the 4 models based on beta estimates. All analyses were done separately for each species using package *jagsUI* (Kellner 2017) in program R (R Core Team 2017).

RESULTS

Across our 16 study species, we identified 18,574 individuals that were classified as breeders (i.e. captured at least once in breeding condition); 7,622 molters, individuals captured at least once undergoing prebasic molt; and 2,763 individuals identified as both, being captured exhibiting both breeding and molting activity at the same site (but not at the same

time). We also identified 19,154 unclassified individuals that were never captured exhibiting breeding or molting activity (see Table 1 for proportions of breeders, molters, both, and unclassified for each species).

Our results describe variation at both the individual and species level with regard to either molting on or off breeding sites (Figure 2). Most species, 14 out of 16, exhibited a gradual variation in the proportions of breeders and molters across sites (Figure 2). By gradual variation we mean that the same species occurred at sites with different proportions of breeders and molters, going from sites dominated by breeding activity to sites dominated by molters. Two species showed a less variable pattern of use across sites (Figure 2). The first was the Wrentit (*Chamaea fasciata*), which was captured only at sites where it both bred and molted, with little variation in proportions between sites. The second species was the White-crowned Sparrow (*Zonotrichia leucophrys*), which was captured at sites where it neither bred or molted (only unclassified individuals), and at other places where it both bred and molted, but no gradual variation in between. No species exhibited complete distinction between molting and breeding sites.

Site Fidelity

Our results showed molt as having little influence on interannual site fidelity (Appendix Figure 3). Locations with higher proportions of breeders exhibited relatively higher site fidelity for most species, while the increased proportion of molters did not increase site fidelity, except in one species, the Dark-eyed Junco (*Junco hyemalis*). For this species, although breeding had a stronger effect on fidelity in all models, molt also had a significant (credible interval above 0) positive effect on site fidelity (see Table 2 for mean and 95% credible interval for each model/species). As the junco was found to both breed and molt at most sites where it occurred (Figure 2), the effect size of breeding and molting activity may have been confounded in the breeding fidelity, molting fidelity, and activity fidelity models. That is, if site fidelity was high because of breeding activity, and as molt occurred at breeding sites, molt is also linked to high site fidelity. However, the effect of molt on site fidelity was also influential when considering the Dark-eyed Junco interaction fidelity model. We found a smaller but positive relationship between molt and site fidelity in this fourth model, indicating that even when accounting for breeding fidelity, molt still had some positive effect. Our results suggest that Dark-eyed Juncos were more likely to return to a site where they bred, and exhibited an even higher chance of returning to a site if they also underwent molt at that site.

Neither breeding or molting proportions explained site fidelity variation across sites for 6 species: Wrentit, Song

Sparrow (*Melospiza melodia*), Yellow-breasted Chat (*Icteria virens*), and the Yellow-rumped (*Setophaga coronata*), Hermit (*S. occidentalis*), and Nashville (*Oreothlypis ruficapilla*) warblers. In the case of the nonmigratory Wrentit, the lack of relationship between local breeding or molting activity and site fidelity simply reflected the lack of variation in the proportions of breeding and molting individuals across sites. All 6 banding sites where the Wrentit was studied had mostly uniform proportions of breeders, molters, both, and unclassified individuals (Figure 2). A principle of linear regression is that if there is no variation in explanatory variables (i.e. activities), there will be little correlation with a response variable (in this case, fidelity).

The Song Sparrow exhibited breeding activity throughout our study area and at least some molting individuals occurred at all sites as well. Although site fidelity had a slightly higher positive relationship with molt than breeding (Table 2), credible intervals for all 4 models overlapped 0, indicating no measurable effect of breeding or molting on Song Sparrow site fidelity. Yellow-rumped, Hermit, and Nashville warblers and the Yellow-breasted Chat all followed the general tendency of heightened site fidelity with increased proportions of breeders. However, similar to the Song Sparrow, effect size was associated with substantial uncertainty whereby credible intervals for all 4 models overlapped 0 (Table 2) indicating no measurable effect.

