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RESOURCE SELECTION BY JUVENILE SWAINSON'S THRUSHES DURING THE POSTFLEDGING PERIOD

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Abstract. Resource-selection studies of passerine birds during the breeding season have mainly been limited to understanding those factors important to nesting. However, little is known about what resources are selected by juveniles that are no longer dependent on their parents. The postfledging period may be a critical part of the breeding season for independent juveniles because they must avoid predators and learn to forage on a changing resource base. We used radio-telemetry to study postfledging habitat use and resource selection of juvenile Swainson's Thrushes (*Catharus ustulatus*) in coastal California from 2000 to 2002. We generated population-level contours (50% and 95% fixed-kernel) to describe habitat use by independent juveniles, and we determined juvenile resource selection by comparing vegetation characteristics at sites used by juveniles versus random sites. Juvenile Swainson's Thrushes used mixed-hardwood forest and coastal scrub during the postfledging period as well as riparian vegetation used by nesting adults. The most parsimonious predictors of resource selection were fruit abundance variables, suggesting that postfledging habitat selection by the Swainson's Thrush is best explained by the optimal-foraging hypothesis. We suggest that juvenile thrushes can track food resources in a habitat mosaic and use vegetation types distinct from what is traditionally considered Swainson's Thrush breeding habitat.

Key words: Catharus ustulatus, *habitat use, optimal foraging, postfledging period, radio-telemetry, resource selection, Swainson's Thrush.*

Selección de Recursos por Juveniles de *Cathatus ustulatus* Durante el Periodo de Emancipación

Resumen. Los estudios de selección de recursos en aves paserinas durante la estación reproductiva, se han centrado principalmente en entender los factores importantes para la anidación. Sin embargo, se sabe poco acerca de los recursos seleccionados por los juveniles que ya no dependen de sus padres. Para los juveniles independientes, el periodo de emancipación podría ser una parte crítica de la estación reproductiva en la que deben evitar depredadores y aprender a forrajear sobre una base de recursos fluctuante. Por medio de telemetría, estudiamos el uso de hábitat y selección de recursos en juveniles del zorzal *Catharus ustulatus* en la costa de California entre los años 2000 y 2002. A nivel de población, generamos polígonos (de 50% y 95% de ''kernel'' fijo) para describir la utilización de hábitat por juveniles independientes, y para determinar la selección de recursos comparamos las características de la vegetación de los sitios utilizados con la de sitios aleatorios pareados. Los juveniles utilizaron bosques mixtos y matorral costero durante el periodo de emancipación, así como la vegetación riparia utilizada por adultos nidificantes. Las variables con las predicciones más parsimoniosas del uso de recursos fueron las relacionadas con la abundancia de frutos, lo que sugiere que la selección de hábitat de emancipación por *C. ustulatus* es explicada en mejores términos por la hipótesis de forrajeo óptimo. Sugerimos que los zorzales juveniles pueden encontrar recursos alimenticios en mosaicos de hábitat y usar tipos de vegetación distintos a los que tradicionalmente se consideran como hábitat de anidación.

INTRODUCTION

Resource-selection studies of passerine birds during the breeding season have mainly been limited to understanding those factors important to nesting. However, we know little about what resources are selected by juveniles during the postfledging period (Anders et al. 1998, Vega Rivera et al. 1998, Lang et al. 2002). This period, between fledging from the nest and fall migration, may be critical for juveniles, particularly for those no longer dependent on their parents, because they must avoid predators and

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learn to forage on a changing resource base. Juvenile birds may have habitat requirements different from those of nesting adults, where nest-site selection may be the primary factor in habitat selection.

Radio-telemetry studies of the Wood Thrush (*Hylocichla mustelina*) indicate that independent juveniles use early-successional habitats rather than the mature forests used by adults (Anders et al. 1998, Vega Rivera et al. 1998, Fink 2003). These researchers hypothesized that juvenile Wood Thrushes were using early-successional habitats because of abundant fruit resources (optimal-foraging hypothesis) and thick vegetation allowing protection from predators (predator-avoidance hypothesis) for molting birds (Anders et al. 1998, Vega Rivera et al. 1998). Fink (2003) also found support for the predator-avoidance hypothesis by determining juvenile resource selection for Wood Thrushes. However, juveniles did not always select sites with thick cover; Lang et al. (2002) found that juvenile Wood Thrushes selected vegetation types similar to their natal sites and that they used a variety of cover types, ranging from dense to sparse cover. Likewise, Vega Rivera et al. (1998) found that juvenile Wood Thrushes used open or early-successional areas early in the season then switched to more mature vegetation types later in the season as fruits matured.

Other juvenile resource-selection hypotheses during the postfledging period include prospecting (searching for a future breeding site), migration commencement (southerly movements), intraspecific competition (adults excluding young from breeding areas), and socialization (associating with and learning from conspecifics; Vega Rivera et al. 1998). However, recent studies have found little support for these alternate hypotheses (Lang et al. 2002, Fink 2003, Kershner et al. 2004).

