

STOPOVER ECOLOGY AND HABITAT SELECTION OF JUVENILE SWAINSON'S THRUSHES DURING FALL MIGRATION ALONG THE NORTHERN CALIFORNIA COAST

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Abstract. We investigated selection of stopover habitat by juvenile Swainson's Thrushes (*Catharus ustulatus*) during fall migration at a site along the northern California coast. The study site vegetation consisted mainly of coniferous forest (pine [*Pinus*] and spruce [*Picea*]), with interspersed patches of broadleaf forest (willow [*Salix*] and alder [*Alnus*]) in poorly drained swales. For 26 birds captured and radio-tracked in 2002 and 2003, the average minimum stopover duration was 8.9 ± 1.0 days. For 20 of these birds with a sufficient number of locations, the average home range size was 1.9 ± 0.3 ha. Thrushes showed no overall pattern of selection for forest type within the study area or for forest type used inside their home range. Fat and lean birds selected forest types similarly within the study area and their home ranges. However, locations occupied by lean birds had twice as much huckleberry (*Vaccinium ovatum*) shrub cover and were 1.3 times more concealed by vegetation than locations occupied by fat birds. There were 2.5 times more huckleberries at occupied than random locations, and locations occupied by lean birds had 2.1 times more berries overall than those frequented by fat birds. Fecal analyses confirmed that huckleberries were a commonly consumed food (70% of sampled thrushes), but also revealed that thrushes ate arthropods (87%) and wax myrtle (*Myrica californica*) bracteoles (43%). The overall lack of forest type selection coupled with differences between fat and lean birds in selection for cover and fruit abundance suggests that fat level may influence microsite selection.

Key words: *Catharus ustulatus*, energetic condition, fall migration, fruit, habitat selection, stopover, Swainson's Thrush.

Ecología de las Paradas Migratorias y Selección de Hábitat por parte de Individuos Juveniles de *Catharus ustulatus* durante la Migración de Otoño a lo Largo de la Costa del Norte de California

Resumen. Investigamos la selección de hábitat durante las paradas migratorias por parte de individuos juveniles de *Catharus ustulatus* durante la migración de otoño en un sitio a lo largo de la costa del norte de California. La vegetación en el sitio de estudio consistió principalmente en bosques de coníferas (*Pinus* y *Picea*) con parches dispersos de bosque latifoliado (*Salix*) y de *Alnus* en las zonas con poco drenaje. Para 26 individuos capturados y monitoreados con radio telemetría en 2002 y 2003, la duración promedio mínima de la parada migratoria fue de 8.9 ± 1.0 días. Para 20 de estas aves con un número de localizaciones suficientes, el tamaño del ámbito de hogar fue de 1.9 ± 0.3 ha. Los individuos de *C. ustulatus* no presentaron un patrón general de selección de algún tipo de bosque en el área de estudio o por algún tipo de bosque utilizado dentro de su ámbito de hogar. Las aves con un contenido de grasa alto o bajo seleccionaron los tipos de bosque de modo similar tanto en el área de estudio como dentro de sus ámbitos de hogar. Sin embargo, los lugares ocupados por las aves magras tuvieron dos veces más cobertura de arbustos de la especie *Vaccinium ovatum* y estuvieron 1.3 veces más cubiertos por la vegetación que los lugares ocupados por las aves con un mayor contenido de grasa. Hubo 2.5 veces más arbustos de la especie *V. ovatum* en los lugares ocupados que en lugares seleccionados al azar, y los lugares ocupados por las aves magras tuvieron 2.1 veces más de frutos que los lugares frecuentados por las aves con mayor contenido de grasa. Los análisis fecales confirmaron que los frutos de *V. ovatum* fueron un alimento consumido con frecuencia (70% de los individuos muestreados), pero también revelaron que estas aves se alimentaron de artrópodos (87%) y de *Myrica californica* (43%). La ausencia general de un patrón de selección de un tipo de bosque determinado, junto con las diferencias en la selección de áreas con mayor cobertura y abundancia de frutos entre aves magras y gordas, sugieren que el nivel de grasa corporal podría estar influenciando la selección a nivel de micro-sitio.

INTRODUCTION

For migratory birds, migration is a dangerous and unpredictable period of the annual cycle (Sillet and Holmes 2002), and thus has a profound impact on an individual's fitness. Individuals that cope poorly with the hazards and stresses of migration may succumb to starvation or predation, arrive too weak or too late at their destination to obtain and defend a breeding or nonbreeding territory, or suffer reduced reproductive success (Moore 2000). Since stopover represents a much greater proportion of the migratory phase than flying (Hedenström and Alerstam 1997), the selection of appropriate stopover sites and habitats for resting, refueling, and refuge from predators is critical to the success of a migrant bird (Schaub and Jenni 2001).

The energetic condition of a migrant arriving at a stopover site may affect which stopover strategy is favored. Fat and lean birds have been shown in previous research to select different stopover habitats (Moore and Aborn 2000), forage using different behaviors (Loria and Moore 1990), and remain at stopover sites for different lengths of time (Yong and Moore 1997). One line of reasoning suggests that in order for lean birds to continue their migration, they should select stopover habitats rich in foods that will meet their physiological demands and allow them to quickly regain body mass and fat stores. Fat birds, on the other hand, simply need to conserve energy and avoid predators, since they may already have sufficient energy stores to continue migration (Moore and Aborn 2000). This contrast in strategies may be most relevant for time-constrained individuals, such as birds heading north to their breeding grounds, for which early nest initiation dates are correlated with increased reproductive success (Norris et al. 2004, Smith and Moore 2005), or for adults heading south that need to reclaim a winter territory (Stutchbury 1994, Schmaljohann and Dierschke 2005). For juvenile migrants heading south for the first time, there may not be a clear advantage to arriving on the wintering grounds as early as possible because dominant adults may evict subordinate juveniles (Marra 2000). If food is relatively abundant along the migration route, as it may be for frugivores in the fall (Thompson and Willson 1979, Burns

2002), then a juvenile migrant might benefit during stopover by conserving energy, avoiding predators, and using risk-averse behaviors while foraging (Alerstam and Lindström 1990, Hedenström and Alerstam 1997).