Swainson's Thrush, American Robin (*Turdus migratorius*), Orange-crowned Warbler (*O. celata*), Spotted Towhee (*Pipilo maculatus*), White-crowned Sparrow, and Purple Finch (*Haemorhous purpureus*) all had positive and significant effects of breeding, but no measurable effect of molt, on site fidelity (Table 2). Yellow Warbler (*Setophaga petechia*) showed a small but significant effect of molt on site fidelity with the molter fidelity model (Table 2). However, within the interaction fidelity model, the effect on site fidelity was associated with breeding, while molt had no measurable effect. Because molting largely occurred at the same sites as breeding for Yellow Warbler, the results of the molter fidelity model were likely associated with fidelity resulting from breeding individuals.

DISCUSSION

In this study we examined how variation in breeding and molting activities affected site fidelity for 16 species of songbirds. We found that while site fidelity is related to breeding activity for most species, the occurrence of molt seems to have little influence on the probability of an individual returning to a location. Our study adds to a growing body of research demonstrating that western songbirds

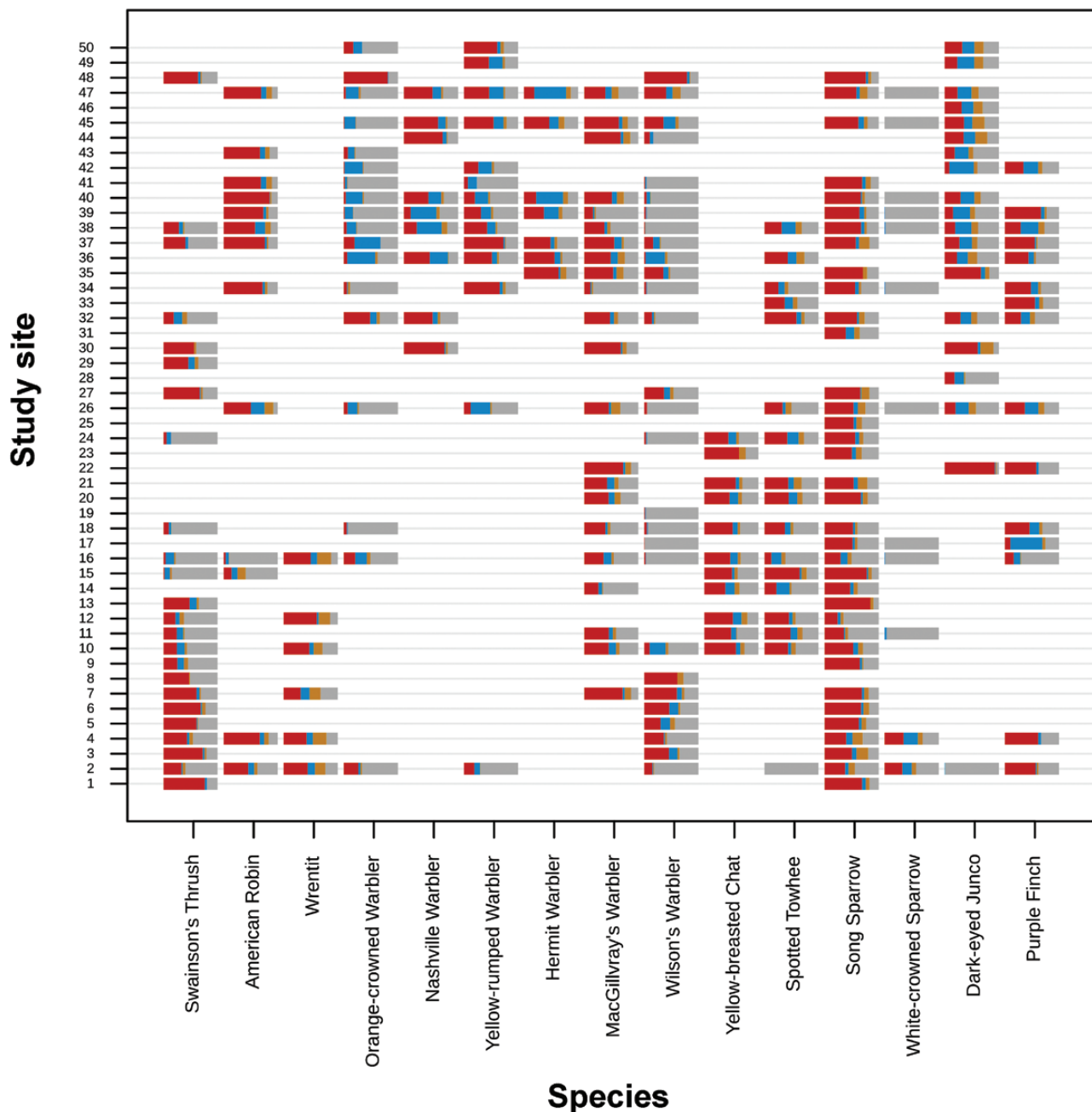


FIGURE 2. Proportion of local breeders (red), molters (blue), both (orange), and unclassified (gray) for each of the 16 species (x-axis) by study site (y-axis). Sites closer to one another on the y-axis have more similar elevation with sites at the top of y-axis at higher elevation; Species are included at a site only if ≥ 50 individuals were captured.

exhibit substantial variation in molt activity on and off their breeding sites, within and between species (e.g., [Cherry 1985](#), [Vega Rivera et al. 1999](#), [Wiegardt et al. 2017](#), [Pyle et al. 2018](#), [Tonra and Reudink 2018](#); Appendix Figure 4).

The relationship between breeding and site fidelity is well known across species ([Newton 2008](#)). Birds that nest successfully are more likely to return to the same site for breeding in the following year (e.g., [Hoover 2003](#),

[Pageau et al. 2020](#)). The previous knowledge of a particular location likely benefits the outcome of nest success and survival during the breeding period in subsequent years. However, when considering molt, previous knowledge of the molting location may be less important to the success of this activity, although to our knowledge this has not been studied. It does seem likely that other pressures—like timing and weather conditions—might be