We studied Swainson's Thrushes (*Catharus ustulatus*) in central coastal California. Our study subspecies (*C. u. oedicus*) is endemic to California where it is listed as a species of special concern by the California Department of Fish and Game (CDFG and PRBO 2001). This subspecies nests in shrubs and is unique among Swainson's Thrushes in that it breeds primarily in riparian rather than coniferous forests. These forests are typical of western riparian forests in that they are narrow strips of mesic forest surrounded by more arid vegetation types. Riparian forests at our study sites were also bordered by different land uses, including grazed pasture, human habitation, or roads. We know little about what aspects of the riparian vegetation might be important to Swainson's Thrushes postfledging, or the extent to which thrushes might use adjacent vegetation types.

Our goal was to use radio-telemetry to determine the mechanisms behind postfledging juvenile habitat use and resource selection. Our first objective was to document vegetation types used by juvenile thrushes and to determine important vegetation components by comparing habitat characteristics at bird locations to paired random sites. Our second objective was to determine whether the predator-avoidance hypothesis (cover from predators) or the optimal-foraging hypothesis (abundant food resources) best explained juvenile use of a site.

METHODS

STUDY AREA

We studied Swainson's Thrushes in two riparian forests, Redwood Creek Muir Woods National Monument (37°51′N, 122°34′W), and Lagunitas Creek Golden Gate National Recreation Area (38°02′N, 122°45′W) located in Marin County, California. Riparian vegetation was typical of central coastal California and was comprised primarily of red alder (*Alnus rubra*) and arroyo willow (*Salix lasiolepis*). The surrounding vegetation types were grazed and ungrazed annual grasses, mixed-hardwood forest, and coastal scrub. Dominant trees found in mixed-hardwood forest were California bay (*Umbellularia californica*) and coast live oak (*Quercus agrifolia*).

Coastal scrub is a shrubland community composed of drymophytic plants, or plants that experience short ''wet seasons'' and long ''dry seasons'' (McMinn 1939). At our study sites, the coastal scrub could be broken down into two distinct vegetation types found on south and north-facing slopes. Dominant shrubs on the south-facing slope (hereafter referred to as south-slope coastal scrub) were coyote brush (*Baccharis pilularis*) and California sagebrush (*Artemisia californica*). The north-facing slope (hereafter referred to as north-slope coastal scrub) had a much more diverse shrub community and included coyote brush, California blackberry (*Rubus ursinus*), thimbleberry (*R. parviflorus*), California coffee berry (*Rhamnus* *californica*), blue blossom (*Ceanothus thyrsiflorus*), and California wax myrtle (*Myrica californica*).

FIELD COLLECTION

We used radio-telemetry to study postfledging habitat use and resource selection of juvenile Swainson's Thrushes from 2000 to 2002. We searched for, and monitored, nests following standardized protocols (Martin and Geupel 1993) on four pre-existing nest plots (two plots per site) established by PRBO Conservation Science (PRBO). Nest plots at Lagunitas Creek were 640 m apart and plots A and B were approximately 7.4 and 3.9 ha, respectively. Nest plots at Redwood Creek were 1400 m apart and plots A and B were 4.9 and 4.2 ha, respectively. Each nest plot had an average of 21 Swainson's Thrush territories each year from 2000–2002 (JDW, unpubl. data). Most nestlings were banded on days 9 or 10 of the nestling period, approximately 3 to 4 days before fledging, and each nestling received a Fish and Wildlife Service aluminum band and a unique combination of three colored bands.

At least one nestling per brood was fitted with a radio-transmitter using the leg-harness method (Rappole and Tipton 1991) with a modified adjustable harness. During 2000, we used 1.4 g transmitters with an average life of 60 days (Advanced Telemetry Systems [ATS], Itasca, Minnesota). During 2001, we used refurbished ATS transmitters and new 1.1 g transmitters with an average life of 50 days (Holohil Systems Ltd., Ottawa, Ontario, Canada). Transmitters weighed 4% (2000) and 3% (2001–2002) of adult thrush body mass (30 g), respectively. We used handheld receivers (model R-1000) and Yagi three-element directional antennas (model RA-150, Communications Specialists, Inc., Orange, California).

We limited our resource-selection study to juveniles that left the natal territory without returning and were no longer observed with parents or siblings. We consider juveniles to be biologically independent at this time, rather than at nutritional self-sufficiency, because juveniles may associate with parents after parental feeding has ceased. After juveniles are biologically independent from parents, siblings are expected to show spatially independent dispersal from other members of their family group, as was found for Wood Thrushes (Anders et al. 1998, Vega Rivera et al. 1998). Siblings are considered spatially independent as long as their locations do not track each other in space or in time (Erickson et al. 2001). We plotted locations of biologically independent siblings in ArcView GIS (ESRI 2000) to determine visually if sibling locations tracked each other; in no instance did independent siblings or nonrelated individuals track each other in space or time. Marked birds that occurred at the same fruiting-shrub thicket were considered independent experimental units because we assumed animals were likely congregated to use the same resource (Millspaugh et al. 1998).