We investigated stopover habitat selection by juvenile Swainson's Thrushes (*Catharus ustulatus*) during fall migration at a site along the northern California coast. Habitat selection is a hierarchical process whereby an individual chooses amongst available habitats, and is most appropriately tested by comparing used locations to random locations that are accessible to the individual (Block and Brennan 1993, Jones 2001). Because habitat selection can occur at a variety of scales (Johnson 1980), we tested whether the observed selection of forest types by thrushes differed from expected within the 66 ha study area (Johnson's [1980] 2nd order selection) and within an individual bird's home range (Johnson's [1980] 3rd order selection). Since differences in food availability and predation risk among habitats have been shown to affect stopover site selection (Hutto 1985, Lindström 1990, Sapir et al. 2004), we examined whether fruit availability, shrub cover, and concealment differed between occupied and random locations within home ranges. We also compared the habitat selection of fat and lean birds to determine whether energetic condition upon arrival played a role in shaping stopover strategy. In addition, we analyzed fecal samples to determine what foods were being consumed, how prevalent these food types were in the birds' diets, and whether the fecal samples of fat and lean birds differed.

METHODS

We conducted our field research at the Lanphere Dunes unit of the Humboldt Bay National Wildlife Refuge and on two adjacent private properties on the North Spit of the Humboldt Bay dunes (Fig. 1). This location is well situated for concentrating migrant songbirds because it contains a narrow strip of forest bordered on the west by sand dunes and the Pacific Ocean and on the east by Humboldt Bay, a tidal estuary, and dairy pasture.

CAPTURE AND MARKING

In 2002 and 2003, we captured Swainson's Thrushes in 13 12 m mist nets placed in coniferous forest and 11 12 m nets and one

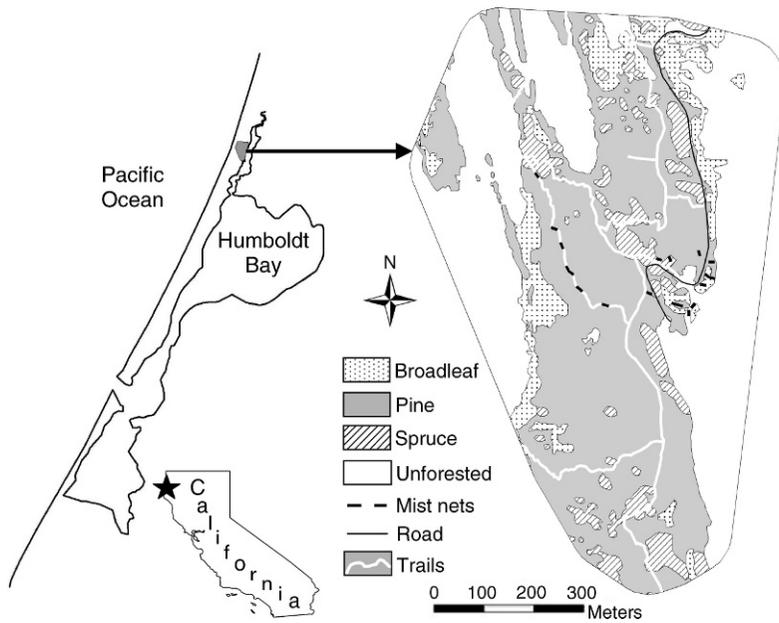


FIGURE 1. Map of the study area showing forest types and locations of mist nets and trails used to study Swainson's Thrushes during their fall stopover along the northern California coast.

6 m net placed in broadleaf forest (Fig. 1). Adult fall migrants are rare along the immediate coast (Ralph 1971), and small sample sizes prohibited examining age effects. We therefore focused only on juveniles. Since two-thirds of the nets were operated in a year-round constant effort by the Humboldt Bay Bird Observatory (HBBO), we followed their operating and banding procedures. Mist nets were opened at dawn on Wednesdays, Fridays, and Sundays for 5 hr from 4 September to 10 October. We chose this period after examining ten previous years of banding data (HBBO, unpubl. data), which indicated that peak fall migration for juvenile Swainson's Thrushes occurs between these dates and that the capture rate of local juveniles declines by over 90% from early August to 4 September.

Mist nets were checked every 30 min and captured Swainson's Thrushes were brought to a central banding station in brown paper bags for processing (bags were used to collect fecal samples; see below). All birds were aged by degree of skull ossification, standard morphometric measurements were taken (Ralph et al. 1993), and each bird received a uniquely numbered U.S. Geological Survey leg band. Energetic condition was determined by the

amount of subcutaneous fat in the furcular hollow. Birds with their furcular hollow <5% full were considered lean, while birds with their furcular hollow >50% full were considered fat. Birds with intermediate fat scores were excluded from analyses in which energetic condition was used as an independent variable. Newly captured juvenile birds not exhibiting physical abnormalities and that had completed their first prebasic molt were fitted with radio-transmitters (Holohil Systems Ltd., Carp, Ontario, Canada) with a minimum battery life of three weeks. We did not attach transmitters to birds still undergoing their first prebasic molt because we believed that they were probably lingering local juveniles. This belief was based on a few molting individuals that we radio-tracked which remained in the study site much longer than nonmolting juveniles. Although these birds may have migrated to the study site to molt, we excluded them from analyses because their use of the study area was clearly different than that of nonmolting birds. Transmitters were attached using a leg harness system designed for songbirds (Rappole and Tipton 1991). In 2002, we used a nonelastic thread to attach the harness. In 2003 we used elastic thread, which greatly expedited the harnessing

procedure. Birds were released within 10 m of the net in which they were captured during the next routine net check.