TABLE 2. Results from weighted linear regressions assessing effects of breeding and molting activity on site fidelity. We tested 4 models; for each model, the response variable was the estimated site fidelity for each site, weighted by its estimated uncertainty (variance). Explanatory variables (beta) were for model "Breeding fidelity," the percentage of local breeders for each site; model "Molting fidelity," the percentage of local molters for each site; model "Activity fidelity," the sum of the percentages of local breeders, molters, and both, that is, the total percentage of individuals showing any kind of activity; and for model "Interaction fidelity," the percentage of local breeder and of local molter with independent slopes. The asterisk (*) highlights estimated parameters where credible intervals did not overlap 0, meaning a measurable effect of explanatory variable on site fidelity.

Species	Model 1				Model 2				Model 3				Model 4							
	Breeding fidelity				Molting fidelity				Activity fidelity				Interaction fidelity							
	beta. breed	95% CI			beta. molt	95% CI			beta.all	95% CI			beta. breed	95% CI			beta. molt	95% CI		
		lower	upper			lower	upper			lower	upper			lower	upper			lower	upper	
Swainson's Thrush	0.18	0.14	0.226*		-0.06	-0.14	0.01		0.17	0.13	0.207*		0.19	0.14	0.24		0.02	-0.03	0.06	
American Robin	0.08	0.04	0.109*		0.03	-0.05	0.11		0.06	0.03	0.087*		0.08	0.04	0.116*		-0.01	-0.06	0.04	
Wrenit	-0.03	-0.17	0.12		0.01	-0.13	0.15		-0.03	-0.14	0.08		-0.07	-0.35	0.24		-0.04	-0.32	0.23	
Orange-crowned Warbler	0.06	0.03	0.088*		-0.01	-0.04	0.02		0.03	0	0.059*		0.06	0.02	0.09*		0	-0.02	0.02	
Nashville Warbler	0.02	-0.03	0.08		-0.03	-0.09	0.03		0.02	-0.04	0.08		-0.04	-0.31	0.22		-0.08	-0.38	0.22	
Yellow Warbler	0.11	0.08	0.151*		0.06	0.01	0.119*		0.11	0.08	0.144*		0.11	0.06	0.157*		0.01	-0.04	0.05	
Yellow-rumped Warbler	0.01	-0.01	0.02		-0.01	-0.02	0.01		0	-0.02	0.02		0	-0.03	0.02		-0.01	-0.03	0.02	
Hermit Warbler	0.01	0	0.03		-0.01	-0.02	0.01		-0.01	-0.02	0.01		0.05	-0.04	0.14		0.03	-0.05	0.11	
MacGillivray's Warbler	0.12	0.03	0.204*		-0.04	-0.13	0.05		0.12	0.03	0.197*		0.12	0.04	0.208*		-0.05	-0.12	0.02	
Wilson's Warbler	0.15	0.1	0.199*		0.05	-0.01	0.12		0.13	0.09	0.179*		0.15	0.1	0.201*		0.01	-0.04	0.05	
Yellow-breasted Chat	0.05	-0.02	0.13		-0.05	-0.13	0.03		0.04	-0.03	0.12		0.04	-0.09	0.16		-0.02	-0.15	0.1	
Spotted Towhee	0.06	0	0.109*		0.03	-0.04	0.1		0.07	0.02	0.118*		0.06	0.01	0.113*		0.04	-0.02	0.1	
Song Sparrow	0	-0.04	0.04		0.03	-0.01	0.07		0.03	-0.01	0.07		0.03	-0.03	0.07		0.05	-0.01	0.1	
White-crowned Sparrow	0.11	0.09	0.135*		0.1	0.06	0.14		0.11	0.08	0.139*		0.14	0.06	0.208*		-0.03	-0.1	0.05	
Dark-eyed Junco	0.21	0.16	0.261*		0.11	0.07	0.16		0.1	0.09	0.12		0.16	0.11	0.208*		0.05	0.02	0.084*	
Purple Finch	0.05	0.01	0.102*		-0.03	-0.11	0.06		0.04	0	0.072*		0.06	0	0.12		0.02	-0.07	0.11	