Once juveniles fledged, we checked individuals and broods once every 2–4 days until juveniles were no longer associating with their parents or siblings. We recorded the GPS location of radio-tagged juveniles still with their parents and siblings, but did not record vegetation data for dependent juveniles. After juveniles became biologically independent from their parents we checked them every other day, homing in on the juvenile until it was observed then recording its location (White and Garrott 1990). We recorded two GPS locations per day for a total of 20–30 locations per bird. We alternated checks of individuals between morning and afternoon time periods on subsequent visits to ensure that each bird was monitored during different time periods throughout the day. Twice-daily locations were separated by two hours to ensure that the juvenile had enough time to move if it desired (Pasinelli et al. 2001) and to guard against autocorrelation of data points (Otis and White 1999). We monitored juveniles for 15–30 min and recorded behavior, food items taken, and presence of conspecifics or other avian species. We believe the animals we followed were a representative sample of the population because they were captured in a random fashion from nests found on the nest plots and because they behaved similar to unmarked conspecifics (Garton et al. 2001).

POPULATION-LEVEL HABITAT USE

Locations for all nests, all dependent juvenile locations, and all independent juvenile locations were pooled by plot and projected onto vegetation layer maps generated by the National Park Service. Our objective was to show population-level habitat use and to identify areas of concentrated use at the population level. We defined habitat use as the use of a certain vegetation type, and defined resource selection as nonrandom use of measured vegetation features. There are many levels at which an animal can decide to use a site; here, we focus on selection of the foraging patch (third-order selection, Johnson 1980). We used the Animal Movements Program in ArcView (Hooge and Eichenlaub 1997) to generate population-level contours from locations of independent juveniles. We used the least-squares cross-validation smoothing parameter and the fixed-kernel method to generate 50% and 95% contours. Animals often use space nonuniformly, and areas of concentrated use within an animal's home range (e.g., greater than 50% of an animal's locations) are referred to as core areas (Samuel et al. 1985). Likewise, at the population level we found areas of concentrated use. These areas were used by more than one radio-tagged juvenile at a time or were used during each year of the study. We refer to these areas as population-level core areas; they are represented by the 50% fixed-kernel. Areas of concentrated use were likely important areas at the population level. Although locations of individuals were pooled, we still consider independence among juveniles to be important because we can be more confident in our assumption that birds were at a site because of a resource rather than a connection to another individual. We did not require individuals to have a minimum number of locations to be included in population-level habitat-use analyses. Including individuals with few locations to the analysis might alter the outer boundaries of the population-level habitat-use contour but was unlikely to change identification of areas of concentrated use within the population-level habitat-use range.

VEGETATION MEASUREMENTS

We assessed vegetation characteristics at random sites and sites used by independent juveniles during 2001 and 2002. Because measuring vegetation is time intensive, we could not measure vegetation at every juvenile location. Therefore, we subsampled vegetation measurements at juvenile-use sites by systematically recording data every third visit. Juvenile-use and random site vegetation measurements were taken on the same day to remove any temporal effect of fruit availability (Compton et al. 2002). Random sites were located 50 m away from used sites, at random cardinal directions selected by a series of two coin tosses. We considered random sites to be available to juveniles because of their close proximity to used sites. Therefore, random sites were likely to be a part of the birds' home range and were close enough to be accessible to the bird.

When selecting random sites, we controlled for vegetation type; for example, if a used site was in coastal scrub then the paired random site also was in coastal scrub. In this way, we removed the potential effects of differences in vegetation types (e.g., between shrub and forest communities), and we ensured that random sites were not in unsuitable vegetation types (e.g., grasslands; Johnson 1980, Jones 2001).

To broadly describe the vegetation features at a foraging site, we measured percent tree cover, percent shrub cover (i.e., percent cover of tree and shrub canopy without stem counts), and tree and shrub species composition at a 50-m radius circular plot centered on the juvenile's location (Ralph et al. 1993). We measured the abundance of ripe fruits by species within a 5-m radius circular plot to describe the crop size at the foraging patch, using five categories: 1) 0 berries, 2) 1–50 berries, 3) 50–100 berries, 4) 100–500 berries, and 5) >500 berries. For analysis, we did not use the total number of fruits from all species at a site but rather we used the species with the largest number of fruits at used and random sites for comparison. In most cases, there was only one species present or where there was a second species, the number of fruits was minimal. Finally, we also measured fruit by species within a 0.5-m^2 plot, recording condition (flower, ripe, dry, or missing berry) and number of ripe fruits (Fantz and Hamilton 1997). If a juvenile used the same patch (within 10 m) on a subsequent visit then fruit measurements were repeated, but cover and species composition were not remeasured because these are not expected to change over a short time period.

By noting the date of the first flower or ripe fruit of each species observed on the study plots during 2001 along with flower and fruiting dates from the California Academy of Sciences herbarium collection and CalPhotos (2002), we found that fruit was available in central coastal California from mid-March through at least mid-November. Additionally, we measured fruit diameter, whole fruit weight, and dry weight of seeds of main species consumed by Swainson's

TABLE 1. Description of variables included in resource selection models for juvenile Swainson's Thrushes, from 2001 and 2002, Marin County, California. All variables were based on measurements from a 50-m radius from the location where individual thrushes were observed and from paired random sites, unless otherwise indicated.

