

## SITE USE AND SITE FIDELITY OF POST-BREEDING SWAINSON'S THRUSHES IN SOUTHERN OREGON

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**ABSTRACT:** Because the relative threats to survival during each stage of the life cycle remain uncertain, understanding all aspects of the full annual cycle has become a priority for bird conservation. The time between the end of breeding and the onset of fall migration is poorly known in most neotropical migrants and may be fraught with peril as birds move away from accustomed breeding areas to find food sufficient to prepare for migration. Therefore, we explored the use by post-breeding adult Swainson's Thrushes (*Catharus ustulatus*) of two bird-banding stations in southwestern Oregon over a combined total of 31 years. Though the stations are within the species' breeding range it nests at neither. Of 547 nonbreeding adults captured, 15.5% (85) were molting flight feathers during at least one capture. On average, these molters arrived and left earlier (2 August–29 September) and stayed longer (18.5 days) than nonmolters (30 August–21 October; 7 days). Molters' probability of being recaptured at the same site in subsequent years was higher. The estimated fidelity of molters was 0.35; that of nonmolters was 0.15. We infer that both categories represent short-distance movements of birds nesting nearby.

Understanding a species through all phases of its life cycle is paramount for its conservation (e.g., Faaborg et al. 2010, Marra et al. 2015). The importance of breeding, winter, and migration periods is well recognized, but the post-breeding period, between the end of reproduction and the departure for migration, is also critical to the success of subsequent stages of the annual cycle (e.g., Vega Rivera et al. 1998, 1999, Pagen et al. 2000, Vitz and Rodewald 2006). Among the essential aspects of the post-breeding period are the accumulation of energy for migration, imprinting on sites for future breeding, and, in some cases, the pre-basic molt prior to migration.

Most North American birds that migrate to the Neotropical Region molt after breeding but before departing for migration (Leu and Thompson 2002). Contrary to common assumptions, this molt may not actually be completed on a bird's breeding territory. Some individuals might move short distances seeking different habitats and resources to support the energetically costly activity of molt (e.g., Vega Rivera et al. 1999, Vitz and Rodewald 2006). Others may undertake long-distance flights, along or across elevational gradients, to molt at sites still within the breeding range (Rohwer et al. 2008, Wiegardt et al. 2017, Pyle et al. 2018).

In avian ecology, the post-breeding period has been less studied than other phases of the life cycle and is commonly not considered as a separate period (e.g., Marra et al. 2015). In part, this is because of the difficulty of

distinguishing the post-breeding period and migration in migratory birds. It is also challenging to distinguish whether a bird is molting at a site during the post-breeding period before migration, or if the bird is using the site for a stopover during migration. Further, it is difficult to determine how far a bird disperses from its breeding site before starting the migration. Gow and Stutchbury (2013) demonstrated that off-territory movements for molt, whether during breeding period or after, are difficult to identify without radio-telemetry.

In this study, we investigated the use of two sites by post-breeding adults of Swainson's Thrush (*Catharus ustulatus*), a Neotropical migrant, both within a season and in successive years. At these sites of long-term monitoring we captured and banded thrushes both in and after flight-feather molt. On the basis of the capture–recapture data this effort generated, we tested the hypothesis that whether an individual was molting should affect the way it used these sites. Specifically, should a thrush in molt (1) arrive earlier, (2) stay longer, or (3) be more likely to be recaptured the following year. This study sheds light on the post-breeding period of the Swainson's Thrush's annual cycle and highlights the importance of sites that are used during this less-studied period.

## METHODS

### Data Collection

We used capture–recapture data on adult Swainson's Thrushes from two banding stations in southern Oregon. We selected these two stations because of the large number of thrushes captured there (more than 100 across all years sampled). Also, the proportion of breeding adults among these captures was low, minimizing the issue of calculated fidelity rates being inflated with breeding birds still on their territories. Specifically, since fewer than 5% of Swainson's Thrushes captured showed any signs of breeding (e.g., a medium to large cloacal protuberance or a vascularized or wrinkled brood patch) as described in Ralph et al. (1993), we categorized these stations as “post-breeding.”