more influential on decisions about where to molt. Also, unlike breeding birds that constrain movements to areas immediately around their active nests, post-breeding birds face fewer movement constraints when selecting high-quality habitats to successfully complete their molt. Our study found that the proportion of molting birds within a species varied at breeding sites across the landscape. This observation begs the question: Why do some individuals molt on breeding territories and others do not? Factors driving these differences likely vary. For example, Pyle et al. (2018) demonstrated that breeding songbirds in the southern portions of North America—where birds have fewer seasonal constraints after the breeding period—were more likely to be captured in molt than their northerly counterparts. Additionally, an individual bird's decision to stay or leave a breeding site prior to molt is possibly associated with the timing and success of breeding (Vega Rivera et al. 1999, Pyle 2018, Tonra and Reudink 2018). In northerly latitudes, late breeders are likely to be late molters (Stutchbury et al. 2011) and might not have time to molt before food resources become seasonally scarce. Feather condition could also affect an individual's decision to vacate its breeding territory prior to molt: birds with heavier feather wear can be limited in their flight capacity making them more vulnerable to depredation and less mobile (Vega Rivera et al. 1999). In these cases, delaying movement and being able to replace feathers within the breeding site is likely more advantageous.

The 2 species that exclusively molted at breeding sites, Wrentit and White-crowned Sparrow, may have exhibited this behavior for different reasons. For example, the Wrentit is a sedentary species that is believed to live year-round within a single territory (Geupel and Ballard 2020) and has a small distribution range, mostly in California. Given their sedentary behaviors, Wrentits likely remain within their breeding territories to molt. By contrast, White-crowned Sparrows are widely distributed and abundant with diverse migratory behaviors, varying between populations and subspecies. Within our study area, White-crowned Sparrows are year-round residents as well as short- and long-distance migrants (Rising 2018). Because subspecies were not identified consistently in our dataset, we are not certain of the migratory status at each of our study sites. We know that at some of our coastal sites had a combination of Nuttall's (*Z. l. nuttalli*) and Puget Sound (*Z. l. pugetensis*) subspecies, and based on our observations, while some were migratory, most were resident birds. The proportion of migratory and resident White-crowned Sparrows likely varied across our study sites, with more migratory populations to the north and residents to the south (Chilton et al. 2020). Thus, similar to Wrentits, resident White-crowned Sparrows may have molted at breeding sites. Migratory White-crowned

Sparrows captured at nonbreeding wintering sites had no prebasic molt activity detected, indicating that it was completed prior to arrival in our study area.