Variable	Abbreviation	Description
Number ripe[a]	RIPE	Number of ripe fruit
Crop size[b]	CROP	Crop size of ripe fruit categorized into groups based on abundance
1–50 berries	X1	
50–100 berries	X2	
100–500 berries	X3	
>500 berries	X4	
Shrub richness	SRICH	Number of fruiting shrub species
Tree cover	TCOV	Percent tree cover
Shrub cover	SCOV	Percent shrub cover
Cornus sericea	COSE	Percent cover
Sambucus racemosa	SARA	Percent cover
Rubus discolor	RUDI	Percent cover
Lonicera involucrata	LOIN	Percent cover
Shrub cover × shrub richness	SCOV × SRICH	Interaction term
Shrub cover × crop size	SCOV × CROP	Interaction term
Shrub richness × crop size	SRICH × CROP	Interaction term

[a] The number of fruit was calculated from a 0.5-m^2 plot.

[b] Crop size was based on the amount of fruit within a 5-m radius. An additional category of no ripe fruit was included as a reference category.

Thrushes: Pacific red elderberry (*Sambucus racemosa* var. *racemosa*), Himalayan blackberry (*Rubus discolor*), California coffee berry, creek dogwood (*Cornus sericea*), and twinberry (*Lonicera involucrata*).

MODEL BUILDING

To identify which vegetation components and hypotheses (predator avoidance or optimal foraging) were important in determining resource selection by juvenile Swainson's Thrushes, we developed eight *a priori* models that included nine variables and three interaction terms (Table 1). These interaction terms should account for the possible increase in shrub richness or fruiting-shrub display with an increase in shrub cover, and the possible increase in the likelihood that any one species will display fruit at a given time with an increase in the number of shrub species. We included all variables in the ''global'' model, all variables except the interaction terms in the ''main effects'' model, and included no variables in the ''null'' model (Table 2). With the remaining models, we evaluated support for either the optimal-foraging or the predator-avoidance hypotheses, or determined the importance of different fruiting-shrub species or fruiting-shrub species richness to resource selection (Table 2).

Under the optimal-foraging hypothesis, postfledging juvenile habitat selection is based on the need for young birds to find enough food for immediate growth and survival, to undergo the first-basic molt, and to store fat for migration. If postfledging habitat selection is due to optimal foraging then Swainson's Thrush juveniles will be found in sites with abundant food resources regardless of the major vegetation type. Under this scenario the ''fruit'' model should gain support; this model included the number of ripe fruits and the crop size of a given species (Table 1). The display of a large number of brightly colored ripe fruit (crop size) is expected to attract the attention of birds and lead to increased use of shrubs with abundant and conspicuous fruits (Snow 1971, Sargent 1990, Sallabanks 1992).

If fruiting-shrub species richness or percent cover of the four main food species are important in determining juvenile use of a site, then the ''fruiting-shrub richness'' and the ''fruiting-shrub species'' models will gain support. These models would lend additional support to the optimal foraging hypothesis; however, if these models are not important but the ''fruit'' model is, then ripe fruit is more important than species richness or cover of certain shrubs.

TABLE 2. Description of *a priori* models and an additional model (fruit and cover) used in modeling resource selection by juvenile Swainson's Thrushes, 2001 and 2002, Marin County, California. The global and null models (not shown) contained all variables and none of the variables, respectively. The conditional logistic regression model has an event probability (π_{hi}) for the ith observation in stratum h, the stratum-specific intercepts (α_h) are nuisance parameters to be conditioned out. Variable coefficients (β) are listed for each variable (x'_{hi}). See table 1 for a description of variables.

Model	Model Structure
Main effects	$\text{logit}(\pi_{hi}) = \alpha_h + \beta_1(\text{TCOV}) + \beta_2(\text{SCOV}) + \beta_3(\text{SRICH}) + \beta_4(\text{RIPE})$ $+ \beta_5(\text{X1}) + \beta_6(\text{X2}) + \beta_7(\text{X3}) + \beta_8(\text{X4}) + \beta_9(\text{COSE})$ $+ \beta_{10}(\text{SARA}) + \beta_{11}(\text{RUDI}) + \beta_{12}(\text{LOIN})$
Shrub cover and fruit	$\text{logit}(\pi_{hi}) = \alpha_h + \beta_1(\text{SCOV}) + \beta_2(\text{SRICH}) + \beta_3(\text{SCOV}*\text{SRICH}) + \beta_4(\text{RIPE})$ $+ \beta_5(\text{X1}) + \beta_6(\text{X2}) + \beta_7(\text{X3}) + \beta_8(\text{X4}) + \beta_9(\text{COSE})$ $+ \beta_{10}(\text{SARA}) + \beta_{11}(\text{RUDI}) + \beta_{12}(\text{LOIN})$
Fruit	$\text{logit}(\pi_{hi}) = \alpha_h + \beta_1(\text{RIPE}) + \beta_2(\text{X1}) + \beta_3(\text{X2}) + \beta_4(\text{X3}) + \beta_5(\text{X4})$
Cover	$\text{logit}(\pi_{hi}) = \alpha_h + \beta_1(\text{TCOV}) + \beta_2(\text{SCOV})$
Fruiting shrub species richness	$\text{logit}(\pi_{hi}) = \alpha_h + \beta_1(\text{SRICH})$
Fruiting shrub species	$\text{logit}(\pi_{hi}) = \alpha_h + \beta_1(\text{COSE}) + \beta_2(\text{SARA}) + \beta_3(\text{RUDI}) + \beta_4(\text{LOIN})$
Fruit and cover	$\text{logit}(\pi_{hi}) = \alpha_h + \beta_1(\text{RIPE}) + \beta_2(\text{X1}) + \beta_3(\text{X2}) + \beta_4(\text{X3}) + \beta_5(\text{X4})$ $+ \beta_6(\text{SCOV})$

Alternatively, if habitat selection is primarily due to predator avoidance then use of a site should be best explained by percent shrub or tree cover and food variables will be less important. Under this scenario the "cover" model might gain the most support (Table 2). If both abundant food resources and percent shrub cover are important, then the "shrub cover and fruit" model should be supported more than the "fruit" or "cover" models (Table 2).