The two stations are located within the breeding range of the Russet-backed Swainson's Thrush (*ustulatus* subspecies group) in the forests of the Pacific coast of North America (Mack and Yong 2020). The stations are along the Rogue (42.49° N, 123.48° W) and Applegate (42.29° N, 123.23° W) rivers just under 30 km apart and are part of the Klamath Bird Monitoring Network, which encompasses more than 100 mist-netting stations where effort is consistent (Alexander et al. 2004, Alexander 2011). Both stations included mist nets located in riparian habitat dominated by invasive Himalayan blackberry (*Rubus armeniacus*) with willows (*Salix* spp.), cottonwood (*Populus trichocarpa*), and alder (*Alnus rubra*). One site also included cultivated fruit trees. Monitoring at both stations followed a constant-effort mist-netting protocol (Ralph et al. 1993, Stephens et al. 2010). Capture and banding were scheduled once every 10 days between May and August, and as much as weekly or three times a week from September to early November. Ten to twelve mist nets were opened for 5 to 6 hours per day, beginning 15 minutes prior to sunrise.

Stations were operated from 1994 to 2013 at the Rogue River station (WIIM) and from 1997 to 2007 at the Applegate River (APRI) station. For the analysis, we considered all efforts at these stations, even if no thrushes were captured. Recording of morphometric data followed Ralph et al. (1993), and the birds' identification to species, age, and sex followed Pyle (1997).

### Data Analysis

For analysis, we categorized each nonbreeding adult Swainson's Thrush as a molter or a nonmolter. If an individual was captured in symmetrical flight-feather molt in at least one year, we categorized it as a molter across all years. Individuals that were never captured in molt we categorized as nonmolters. We believe that these nonmolting, post-breeding birds very likely had already undergone their prebasic molt, but we did not collect sufficient data on this for analysis. The <5% of individuals captured at least once with the characteristics of breeding mentioned above were excluded from the analysis.

In our analysis we quantified the extent to which Swainson's Thrushes used each site during their post-breeding period or during their migration. Specifically, we examined (1) when and for how long each individual occupied the site; and (2) calculated the probability of molters and nonmolters being recaptured in a following year. We analyzed captures both within a year and in successive years. The within-year analysis aimed to estimate the (1) length of stay at the site, (2) dates over which birds were encountered at the site (the period), and (3) probability of recapture, that is, the chance of individual being detected on a given day, provided that the individual was at the site. For the within-year analysis, we used Pradel's (1997) reverse-time model. This model runs a Cormack-Jolly-Seber (Cormack 1964, Jolly 1965, Seber 1965, Lebreton et al. 1992) analysis of each individual's history of capture within a year in two directions: (1) forward, estimating the probability of the departure date being in fact after the last date the individual was detected; and (2) backward (i.e., reverse-time), estimating the probability that the arrival date was in fact before the date it was first detected. The reverse-time model also estimates the probability of recapture, both forward and backward. We kept probability of recapture constant in both directions, meaning that the model assumes that an individual's chance of being detected before its first capture is the same as its chance of being detected after its last capture. The output of the reverse-time model provides the estimated time of arrival and departure of individual birds (and consequently the period that the molter and nonmolter groups spend at the site) and the estimated probability for the species' recapture. We used the model's estimated dates of arrival and departure of each individual to calculate the molter and nonmolter groups' estimated length of stay at the post-breeding sites.

Our models of Swainson's Thrush use of the sites included dates much earlier than any confirmed arrival and after most departures. During these early and late periods, birds were almost certainly absent (before the onset of post-breeding movements into the area and after individuals had migrated farther south, respectively), so the model did not provide any reliable estimate of presence. We removed these intervals from posterior analysis (quantified as time periods with posterior standard deviation >0.25).