RADIO-TELEMETRY

We located marked birds using radio-telemetry six days per week during morning (07:00–11:00) and afternoon (13:00–17:00) sessions on days when the mist nets were not in operation. On banding days radio-telemetry was done only in the afternoon. During a session, two or three technicians radio-tracked the movement of each bird to obtain biangulated or triangulated positions, respectively, from marked reference points located with a GPS unit (GeoExplorer 3, Trimble Navigation Ltd., Sunnyvale, California) and postprocessed to minimize error. During a bird's first three tracking sessions (e.g., afternoon of capture day, morning and afternoon of the following day), we obtained its location every 5 min for one hour and used two-way radios to synchronize our work. Because a 5 min interval was sufficient time for a Swainson's Thrush to traverse its home range, we considered these locations independent of each other for the purposes of creating a home range (Swihart and Slade 1985, White and Garrott 1990). For other habitat selection analyses, we avoided pseudoreplication by averaging data at each bird's locations so that the bird was the sample unit. Since we could not know at the time of initial capture how long a radio-marked bird would stop over, we focused the collection of radio-telemetry data for all birds on the first two days of their stopover. This ensured that birds that stopped over for shorter periods of time would not be excluded from analyses and controlled effects of time since capture on comparisons across birds. After the first two days of a bird's stopover, its presence or absence at the site was determined once per day. If, at that point, we did not have a minimum of 20 locations or the bird expanded its home range to another part of the study area, we collected more data as described above.

Minimum stopover duration for all radio-tagged birds was estimated as the number of days between initial capture and the day the bird left the study area. A bird was considered to have left the study area if within three weeks of a bird receiving a transmitter (battery life of the transmitter) its radio signal could no longer

be detected after a thorough search of Lanphere Dunes and the surrounding properties. Daily checks were conducted for the remainder of the battery life to ensure that the bird did not return to the study area. All birds appeared to either leave the study area or die prior to their transmitter battery running out of power.

Radio-telemetry locations and their errors were determined using the computer program LOAS 3.0.2 (Ecological Software Solutions LLC, Urnäsch, Switzerland). Locations with error areas (ellipses for triangulated points and polygons for biangulated points) larger than 400 m² were not used, as areas larger than this can cause bias and lead to type II errors (Conner and Plowman 2001). A pilot study conducted in 2001 suggested that a minimum of 20 locations was necessary to define 90% of a bird's home range, so birds with fewer than 20 acceptable locations were not used in this analysis. Acceptable locations were imported into ArcView version 3.3 (ESRI, Redlands, California), where the Animal Movement extension (Hooge and Eichenlaub 2000) was used to create minimum convex polygon home ranges. These home ranges were then overlaid onto a vegetation map created from aerial photographs that delineated four vegetation types: pine, spruce, broadleaf, and unforested. Pine was composed mostly of beach pine (*Pinus contorta contorta*), spruce of Sitka spruce (*Picea sitchensis*), and broadleaf of red alder (*Alnus rubra*) and willow (*Salix* spp.). Unforested areas were composed of sand dune, dune mat, pasture, tidal estuary, and buildings. Since shrub composition and density in pine and spruce vegetation types were found to be similar, they were combined for several analyses into a forest type called conifer. Only the forested vegetation types were included in habitat analyses since Swainson's Thrushes rarely use unforested areas during stopover (Evans Mack and Yong 2000; JRT, pers. obs.) and radio-tagged birds were never seen or detected in unforested vegetation types. Furthermore, since the mist nets were concentrated across the center of the study area, we constrained analyses to a 66 ha area by placing a 77 m buffer around a minimum convex polygon constructed from all the birds' locations. This buffer distance was derived by taking the radius of a circle that was the size of the mean area of the stopover home ranges.

The resulting study area was 72% pine, 14% spruce, and 14% broadleaf forest.

VEGETATION MEASUREMENTS

During winter, spring, and fall of 2004, we measured understory structure and vegetation composition to determine their roles in habitat selection. Using a GPS unit (12XL, Garmin International Inc., Olathe, Kansas), we located five occupied and five random points within each bird's home range. Occupied points were located at the centroid of the error area as determined by telemetry while random points were determined with the Animal Movement extension in ArcView version 3.3. At each point, we measured vegetation cover using a line intercept technique, which consisted of laying out a 10 m tape centered on the point in both the north-south and east-west directions and measuring the length of tape covered by each plant species in decimeters. Only plants 0.5-3 m tall were measured (i.e., shrubs).

Understory structure was measured by taking two concealment readings at the same occupied and random points used for vegetation cover. A 1 m² cloth checkerboard with 100 10 × 10 cm squares was held 0.5 m above the ground at each point, and JRT stood 3 m to the east and south and counted the number of squares >50% visible. This value was then subtracted from one hundred to obtain percent concealment. To maintain consistency, JRT was the only observer.

To maximize our time available to track birds in the fall, we measured coniferous habitats in the winter and spring, because the understory was almost completely evergreen and therefore did not change seasonally. However, we measured broadleaf habitat in fall (September to mid-October) because it had a higher proportion of deciduous vegetation. By regressing concealment from all locations against ordinal date, we verified that concealment measurements did not vary by season ($r^2 < 0.001$, $t = 0.4$, $P = 0.66$).