After examining the results of the *a priori* models (Table 3) we included a "fruit and cover" model with fewer parameters ($k = 6$, Table 2), because it was potentially a more competitive model than the initially hypothesized "shrub cover and fruit" model ($k = 12$, Table 2).

STATISTICAL ANALYSES

Vegetation assessment. To characterize the overall cover and fruit abundance at used and random sites we tested for differences in the average percent tree and shrub cover and the average number of ripe fruit between used and random sites by vegetation type (riparian, mixed hardwoods, and coastal scrub) using a nonparametric one-way Kruskal-Wallis test (PROC NPAR1WAY, SAS Institute Inc. 1999). Results are reported as mean ± SE unless otherwise indicated.

TABLE 3. *A priori* conditional logistic regression models used in modeling resource selection by juvenile Swainson's Thrushes from 2001 to 2002, Marin County, California. Models are ranked in ascending order by Akaike's Information Criterion adjusted for small sample sizes (AIC_c). The difference between the best model and all other models (ΔAIC_c), the relative likelihood of a model, AIC_c weights (w_i), and the number of parameters (k) are given for each model.

Model	$-2\log(L)$[a]	k	ΔAIC_c[b]	w_i
Fruit only	62.19	5	0.00	0.89
Main effects	50.66	12	4.30	0.10
Shrub cover & fruit	55.96	12	9.61	0.01
Global	49.96	15	10.89	0.00
Cover only	87.22	2	18.70	0.00
Fruiting shrub species	83.17	4	18.84	0.00
Fruiting shrub richness	101.60	1	31.03	0.00
Null	105.36	0	32.77	0.00

[a] Maximized log-likelihood value multiplied by (−2).

[b] The lowest AIC_c score in the analysis was 72.6.

Resource selection modeling. We analyzed paired data from used and random site vegetation measurements using matched-case control-logistic regression with PROC PHREG (SAS Institute Inc. 1999) to estimate the conditional-logistic model (Allison 1999, Vierkant et al. 1999). This is similar to discrete-choice analysis in that it uses the conditional logistic-regression model and paired observations to control for changes in resource availability over time (Cooper and Millspaugh 1999). We wanted to take changing resources into account because the availability of fruit changes with the fruiting phenology of different species and when animals consume fruits. To pool observations within and among individuals and make inferences about a population of animals in a resource-selection study, we assume that a choice between each pair of locations (used and nonused) is the result of an independent trial and we assume the underlying resource-selection function is the same for all individuals in the population (Cooper and Millspaugh 1999, Manly et al. 2003).

We used an information-theoretic approach to evaluate the *a priori* models and the additional ''fruit and cover'' model (Table 2) that we considered biologically relevant (Burnham and Anderson 2002). We tested the fit of the global model using the deviance goodness-of-fit test (Neter et al. 1996). We assessed the global measure of influence using the likelihood displacement statistic (LD) and the influence of individual points on parameter estimates by deletion of each point (DFBETA, Allison 1995, Vierkant et al. 1999). We found two influential points, but these were influential in the opposite direction of the rest of the data so we considered these points conservative and left them in the dataset.

We used Akaike's Information Criterion for small sample sizes (AIC_c) to identify the best approximating model for the data set (Burnham and Anderson 2002). We also calculated the absolute difference between models (ΔAIC_c). The best model in the set will have a ΔAIC_c of zero, models with a ΔAIC_c of 1–2 have good support, and models with a ΔAIC_c of greater than 10 have essentially no support (Burnham and Anderson 2002).

We calculated AIC_c weights (w_i), which estimate the likelihood that a given model is the true Kullback-Leibler best model given the set of models (Burnham and Anderson 2002). We assessed relative importance (RI) of individual variables by summing AIC_c weights for each model in which a variable appeared (Burnham and Anderson 2002). Larger relative importance values indicate higher importance of that variable relative to other variables, however only variables that are in the same number of models can be directly compared. By considering the relative importance of each variable, we will not overlook an important variable that was not present in the best model (Anderson and Burnham 2002, Burnham and Anderson 2002).

We interpreted the effect size of explanatory variables using the odds ratio; the odds ratio (OR) measures the odds that a particular variable influences use of a site while controlling for other variables (Allison 1999). The effect size statistic is calculated from the odds ratio as 100 $(OR - 1)$ for continuous variables and categorical variables greater than 1 (Allison 1999). The farther an odds ratio is from one the larger the effect (positive or negative) a variable had on the odds that a site was used. Therefore, an increase in the odds ratio represents selection for a resource, whereas a neutral effect size (odds ratio = 1.0) represents no selection (Compton et al. 2002). Here, we used a conservative interpretation in the decrease in the odds ratio and assumed that it represented a resource that was not selected at the time rather than assuming that it was avoided. Indeed, a site that was designated as random on one visit might be used on another (Marzluff et al. 2001).