For the within-year analysis, with both the Pradel's reverse-time model

and length-of-stay calculation, we compared two models: (1) an “all birds” model, in which molters and nonmolters were pooled, and (2) a “split groups” model with molters and nonmolters grouped separately. We compared the two models by the deviance-information criterion (Ando 2011). The results of the best model then served as the basis for the analysis of successive years. The multi-year analysis aimed to estimate site fidelity. We adapted a Cormack–Jolly–Seber model by adding “fidelity” as a third parameter, in addition to survival and recapture. The drawback of adding this new parameter is that an apparent lack of fidelity can also represent the bird’s death, confounding fidelity and survivorship. Similarly, an apparent lack of fidelity can also represent failure to recapture a bird that is in fact present. To solve this issue, we fed the model with prior information on probabilities of survival and recapture based on the literature and from our within-year analysis, reducing its uncertainty.

The distributions for probability of survival were based on DeSante et al. (2015). We used these to build a normal distribution for survival priors with values from the averaged spatial model for Swainson’s Thrush (mean = 0.60, SD = 0.02). We used the estimated probability of recapture and length of stay from our within-year analysis as the prior distribution for recapture, combined with the sampling schedule (dates of mist netting). Since the sampling schedule varied both by station and season, we used different distributions of recapture probabilities for each year and site.

With these priors for probabilities of survival and recapture, we focused the Cormack–Jolly–Seber model on our latent parameter to quantify fidelity. To better understand how the fidelity of molters and nonmolters differed, we calculated the two groups’ overlap in posterior distribution of probability of fidelity. For this, we used the function “overlap,” from the package “Overlapping” (Pastore et al. 2025) in program R (R Core Team 2019). The models were built on a Bayesian framework and were run on six Markov Chain Monte Carlo chains of 75,000 iterations each, burn-in of 50,000, and thinning of 100, by means of the package “jagsUI” (Kellner 2017) in program R. We assessed convergence by using the Gelman–Rubin potential scale-reduction factor ( $\hat{R}$ ) (Gelman and Rubin 1992).

## RESULTS

Our dataset from the two stations included 608 captures of 547 individual nonbreeding adult Swainson’s Thrushes. Of those, 15.5% (85) were molting during at least one capture so that they were put in the “molter” group. The remainder of individuals using these stations we categorized as “nonmolters,” captured neither breeding nor molting. Sixteen individuals from the nonmolter group (3% of the total captured) and 10 individuals (12%) from the molter group were captured in more than one year, thus showing some degree of site fidelity across years.

We found that treating the captured thrushes as two independent, distinct groups, molters and nonmolters, better fit our data. Specifically, the value of the deviance-information criterion being lower for the model “split groups” (3689), than for the model “all birds” (3888) indicated that allowing independent estimates for molter and nonmolter described our data better.

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All further results are based on categorizing the birds as two groups, molters or nonmolters.

We found that molters occurred at the banding stations earlier than did nonmolters. Within our defined period of post-breeding and migration (2 August–21 October), molters were confined to the interval 2 August–29 September, while nonmolters occurred later, 10 September–21 October (Figure 1).

The two groups' estimated length of stay (Figure 1) also differed. Molters spent more time at the sites than did nonmolters (median of 18.5 and 7.0 days, respectively). Notably, however, in both groups, we found that the length of stay varied widely, depending on when the bird was captured. In both the molter and nonmolter groups, birds captured earlier or later during the post-breeding period tended to spend less time at the site than those captured toward the middle of the period (Figure 1).