Due to the substantial variation in molt activity both on and off breeding sites within and across our study area, in light of the informative review of Tonra and Reudink (2018) and the recent work of Pyle et al. (2018), it remains unlikely that most migratory songbirds follow simple rules that govern the temporal and spatial dynamics of molt. Rather, their behavior is likely a result of multiple and interacting factors and cues, including age and sex class, timing of breeding, available resources, and environmental conditions. In that sense, although mandatory and predictable, molt still seems to be spatially and temporally flexible to environmental and individual conditions.

Overall, we captured fewer molting individuals than breeding birds. This is a common phenomenon, as molting birds are relatively rare in museum collections (Leu and Thompson 2002) and detected less frequently than breeding birds in similar studies (e.g., Pyle et al. 2018). This is likely due to the shorter time interval for molting vs. breeding in birds, or the diminished detectability of molting birds as compared to breeding individuals (Vega Rivera et al. 1998, 1999), or both. Such retiring behaviors may be in response to impaired flight during molt, making individuals prone to depredation. The Orange-crowned Warbler was unique in that we captured more molting than breeding individuals. According to Pyle et al. (2018), elevated capture rates of molting individual Orange-crowned Warblers may indicate sedentary behaviors during the breeding season, coupled with more movement during prebasic molt, perhaps including foraging lower to the ground (at the height of mist nets). Additionally, this warbler exhibits post-breeding altitudinal movements, leaving breeding territories and moving upslope to molt (Leu and Thompson 2002, Wiegardt et al. 2017), showing a distinction between breeding and molting site habitat selection that may have influenced capture rates in our study.

Differences in detectability between individuals that are breeding or molting is a relevant caveat when considering the effect of molt activity on site fidelity. If birds are more secretive during molt (Vega Rivera et al. 1998), then the probability of between-year recaptures of molting birds would be lower relative to breeding birds. This lower recapture of molting birds may have limited our ability to detect the influence of molt activity on site fidelity. Despite such confounding factors, our results indicated that for at least one species, the resident and short-distance migrant Dark-eyed Junco, site fidelity increased when individuals both bred and molted at the same site. Thus, molt activity may elevate site fidelity among short-distance migrants and resident species—those species with fewer post-breeding time constraints relative to long-distance migrants. Molt

site fidelity might be increased for other species as well and we suggest emerging technologies will help determine if individual birds return to molting sites (e.g., satellites, geolocators, cellular systems: McKinnon et al. 2013; Motus wildlife tracking and automated telemetry: Taylor et al. 2017, Schofield et al. 2018, Wright et al. 2018).

Our results demonstrate that songbirds vary their post-breeding movements and molt activity, yet, for most species, molting behavior did not increase across-year fidelity. In many instances, birds depart breeding territories and move to sites that provide the necessary resources to successfully complete molt, likely in response to environmental conditions (Pageau et al. 2020). These molting sites exhibit high ecological value given their apparent capacity to sustain avian food resources late into the summer and fall. Variation in the quality of molting sites, coupled with divergent migratory behaviors, likely resulted in the dissimilar locations used by molting individuals of different species (Figure 2). The diversity of molting and breeding behaviors exhibited among our study species supports an assertion made by Boyle (2017) that “no avifauna, including that of North America, consists of species falling neatly into tidy migrant and resident categories.” Our study highlights the multitude of dynamic behaviors birds exhibit to successfully complete their spatially flexible prebasic molt. It is likely that ecological flexibility trumps site fidelity when considering molt. Identifying those factors that limit successful completion of the prebasic molt and post-breeding period represents a necessary scientific pursuit to understand and conserve birds throughout their entire annual cycle.

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Ethics statement: Our work was conducted following international standards regarding animal welfare, specifically the code of ethics and bander training provided by the North American Banding Council.

Author contributions: L. Figueira, P. V. Martins, J. D. Wolfe, and C. J. Ralph conceived the idea, design, experiment (supervised research, formulated question or hypothesis). C. J. Ralph, J. D. Alexander and J. L. Stephens performed the experiments (collected data, conducted the research). L. Figueira, J. D. Wolfe, P.V. Martins, C. J. Ralph, J. D. Alexander, and J. L. Stephens wrote the paper. C. J. Ralph and J. D. Alexander developed or designed the methods. L. Figueira and P.V. Martins analyzed the data. C. J. Ralph, J. D. Alexander, and J. L. Stephens contributed substantial materials, resources, or funding.