FRUIT RESOURCES

Fruit availability was measured by counting berry abundance at occupied and random locations within two weeks of a bird's arrival. In 2002, huckleberries (*Vaccinium ovatum*), "native" blackberries (*Rubus ursinus*), salal berries (*Gaultheria shallon*), and bearberries

(*Arctostaphylos uva-ursi*) were counted in a 4 m² (2 × 2 m) plot at five occupied and five random points within each bird's home range located using the same technique as for vegetation measurements (see above). If a plot contained too many berries to be counted individually, berry abundance was extrapolated for a plot by multiplying the mean number of berries counted within four systematically distributed spherical wire counting frames (0.5 m diameter) by the estimated number of frames of berry-producing shrub volume in the 4 m² plot (Stransky and Halls 1980). In 2003 only huckleberries were counted, since they were by far the most abundant berry in 2002 and the only one that showed promise as a factor in the birds' habitat selection. Huckleberries were classified as ripe (purple to black), unripe (green to reddish), or overripe (shriveled), and tallied separately.

In 2002 and 2003, fecal samples were collected from the paper bags used to transport thrushes and preserved in alcohol until processing. Berries from all fall-fruited plants at Lanphere Dunes were collected and preserved for comparative purposes. Fecal samples were examined using a dissecting microscope and all seeds were counted and identified. Wax myrtle (*Myrica californica*) bracteoles and arthropod body parts were noted to be either present or absent.

STATISTICAL ANALYSES

We used Euclidean distance analysis to determine whether Swainson's Thrushes were selecting forest types during stopover (Conner and Plowman 2001, Conner et al. 2003) at Johnson's (1980) 2nd (selection within study area) and 3rd (selection within home range) orders. In this analysis, selection is revealed if the distance to a particular forest type is significantly shorter from occupied points or areas than from random points. Using the Animal Movement extension in ArcView version 3.3, we generated 3500 random points within the study area and 500 points within each bird's home range. The average distance from occupied and random points to each forest type within the study area was calculated to obtain observed and expected distances, respectively, to each forest type using the Near command in ArcInfo version 8.2 (ESRI, Redlands, California).

Second-order selection was determined by creating a ratio in which the average distance from a home range to each forest type (determined from random points within each home range) was divided by the overall expected distance (from the 3500 random points in the study area) to each forest type (Perkins and Conner 2004). Third-order selection was determined by creating a ratio in which the average distance from occupied points to each forest type was divided by the expected distance from random points within each home range to each forest type (Perkins and Conner 2004). Ratios less than one indicate selection (i.e., the bird was closer to a forest type than expected), while ratios greater than one indicate avoidance (Conner and Plowman 2001). To determine if birds were selecting forest "edge" habitats at either order, we examined whether birds were closer to unforested areas than expected. We used a Wilk's lambda multivariate analysis of variance (MANOVA) in SAS version 8.2 (SAS Institute, Inc., Cary, North Carolina) to test for overall selection in both habitat orders (Conner and Plowman 2001). If overall selection was found in either order, we determined which forest types had distance ratios statistically different from 1.0 by using one-sample *t*-tests. This was followed by ranking the forest types through pairwise comparisons. In addition to this general test of habitat selection, we included year and the energetic condition (fat or lean) of the bird as variables in two separate analyses to determine their effects on habitat selection.

For shrub cover, concealment, and berry abundance, the following four factors were considered: point type (occupied or random), energetic condition of the bird (fat or lean), year (2002 or 2003), and forest type (conifer or broadleaf). For the first three factors, we eliminated pseudoreplication and reduced zeros in the dataset by averaging data for the five occupied and five random points per bird (thus, sample size equals the number of birds in the test). However, since individual home ranges often spanned both coniferous and broadleaf habitats, data points for the last factor (forest type) were not averaged and the individual data points were analyzed. Three-way analysis of variance (ANOVA) of the first three factors was not appropriate given the small sample size ($n = 21$; only two fat birds were captured in

2002), and a MANOVA using all the habitat response variables was not possible because some of the berry data were collected from different birds than were used for shrub cover and concealment. Therefore, we first tested for differences between years for each response variable and examined plots of the data for interactions. There were no significant year effects for concealment or counts of berries. Of the five fruit-bearing shrubs, only blackberry shrub cover showed a difference between years ($F_{1,20} = 4.4$, $P = 0.05$), and there was no year effect of all fruit-bearing shrubs combined ($F_{1,20} = 0.2$, $P = 0.67$). Consequently, data from 2002 and 2003 were pooled for further analysis. For concealment and berry abundance we used two-way ANOVAs with point type and energetic condition as factors. To meet assumptions of normality, counts of berries were log-transformed. For shrub cover, we used a two-way MANOVA to simultaneously examine all shrub species.

Due to a large number of zeros in the raw data, we used pairwise randomization tests in NCSS (Hintze 2001) to compare data from coniferous and broadleaf forests and huckleberry seed counts from fecal samples. Fifty thousand Monte Carlo samples were used for all tests to obtain stable *P*-values. Thus, there are no test statistics or degrees of freedom for these tests, and we report *P*-values and sample sizes for each analysis. Chi-squared tests were used to compare frequencies of arthropods and wax myrtle bracteoles in fecal samples. NCSS (Hintze 2001) was used for all analyses except Euclidean distance-based analyses, for which we used SAS (see above). An alpha value of 0.10 was used for all tests due to small sample size, and descriptive statistics are reported as means \pm SE.

RESULTS

During the fall migration of 2002 and 2003, 28 Swainson's Thrushes were captured and tracked. However, seven of these birds did not remain in the study area long enough to obtain 20 or more useable locations and could not be used for Euclidean distance-based analyses. Another bird could not be included in any analyses because it either lost its transmitter or died (unrecoverable transmitter was motionless for 19 days until the battery died). Of the 20 birds that had greater than 20 useable locations,

10 were initially caught in nets placed in broadleaf forest, while the other 10 were captured in nets in coniferous forest. Upon initial capture, nine birds were considered fat, 10 were lean, and one received an intermediate fat score. One of the fat birds was killed by a Cooper's Hawk (*Accipiter cooperi*; JRT, pers. obs.) after we had obtained 20 locations and was not used in stopover duration calculations.