RESULTS

We color banded 178 Swainson's Thrush nestlings from 62 nests. Sixty-seven nestlings were radio-tagged (18 in 2000, 32 in 2001, 17 in 2002) from 61 nests and of those, 35 juveniles reached biological independence (10 in 2000, 12 in 2001, 13 in 2002) from 30 nests. Vegetation data were collected for 25 juveniles during 2001 and 2002 with a total of 76 paired used versus random site comparisons (total number of vegetation plots sampled, $n = 152$) with 3 ± 1.4 (range = 1–6) matched pairs of vegetation samples taken per individual. To determine population-level habitat use contours we used 21 ± 10 (range = 1–41) locations per individual.

The postfledging period added one to two months to the Swainson's Thrush breeding season (first egg typically laid extends from 7 May to 14 July, JDW, unpubl. data). The postfledging period lasted from 5 June, the date of our earliest

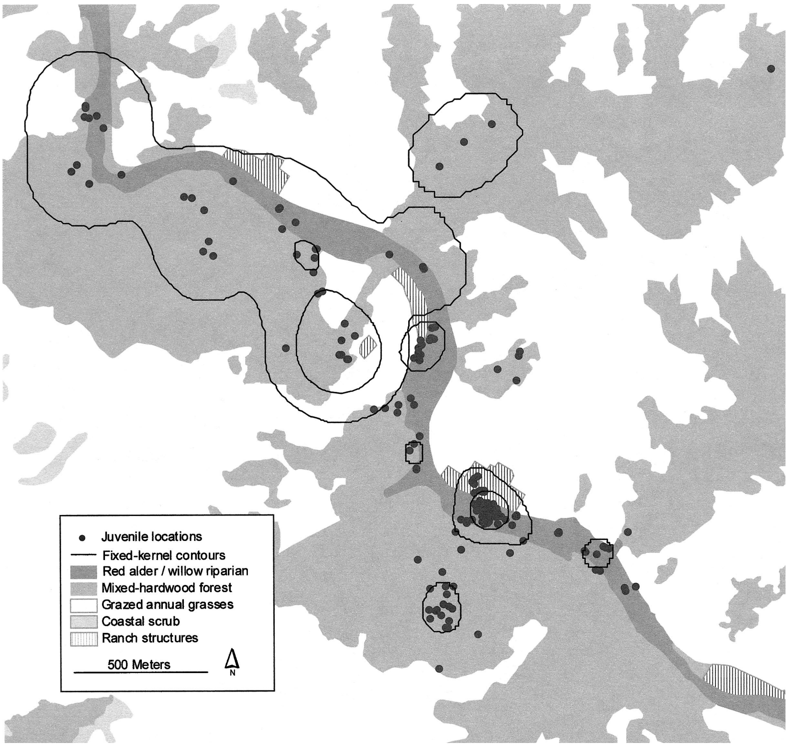

FIGURE 1. Locations of biologically independent juvenile Swainson's Thrushes and population-level contours by nest plot on Lagunitas Creek, Marin County, California, from 2000 to 2002; inner contour = 50% fixed-kernel, outer contour = 95% fixed-kernel.

fledglings, until at least 12 September when the last independent birds were relocated. Most juveniles (70%, $n = 29$) stayed in the watershed where they hatched for at least 95% of the observation time (staying on average 54 ± 1 day, $n = 20$) postfledging before the transmitter batteries wore out. The remaining birds (30%) stayed in the natal watershed an average of 41 ± 2 days ($n = 9$) postfledging before possible dispersal away from the study area.

POPULATION-LEVEL HABITAT USE

Although we found nests only in riparian vegetation, both adults with dependent broods and independent juveniles used vegetation types adjacent to riparian forests (Fig. 1). During the first 2 weeks post-fledging, 27% of parents ($n = 30$) brought their broods to upland vegetation types of mixed-hardwoods or coastal scrub at least once, and broods were found in upland vegetation types on average 38% of the time. Independent juveniles readily used upland areas; 74% of individuals ($n = 35$) used uplands at least once and individuals used upland vegetation types on average 56% of the time. However, Swainson's Thrushes were never detected using annual grasses, grazed annual grasses, or Eucalyptus (*Eucalyptus* spp.) stands, and they only used south-slope coastal scrub when a stream was present. Juvenile Swainson's Thrushes did cross roads to find foraging patches and one individual used the yard of a ranch house.

Population-level core areas for independent juveniles were in mixed-hardwood forests, north-slope coastal scrub, and riparian vegetation types (Fig. 1). In all cases, core areas overlapped fruiting-shrub thickets. Juvenile Swainson's Thrushes often were found with conspecifics and other species in these core areas. We observed juvenile thrushes foraging on fruit and insects in these core areas as well as perching, preening, and sunbathing. We never observed adults excluding juveniles from territories and believe that riparian vegetation was available to juveniles. We witnessed only one antagonistic interaction between an adult and a juvenile, but

TABLE 4. Morphology of fruits eaten by Swainson's Thrush juveniles at Lagunitas and Redwood Creeks, Marin County, California, from 2001 to 2002. Diameter and mass of fruits (mean ± SE), and the mass sum for all fruits and dry seed weight. Sample size (*n*) represents the number of fruits measured; fruits were not all collected from the same plant.