Conflict of interest statement: The authors declare that there is no conflict of interest.

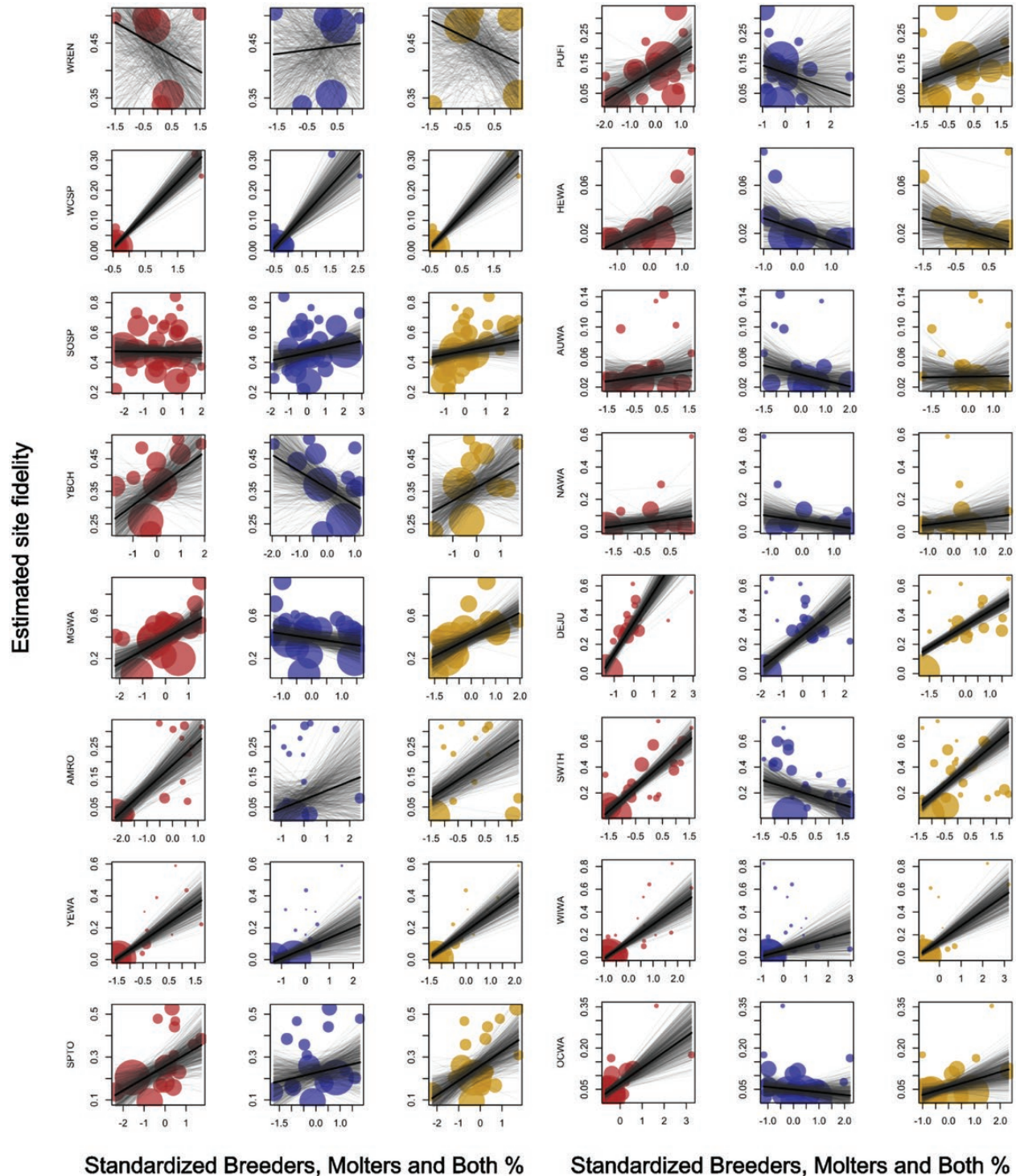
Data depositary: Data are archived in the Avian Knowledge Network and can be accessed at https://data.pointblue.org/apps/data_catalog/dataset/aknw-2020-003.