For 26 birds (28 birds minus one unknown outcome and one mortality), the average minimum stopover duration was 8.9 ± 1.0 days. While there was no significant difference in stopover duration between fat (10.5 ± 1.6 days, $n = 8$) and lean birds (8.6 ± 1.3 days, $n = 17$; $t_{23} = 0.9$, $P = 0.4$), birds stayed 1.8 times longer in 2003 (11.3 ± 1.2 days, $n = 14$) than in 2002 (6.2 ± 1.2 days, $n = 12$; $t_{24} = -2.9$, $P < 0.01$). For birds with greater than 20 locations ($n = 20$), the average home range size was 1.9 ± 0.3 ha. The home range size of lean birds (2.5 ± 0.5 ha, $n = 10$) was twice that of fat birds (1.2 ± 0.3 ha, $n = 9$; $t_{17} = 2.1$, $P = 0.05$), but there was no significant difference between years (2002: 2.0 ± 0.4 ha, $n = 7$; 2003: 1.8 ± 0.4 ha, $n = 13$; $t_{18} = 0.4$, $P = 0.7$).

FOREST SELECTION

Juvenile thrushes showed no consistent selection of forest types within the study area (2nd order selection; $F_{4,16} = 1.2$, $P = 0.34$; Fig. 2A) or within their home ranges (3rd order selection; $F_{4,16} = 1.7$, $P = 0.19$; Fig. 2B). Furthermore, energetic condition (fat or lean) did not affect forest selection at the 2nd order ($F_{4,15} = 0.9$, $P = 0.48$) or the 3rd order ($F_{4,15} = 2.0$, $P = 0.14$). Forest type selection also was not affected by year (2002 or 2003) at the 2nd order ($F_{4,16} = 1.2$, $P = 0.34$; Fig. 2A) or the 3rd order ($F_{4,16} = 1.7$, $P = 0.19$; Fig. 2B). Reanalysis of the data using conifer as a single forest type instead of spruce and pine separately showed no overall selection at the 2nd ($F_{3,17} = 1.1$, $P = 0.38$; Fig. 2A) or 3rd orders ($F_{3,17} = 2.2$, $P = 0.13$). However, pooling masks individual variation (Thomas and Taylor 1990), and the bimodal distance-ratio distribution visible for pine forest at the 2nd order (Fig. 2A) became even more extreme when pine and spruce were combined into conifer forest. Thus, while the "average" thrush showed no selection or avoidance of coniferous forest,

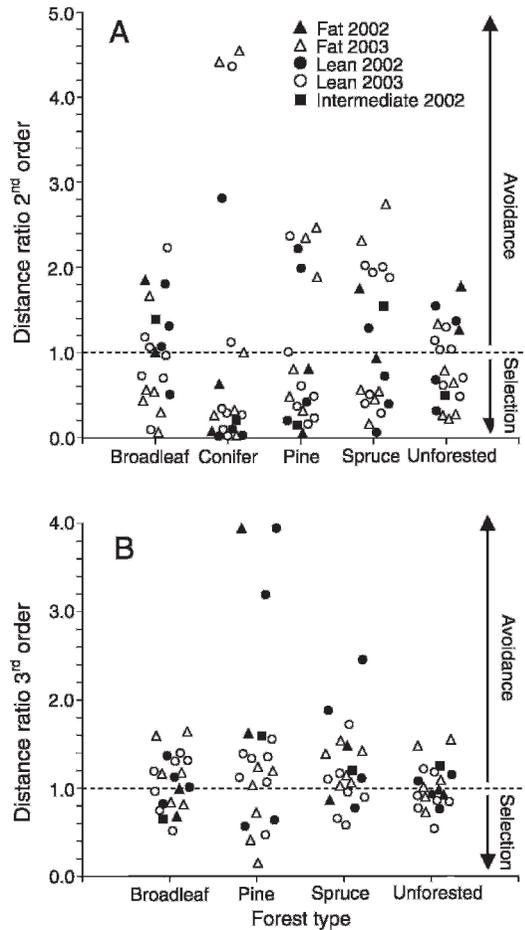


FIGURE 2. Distance ratios of individual Swainson's Thrushes ($n = 20$) along the northern California coast during fall migration to each forest type at Johnson's (1980) 2nd (A) and 3rd (B) orders. Johnson's 2nd order selection compares the selection of forest types within a home range against the available forest types in the study area whereas Johnson's 3rd order selection compares the selection of forest types at occupied locations against the forest types available in the home ranges. A distance ratio is the observed distance from a point or area occupied by a bird to a particular forest type divided by the expected distance to that forest type based on the average distance from randomly selected points. The dashed line at 1.0 represents an observed distance equal to the expected distance to that forest type. Individuals with values less than 1.0 show selection for that forest type, while individuals with values greater than 1.0 show avoidance. The ratios show a lack of overall selection for forest type at both 2nd and 3rd orders.

some individual thrushes appeared to strongly select conifers while others strongly avoided them.

COVER AND CONCEALMENT

Using the line intercept method, we measured 33 species of plants that occurred in the shrub layer, of which only five (blackberry, huckleberry, salal, silk tassel [*Garrya elliptica*], and wax myrtle) averaged greater than 1 m of cover per point (i.e., >5% of the 20 m measured). Thus, we restricted most analyses to these five shrub species, because they all produce berries in the fall and were potential food sources for Swainson's Thrushes. Individually, the amount of cover differed significantly for each species between coniferous and broadleaf forest types (Table 1). The species differed in different directions, however, and when combined, shrub cover in coniferous and broadleaf forest did not differ (Table 1). A two-way MANOVA using these five shrub species as response variables revealed that cover varied significantly between locations used by fat and lean birds ($F_{6,33} = 2.9$, $P = 0.02$), but not between occupied and random points ($F_{6,33} = 0.3$, $P = 0.9$) or the interaction between these factors ($F_{6,33} = 0.7$, $P = 0.7$). Lean birds used areas that had significantly more huckleberry shrub cover and combined shrub cover at both occupied and random points than areas used by fat birds ($F_{1,38} = 16.0$, $P < 0.001$; Table 1, Fig. 3A).