Our results suggest that molters were more likely to use the same post-breeding site in the following years than were nonmolters, though there was

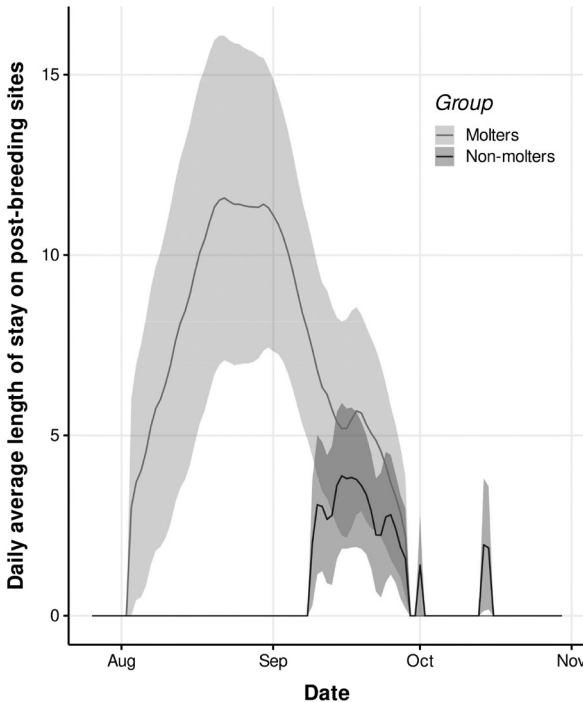


FIGURE 1. Estimated timing of occurrence and average length of stay of post-breeding adult Swainson's Thrushes categorized as molters or nonmolters (see Methods) at two sites in southwestern Oregon. The lines represent the median estimated length of stay value and the gray shadings represent the 95% credible interval. The values on the y axis represent the average length of stay of all individuals of each group at the site at a given time, thus some individuals might be staying longer than the values presented.

considerable (20%) overlap in the two groups' estimated site fidelity (Figure 2). The estimated probability of a Swainson's Thrush returning to the same site in subsequent years was higher among the molters, for which the median value was 0.35 and the 95% credible interval was broader (0.19–0.60). The nonmolters' probability of return was lower (0.16) and the 95% credible interval was narrower (0.10–0.25).

## DISCUSSION

Our examination of Swainson's Thrush's use of and fidelity to post-breeding habitat improves our knowledge of the species' ecology between breeding and winter. At sites we studied, a few individuals (15.5%) were molting in at least one year they were captured, indicating some thrushes leave their breeding territories to molt. We found detectable site fidelity to post-breeding sites by individuals categorized as both molters and nonmolters. Yet the two categories differed in fidelity, as well as in the timing and duration of stay at the site: molters arrived and departed earlier in the season. They stayed longer

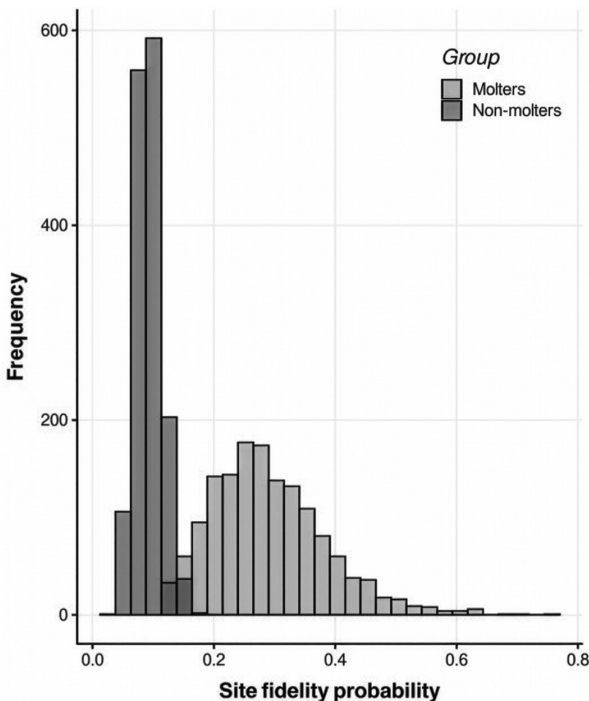


FIGURE 2. Estimated probability of fidelity to two sites in southwestern Oregon by post-breeding Swainson's Thrushes categorized as molters (light gray) or nonmolters (darker gray) (see Methods). The  $y$  axis shows the number of times a given interval of probability of fidelity appears on the posterior distribution of the Cormack–Jolly–Seber model (see text for details).

than nonmolters did, and their site fidelity was greater. Notably, however, length of stay varied widely within both groups, with shorter stays associated with captures earlier or later in the post-breeding period (Figure 1).