LITERATURE CITED

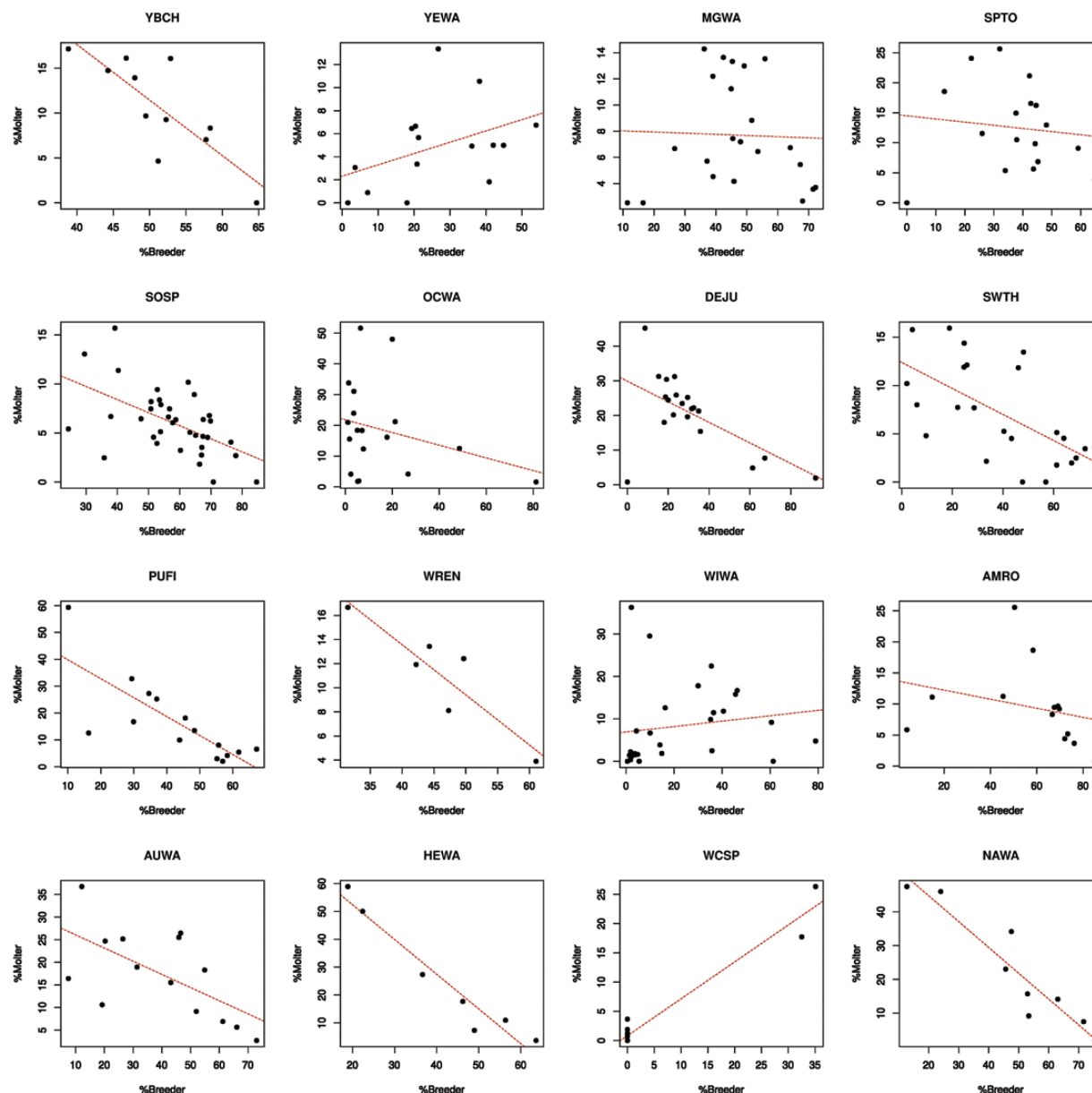
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Appendix Figure 3. Plots of weighted-linear regressions assessing the effect of breeding and molting activity on site fidelity by species (row). Species are identified by their four-letter alpha code. First column (red) for each species shows the relationship between the proportion of local Breeders (individuals captured at least once with breeding condition, but never with molt) and estimated site fidelity for each site, that is, results from weighted-linear regression in Model 1. Second column (blue) for each species shows relationship between proportion of local molters (individuals captured at least once with molt but never with breeding condition) and estimated site fidelity for each site (i.e. results from weighted-linear regression Model 2). The third column (yellow) for each species shows the relationship between the combined proportion of local breeders, molters, and both (individuals captured at least once with molt and at least once with breeding condition) and estimated site fidelity for each site, that is, results from weighted-linear regression Model 3. Size of the circle indicates the weight of each site information to the regression, with larger circles having stronger influence in regression estimation. Black bold line represents the mean estimated relationship values between x and y variables. Gray thinner lines represent all estimated relationship values within 95% credible interval.