Concealment did not differ between occupied and random points overall (occupied = 72% ± 2%, random = 71% ± 2%; $F_{1,38} = 0.2$, $P = 0.66$), but the effect of energetic condition and the interaction between condition and point type were both significant. Lean birds used areas that had more concealment overall (76% ± 2%) than areas used by fat birds (65% ± 2%; $F_{1,38} = 12.4$, $P < 0.001$), and occupied points were more concealed than random points used by lean birds, but less concealed than random points used by fat birds ($F_{1,38} = 3.7$, $P = 0.06$; Fig. 3B). Comparing concealment to huckleberry cover at random locations revealed that they were strongly and positively correlated ($r_s = 0.6$, $P < 0.001$). Concealment did not differ between broadleaf ($n = 12$) and conifer ($n = 98$) forest types at random points within the birds' home ranges (broadleaf = 72% ± 10%, conifer = 70% ± 3%; $P = 0.86$).

BERRY ABUNDANCE

There were, on average, 118.6 ± 53.5 more huckleberries at points occupied by Swainson's Thrushes than at randomly chosen points

TABLE 1. Mean shrub cover measurements (vegetation over two 10 m line intercepts ± SE) of the five most common shrub species within Swainson's Thrush home ranges along the northern California coast during fall migration at random broadleaf ($n = 12$) and conifer forest points ($n = 98$), occupied and random points ($n = 22$), points occupied by fat ($n = 9$) and lean ($n = 12$) birds, and data from points occupied in 2002 ($n = 7$) and 2003 ($n = 15$). The "combined" category is the sum of the five shrub species.

Shrub	Forest type			Point type			Energetic level			Year		
	Broadleaf	Conifer	P	Occupied	Random	P	Fat	Lean	P	2002	2003	P
	Blackberry (<i>Rubus ursinus</i>)	10.2 ± 1.8	1.1 ± 0.3	<0.001	3.3 ± 0.7	2.3 ± 0.6	0.29	4.0 ± 0.7	2.0 ± 0.6	0.10	1.1 ± 0.7	3.9 ± 0.9
Huckleberry (<i>Vaccinium ovatum</i>)	1.4 ± 1.0	9.8 ± 0.7	<0.001	8.0 ± 0.6	8.6 ± 0.6	0.56	6.4 ± 0.7	10.3 ± 0.6	<0.001	10.4 ± 1.8	7.8 ± 1.0	0.20
Salal (<i>Gaultheria shallon</i>)	0.0	2.8 ± 0.4	0.01	2.6 ± 0.6	2.5 ± 0.5	0.90	2.7 ± 0.7	2.5 ± 0.6	0.84	3.2 ± 1.4	2.1 ± 0.7	0.43
Silk tassel (<i>Garrya elliptica</i>)	0.0	1.7 ± 0.3	<0.05	1.4 ± 0.3	1.5 ± 0.2	0.84	1.2 ± 0.7	1.6 ± 0.6	0.30	1.1 ± 0.4	1.4 ± 0.3	0.57
Wax myrtle (<i>Myrica californica</i>)	3.3 ± 1.1	1.6 ± 0.3	0.07	2.3 ± 0.4	1.9 ± 0.3	0.48	2.3 ± 0.7	1.9 ± 0.6	0.4	1.8 ± 0.9	2.8 ± 0.5	0.27
Combined	14.9 ± 2.1	17.0 ± 0.8	0.41	17.6 ± 0.6	16.8 ± 0.7	0.35	16.2 ± 1.0	18.3 ± 0.6	0.03	17.6 ± 1.0	18.1 ± 0.7	0.67

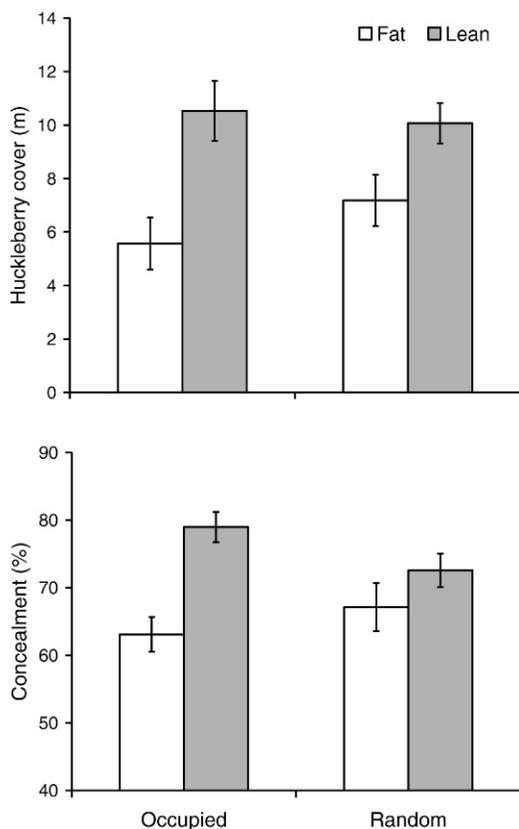


FIGURE 3. Mean (A) huckleberry cover and (B) concealment values (\pm SE) of random points and locations occupied by fat and lean Swainson's Thrushes ($n = 22$) along the northern California coast during fall migration. Huckleberry cover was measured along two 10 m line intercepts at five occupied and five random locations within each bird's home range. Concealment values were the percentage of 100 squares on a 1 m² checkerboard that were greater than 50% obscured through 3 m of vegetation at five occupied and five random locations within each bird's home range.