Species	*n*	Diameter (mm)	Mass (g)	Sum fruit mass	Sum seed mass
Pacific red elderberry (*Sambucus racemosa*)	106	4.2 ± 0	–	5.1	0.4
Creek dogwood (*Cornus sericea*)	41	6.8 ± 0.1	0.15 ± 0.01	6.0	1.5
Twinberry (*Lonicera involucrata*)	25	9.0 ± 0.2	0.37 ± 0.03	9.3	0.6
California coffee berry (*Rhamnus californica*)	20	12.5 ± 0.1	1.06 ± 0.03	21.2	3.1
Himalayan blackberry (*Rubus discolor*)	58	17.6 ± 0.2	2.42 ± 0.10	140.6	6.7

this was postbreeding at a population-level core area.

Juvenile thrushes also used mixed-hardwood forests where there was not an abundance of fruit. In these areas they foraged on moths at coast live oak and California bay trees and on oak moth caterpillars (*Phryganidia californica*) whose populations grew to irruptive outbreak proportions by mid August (JDW, pers. obs.).

VEGETATION MEASUREMENTS

We observed Swainson's Thrushes eating the fruits of creek dogwood, twinberry, elk's clover (*Aralia californica*), California coffee berry, blue (*Sambucus mexicana*) and red elderberry, creek gooseberry (*Ribes divaricatum*), California (*Rubus ursinus*) and Himalayan blackberry, and thimbleberry (*R. parviflorus*). Swainson's Thrushes also ate crab apples and plums (*Prunus* spp.) that had fallen to the ground.

The fruit consumed by Swainson's Thrushes varied from 4.2–17.6 mm in diameter and from 0.1–2.4 g in mass (Table 4). The range of fruit size we measured for native plant species was typical of species from eastern North America (*Sambucus* <5 mm, other species ~7–8 mm, Johnson et al. 1985). However, California coffee berry (13 mm) and Himalayan blackberry (18 mm) were larger than other North American species. Himalayan blackberry is a non-native species and Swainson's Thrushes dropped these berries on occasion, whereupon they would either follow the dropped berry to the ground or pick a new berry (JDW, pers. obs.). Dogwood and California coffee berry have large single seeds, and relatively small pulp to seed ratios (Table 4). Swainson's Thrushes likely regurgitate large seeds (JDW, pers. obs.). Twinberries have two large seeds, elderberries have three small seeds and blackberries have many small seeds; these species, particularly Himalayan blackberry, have a large pulp to seed ratio (Table 4).

Riparian sites used by Swainson's Thrushes had significantly less mean percent tree cover than random sites (Kruskal-Wallis $\chi^2_1 = 8.4$, $P < 0.01$) and had significantly greater mean percent shrub cover (Kruskal-Wallis $\chi^2_1 = 4.5$, $P = 0.03$) and mean number of ripe fruit (Kruskal-Wallis $\chi^2_1 = 25.6$, $P < 0.001$) than random sites (Fig. 2 and 3). Used sites in mixed hardwoods had significantly less tree cover than random sites (Kruskal-Wallis $\chi^2_1 = 5.0$, $P = 0.03$), but there was no difference between shrub cover (Kruskal-Wallis $\chi^2_1 = 0.7$, $P > 0.3$) or number of ripe fruit (Kruskal-Wallis $\chi^2_1 = 0.7$, $P > 0.3$) between used and random sites (Fig. 2 and 3). Used coastal-scrub sites had significantly more ripe fruit than random sites (Kruskal-Wallis $\chi^2_1 = 13.0$, $P < 0.001$), but there was no difference in tree (Kruskal-Wallis $\chi^2_1 = 0.5$, $P > 0.4$) or shrub (Kruskal-Wallis $\chi^2_1 = 0.3$, $P = 0.59$) cover between used and random sites (Fig. 2 and 3).

RESOURCE SELECTION MODELING

The global logistic model had a satisfactory fit (deviance = 105.4, $\chi^2_{15} = 124.3$, $n = 152$). The "fruit" model was the most supported model among the *a priori* candidate models ($w_i = 0.89$, Table 3). The "main effects" model had some support ($\Delta AIC_c = 4.3$) but the likelihood that this was the best model was low ($w_i = 0.10$). The relative importance of variables based on all models indicated that the number of ripe fruit