Appendix Figure 4. Relationship between local proportions of breeders (individuals captured at least once with breeding condition but never with molt – x axis) and molters (individuals captured at least once with molt condition but never with breeding – y axis) for each species. Dashed line represents estimated linear regression for the indicated relationship. Each point for a specific species represents a unique study site. Number of study sites varied between species, as not all species occurred at all sites in sufficient quantities for analyses. Species are indicated by 4-letter alpha code.

Appendix Table 3. Study sites (Figure 2), corresponding identification code, elevation, latitude and longitude.

Station number	Station code	Elevation (m)	Latitude	Longitude
1	SACR	2	40.6758°N	124.2068°W
2	HOME	6	40.8904°N	124.1419°W
3	NAVR	6	39.1973°N	123.7507°W
4	PARK	6	40.8947°N	124.1429°W
5	RECR	11	41.2987°N	124.0360°W
6	LELA	16	40.5398°N	124.1417°W
7	MARI	33	40.8475°N	123.9880°W
8	LOST	42	41.3276°N	124.0234°W
9	RED2	110	41.2621°N	123.6041°W
10	LADY	111	41.2928°N	123.5480°W
11	CAPD	112	41.2604°N	123.6060°W
12	CAMP	119	41.2957°N	123.5587°W
13	MOLI	121	41.2881°N	123.5534°W
14	WHBA	130	40.7544°N	123.2840°W
15	APRI	352	42.2937°N	123.2347°W
16	WIIM	392	42.4907°N	123.4804°W
17	WIWI	397	42.1988°N	122.6906°W
18	PCT1	409	41.8430°N	123.2114°W
19	JENC	429	42.3004°N	122.8414°W
20	HOCK	437	40.7457°N	123.0661°W
21	SFRD	475	40.6539°N	122.9612°W
22	LORI	498	42.2276°N	124.0984°W
23	SBRR	509	40.6772°N	122.9154°W
24	HAMI	532	40.6931°N	122.8568°W
25	SVEN	550	40.7207°N	122.8057°W
26	WILL	556	42.6563°N	121.8542°W
27	YACR	584	40.5601°N	124.0585°W
28	QUIC	589	42.7384°N	123.2622°W
29	SNCO	591	42.8258°N	123.1000°W
30	GBCR	656	42.1498°N	123.4178°W
31	EMMY	720	40.6094°N	123.4126°W
32	HCME	864	42.3850°N	123.6678°W
33	BURN	934	40.9797°N	121.6601°W
34	TOPS	964	42.0261°N	122.1007°W
35	SKSW	1096	42.4637°N	122.3983°W
36	INVA	1187	40.5161°N	123.3528°W
37	GROV	1258	40.9562°N	123.4862°W
38	ODES	1263	42.4304°N	122.0619°W
39	CABN	1264	42.4969°N	122.0797°W
40	7MIL	1279	42.7050°N	122.0739°W
41	WOOD	1283	42.5876°N	121.9326°W
42	BIGS	1401	40.6431°N	121.4690°W
43	GERB	1481	42.1732°N	121.0423°W
44	ORCA	1495	42.0960°N	123.3957°W
45	JOHN	1559	42.2479°N	122.2338°W
46	ASWA	1631	42.1006°N	122.6747°W
47	ANT1	1656	41.4940°N	121.9403°W
48	WREF	1717	40.7820°N	124.1219°W
49	PLME	1846	39.7277°N	122.8485°W
50	MAST	1847	39.7370°N	122.8438°W