within their home ranges ($F_{1,40} = 3.2$, $P = 0.08$; Fig. 4). Although points occupied by lean birds had 2.1 times as many huckleberries (163.9 ± 35.7 , $n = 15$) as points occupied by fat birds (76.8 ± 52.2 , $n = 7$), this result was not statistically significant ($F_{1,40} = 1.1$, $P = 0.30$). There was no significant interaction between point type and energetic condition ($F_{1,40} = 2.7$, $P = 0.11$). Occupied points contained twice as many ripe than unripe berries and six times as many ripe than overripe berries (Fig. 4), but these proportions were not significantly different between occupied and random points

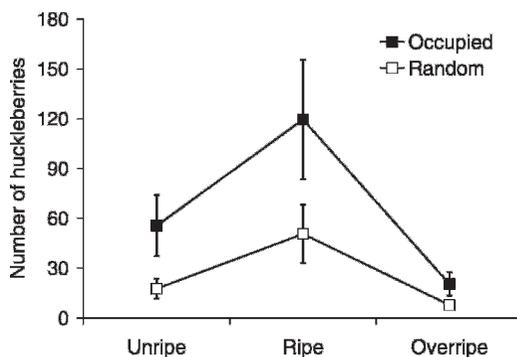


FIGURE 4. Mean numbers of unripe, ripe, and overripe huckleberries (\pm SE) at occupied and random plots (4 m²) within Swainson's Thrush home ranges ($n = 22$) along the northern California coast during fall migration.

(Fig. 4). Due to annual variation in the huckleberry crop, there was no significant difference in huckleberry abundance between coniferous and broadleaf forest types at occupied and random points for both years combined (broadleaf = 154.2 ± 105.5 , conifer = 132.1 ± 19.0 ; $P = 0.74$). In 2002, there were four times as many huckleberries in broadleaf than in coniferous forest (broadleaf = 423.7 ± 283.1 , conifer = 108.7 ± 18.5 ; $P = 0.03$), while in 2003 only six huckleberries were counted in broadleaf forest (broadleaf = 0.2 ± 0.2 , conifer = 158.8 ± 34.8 ; $P = 0.01$).

The most common types of foods in fecal samples from Swainson's Thrushes at Lanphere Dunes ($n = 74$), in descending order of frequency, were arthropods (87%), huckleberries (70%), wax myrtle bracteoles (43%), blackberry spp. (7%), and salal (4%). The mean number of huckleberry seeds per fecal sample was 8.1 ± 1.3 for all thrushes and 11.5 ± 1.7 for thrushes that had huckleberry seeds in their feces. The number of huckleberry seeds counted in fecal samples from birds captured in coniferous and broadleaf forest did not differ significantly in 2002 (conifer = 6.8 ± 2.6 , $n = 16$; broadleaf = 4.1 ± 2.1 , $n = 7$; $P = 0.55$) or in 2003 (conifer = 9.5 ± 2.2 , $n = 28$; broadleaf = 8.5 ± 2.8 , $n = 23$; $P = 0.78$). The presence of wax myrtle bracteoles in thrush feces was 1.6 times more likely for birds captured in nets placed in broadleaf (55%, $n = 31$) than in coniferous forest (35%, $n = 43$; $\chi^2_1 = 3.7$, $P = 0.05$). The number of huckleberry seeds (lean birds = 8.7 ± 1.7 , fat birds = 4.4 ± 1.9 ; $P =$

0.20) and the frequency of wax myrtle bracteoles (fat birds = 50%, lean birds = 39%; $\chi^2_1 = 0.5$, $P = 0.47$) in the feces of fat ($n = 14$) and lean birds ($n = 51$) did not differ statistically.

DISCUSSION

In contrast to several previous studies on stopover ecology that found that habitats were used out of proportion to their availability (Hutto 1985, Martin and Karr 1986, Winker et al. 1992, Moore and Aborn 2000, Rodewald and Brittingham 2004, Sapir et al. 2004), juvenile Swainson's Thrushes in this study did not select among forest types at the scale of the study site (2nd order selection) or within their home ranges (3rd order selection). However, because of the marked difference in shrub composition between the coniferous and broadleaf forest types, we had expected to see these understory-foraging thrushes make a clear selection of one of these vegetation types.

Several explanations may account for this apparent lack of habitat selection. During fall migration, Martin and Karr (1986) measured foliar cover of fruit-bearing plants around mist nets at their study site and found that it correlated positively with net captures of frugivores like the Swainson's Thrush. Although huckleberry, the most commonly ingested fruit as determined by fecal samples, was seven times more common as a cover type in coniferous than broadleaf forests, the abundance of berries in the two forest types was not significantly different when the two years were combined. Thus, even though the birds showed selection for microhabitats with abundant huckleberries, the widespread and variable distribution of huckleberries in our study site may have precluded a consistent selection for or against any particular forest type.

Three major ecological features that migrants may consider when selecting stopover habitat are food abundance, competition, and predation (Petit 2000). Depending on the energetic condition of an arriving migrant, different habitats may optimize a bird's abilities to meet these needs. For instance, Moore and Aborn (2000) found that spring migrant Summer Tanagers (*Piranga rubra*) differing in energetic needs used different stopover habitats. They found that fat birds rested in pine forests where concealment from raptors was greater, while lean birds chose to replenish their fuel reserves

in fruit-rich scrub-shrub habitat. Although we discovered differences in microhabitat selection between fat and lean birds for concealment and huckleberry cover, it was the lean birds that occupied more densely concealed microhabitats, and this did not result in selection of different forest types.

Displacement of subordinates from a habitat may occur when a limited food supply causes competition (Martin 1981, Moore and Yong 1991). Competition for preferred food-rich habitats could erode the ability to detect habitat selection when individuals are pooled, because dominant individuals occupy the preferred habitat and subordinates are forced into poorer habitats. Although food did not appear to be limited, since huckleberries and wax myrtle berries were still present and abundant in late October when the majority of Swainson's Thrushes had already migrated south (JRT, pers. obs.), the remaining berries may have been in riskier areas where the reward was not sufficient to warrant their consumption by subordinates. This explanation could be investigated by testing the prediction that concealment values should be lower at locations where berries remain hanging in late October (after migrants have passed through the area) than at locations where berries have previously been removed.