The groups' differences in post-breeding site use can be related to various factors, both at the individual and population levels. Since it was beyond the scope of this study to determine where the birds captured at these sites bred, we suggest two possible scenarios. First, the molter and nonmolter groups may have come from different regions. In this case, molters would be individuals breeding nearby that moved to a different habitat for at least part of their molt, while nonmolters are migrants, breeding farther north and stopping over at our sites. For example, Delmore et al. (2012) showed that Swainson's Thrushes breeding in coastal British Columbia, Canada, follow a fall migration route that includes our study region in southwestern Oregon. Because the availability of habitat along migration routes varies, however, and as do weather conditions affecting flight route and timing, small birds are not expected to depend on particular sites while en route between their breeding and wintering grounds (Catry et al. 2004). Thus the post-breeding site fidelity of nonmolters in our study either contradicts this premise or makes this scenario unlikely.

The second and more likely scenario is that both molters and nonmolters come from nearby breeding sites in southern Oregon. After the birds have bred, their habitat selection may differ from what is required for a breeding territory, and they may shift to nearby areas, possibly just a few hundred meters from nesting territories (as discussed by Vega Rivera et al. 1999, Pagen et al. 2000, White and Faaborg 2008, Vitz and Rodewald 2011). In this scenario, some thrushes leave their breeding territories to molt at other sites before departing the species' breeding range, consistent with recent studies on other songbird species that disperse within their breeding range to molt away from where they breed (e.g., Wiegardt et al. 2017, Pyle et al. 2018, Figueira et al. 2020). Sites that apparently lack the characteristics required for breeding might nonetheless be of great importance during the post-breeding period (Vega Rivera et al. 1999, Gow and Stutchbury 2013). Post-breeding site fidelity—when a site used after breeding is adjacent to or near the breeding territory—has been previously documented in Swainson's Thrush. Using radio telemetry, White and Faaborg (2008) found that adults were faithful to post-breeding sites located hundreds of meters from where they nested and led fledglings to these same sites. White and Faaborg (2008) also suggested that these sites might have important roles in territory and nest-site selection.

Molters staying longer at our post-breeding sites could be explained by birds' reduced mobility during molt (as shown by Vega Rivera et al. 1999), individuals remaining at the site until molt is complete. Nevertheless, the length of stay our models estimated for the molters is not long enough for them to complete a full molt. Cherry (1985) estimated that it takes a Swainson's Thrush around 32 days to complete the flight-feather molt, almost twice the maximum estimated time molters spent at our sites. While birds might be less mobile during molt, they nevertheless move to some extent. Molt-migration, as defined by Tonra and Reudink (2018), is the temporal overlap of the life-history stages of molt and migration, and is known in Swainson's Thrush (Cherry 1985, Wiegardt et al. 2017, Morales et al. 2022). Morales

et al. (2022) reported the average time molt-migrant Swainson's Thrushes stopped over at a site in Canada as 47 days. In our study, the brevity of stays, shorter than required for molt, suggests either dispersal over molt-migration or methodological constraints, since the low mobility of thrushes during molt might depress capture rates (Poirier et al. 2024).

Studies such as ours that explore birds' fidelity to nonbreeding sites for post-breeding dispersal, molt, or stopover in fall migration, begin to fill an information gap regarding when and where migratory birds are most limited. The post-breeding period, when birds molt, accumulate fat, and migrate, is a critical stage that may determine a bird's fate. The repeated use of a post-breeding site indicates the importance of these habitats and sites that, although not selected for breeding, may provide resources essential for molt and other post-breeding activities. Future studies using new tracking technologies are likely to further clarify the frequency, importance and extent of site fidelity in this and other species.

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