A lack of habitat selection may also have occurred because the birds had insufficient knowledge of the environment. Searching for the most appropriate habitat during stopover can be rewarding if that habitat is found, but it may also increase risk of predation and time spent searching instead of feeding (Alerstam and Lindström 1990). Shochat et al. (2002) found that sylviid warblers during autumn migration in Israel deviated from an ideal free distribution by overexploiting a food-poor habitat compared to a nearby food-rich habitat, and they attributed this to a perceptual limitation of resource distribution and insufficient time for exploration. Since newly arriving juvenile Swainson's Thrushes are naive to the distribution of resources at Lanphere Dunes, it is possible that their lack of knowledge of the landscape caused them to distribute themselves amongst forest types haphazardly.

If migrants arrive with different nutritional needs, and different habitats contain different resources, then individual migrants might be

expected to select habitats differently to replenish nutritional deficiencies, resulting in an overall appearance of no consistent habitat selection. Although huckleberry was the most frequent fruit found in fecal samples, and there were significantly more huckleberries at occupied than random sites, huckleberries alone may not have fulfilled a bird's nutritional requirements, as they contain high amounts of sugar, but low levels of lipids and proteins (Norton et al. 1984). In a review of migratory fattening in birds, Bairlein (2002) stated that a diet high in sugar does not provide efficient fat deposition. Thus, some birds may have preferred lipid-rich fruits such as wax myrtle and spent more time in broadleaf forest where this fruit was twice as common as in coniferous forest. Further research, such as volumetric analysis of fecal samples, nutrient content of fruits, and cage-controlled experiments, would be necessary to determine whether certain fruits at Lanphere Dunes are preferred over others, and whether energetic condition influences this preference.

Equally important and unmeasured in this study were the distributional abundance and composition of arthropods, which were found in 87% of all fecal samples. Fruit is generally low in protein, so thrushes may seek habitats where arthropods are common to replenish protein stores and meet basal metabolic needs (Schwilch et al. 2002). Additionally, since Bairlein (2002) demonstrated that birds put on fat fastest when their diets include both fruits and insects, it would be particularly interesting to investigate whether birds that include different habitats in their home range are benefiting from complementary food resources.

STOPOVER STRATEGIES: FAT VS. LEAN

Lean birds differed from fat birds by having significantly more huckleberry cover and more concealment at occupied points within their home ranges. Since lean birds need to accumulate additional fat to migrate to the next stopover site, it was expected that lean birds would occupy locations where there was a greater food supply. However, since huckleberry cover and concealment were positively correlated, it is not possible to say with certainty that lean birds were selecting locations based on food abundance rather than concealment from predators. Visually oriented predators may

present a hazard to migrants during stopover at Lanphere Dunes. During our study, at least two birds with radio-transmitters (one during a preliminary season in 2001 and one in 2003) were captured and eaten by accipiters. At a stopover site in coastal Alabama, Cimprich et al. (2005) found that as the number of Sharp-shinned Hawks (*Accipiter striatus*) increased, Blue-gray Gnatcatchers (*Poliophtila caerulea*) moved deeper into shrub cover where they moved more slowly and reduced foraging. If concealment is more of a priority for Swainson's Thrushes than food at Lanphere Dunes, then huckleberries may just be the best food available within the dense (safe) huckleberry shrubs. Whether huckleberries or concealment were the priority for lean birds, these birds used a strategy at this study site that provided a reliable food source and dense cover.

Strategies for fat birds remain less clear. In contrast to lean birds, fat birds used more open microhabitats with fewer huckleberry shrubs and thus occupied seemingly more risk-prone locations than lean birds. There are two potential explanations for this. One possibility is that fat birds were subordinate to lean birds and were forced to occupy these locations due to conspecific interactions. If either huckleberries or concealment were a limited resource, then this may be a possible scenario. However, huckleberries, although patchy in distribution, were still on the bushes months after the last of the Swainson's Thrushes had left. Moreover, the average concealment values at locations used by fat birds were actually lower than the average concealment values at random locations within their home ranges, within which they should be free to select.

Another possibility is that fat birds already had sufficient fuel stores to continue with migration and simply needed to avoid predation. Although fat birds had significantly less concealment than lean birds, they still had an average of $63\% \pm 3\%$ concealment at occupied locations, which may have been sufficient to avoid predators if they were not actively foraging. Additionally, the significantly smaller home range size of fat birds might indicate that they did not need to search for food as much as lean birds. This scenario is somewhat different than that described by Moore and Aborn (2000) for spring migrant Summer Tanagers on a barrier island off the coast of Mississippi,

where fat birds took shelter in pine forest and lean birds foraged in the more productive but more exposed scrub habitat. This difference is likely due to the fact that an important food source (huckleberry) at our study site was positively correlated with concealment.

CONSERVATION IMPLICATIONS

This study documents that juvenile Swainson's Thrushes did not select for a particular forest type in our study area on the northern California coast during fall migration, which may suggest that a mixture of habitats is important to fulfill the stopover needs of different individuals. More importantly, though, since not a single bird was seen or located in unforested environments, it can be inferred that Swainson's Thrushes avoided these habitats in favor of forest. Unforested habitats would have been much riskier to inhabit due to their lack of concealment and would have needed a considerable food reward to entice birds to use them. Furthermore, since this study documented high quantities of huckleberry in the forested habitats, the thrushes probably also avoided unforested habitats because they did not contain the bird-disseminated fruits found in fecal samples of these birds. Thus, preserving forested habitats along the west coast of the U.S. that contain bird-disseminated fruits and shrub cover may in turn help protect the migrants that depend on them for refueling during their southbound migrations.

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