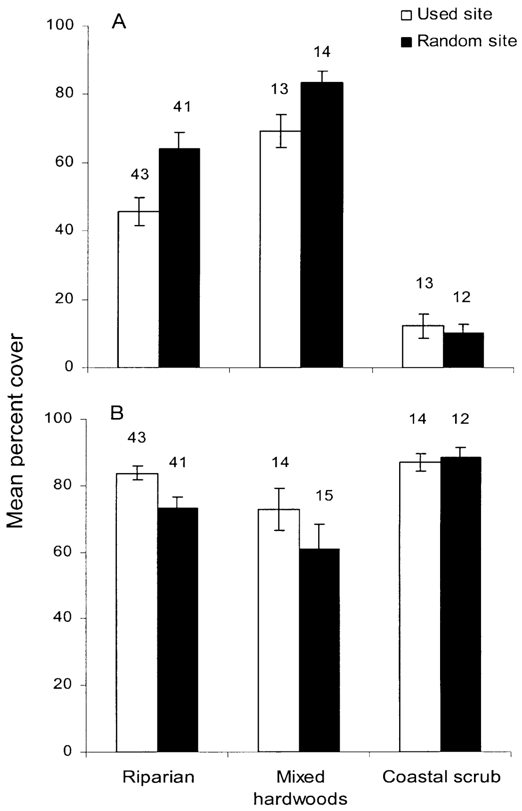

FIGURE 2. Percent tree and shrub cover (mean ± SE) by vegetation type at sites used by Swainson's Thrush juveniles and at random sites, from 2001 and 2002, Marin County, California. Sample sizes are located above each box.

and crop size were the most important variables in the set (RI = 1.0, 4 models). Variables that appeared in the same number of models can be directly compared; the other variables (SCOV, SRICH, and four fruiting-shrub species) with Akaike's weights summed over 4 models all had similarly low levels of relative importance (RI = 0.11). The remaining variables had low relative importance (TCOV RI = 0.11, SCOV*SRICH RI = 0.01, SCOV*CROP and SRICH*CROP RI $<$ 0.01); however, they were summed over fewer models (3, 2, 1, and 1 models, respectively) and thus cannot be directly compared.

When the "fruit and cover" model was added to the *a priori* set of models, it gained the most support ($\Delta AIC_c = 0$, $w_i = 0.55$); however, a great deal of model selection uncertainty existed between this and the "fruit" model ($\Delta AIC_c = 0.6$, $w_i = 0.41$). The relative importance of shrub cover increased with the added model (RI = 0.59, 5 models), but fruit variables still had the highest relative importance (RI = 1.00, 5 models). The shrub cover parameter estimate was 0.02 (±0.02) and the odds ratio and confidence interval was 1.02 (1.01–1.04).

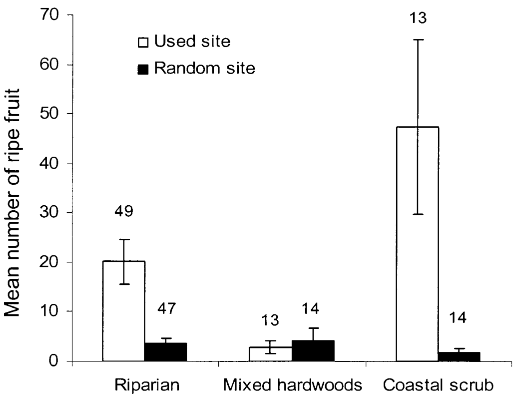

FIGURE 3. Number of ripe fruit (mean ± SE) by vegetation type at sites used by Swainson's Thrush juveniles and at random sites, from 2001 and 2002, Marin County, California. Sample sizes are located above each box.

We based our inferences primarily on the *a priori* "fruit" model because it was the most parsimonious model and because the "fruit and cover" model was derived *post hoc*. We also based inferences on the "fruit" model because of the large effect size and high relative importance of the crop-size variable and the comparatively small effect size and relative importance of the shrub-cover variable found in the "fruit and cover" model.

The odds ratio for all fruit variables was positive, indicating that as the amount of fruit increased the odds that a site was selected also increased (Table 5). There was an estimated 1.4% increase in the odds of selection for each 1 unit increase in the number of ripe fruit at used versus random sites. However, the confidence interval for the ripe fruit variable included one so this variable had a small effect size and therefore, was not as important as the crop-size variable.

DISCUSSION

POPULATION-LEVEL HABITAT USE

During the postfledging period, juvenile Swainson's Thrushes used mixed-hardwood forest and

TABLE 5. The conditional logistic model (''fruit'' only) that best described the likelihood of use of a site by juvenile Swainson's Thrushes at Lagunitas and Redwood Creeks, Marin County, California, from 2001 to 2002. Predictor variables, parameter estimates (±SE), and odds ratios (with 95% confidence intervals) are shown.

Predictor variable	Parameter estimate	Odds ratio
Number ripe	0.01 ± 0.02	1.01 (0.99–1.04)
Crop size		
1–50 berries	1.28 ± 0.62	3.59 (1.93–6.71)
50–100 berries	1.99 ± 0.93	7.31 (2.89–18.52)
100–500 berries	1.87 ± 0.91	6.52 (2.64–16.12)
>500 berries	3.98 ± 1.34	53.28 (13.96–203.41)

north-slope coastal scrub vegetation types as well as riparian vegetation. Therefore, we do not believe that prospecting explained juvenile habitat use or resource selection because juveniles used vegetation types that adults do not use for nesting.

We found juveniles in riparian vegetation used by nesting adults, but found no evidence that adults excluded juveniles from riparian vegetation (intraspecific competition hypothesis). Swainson's Thrush adults have territories with permeable boundaries and defend a small area around the nest (Evans Mack and Yong 2000). At our study sites, pairs tolerate each other at close proximity, and active nests of different pairs may be within 4 to 5 meters of each other (JDW, unpubl. data). Some population-level core areas were found in riparian vegetation; these core areas overlapped fruiting-shrub thickets and usually included many Swainson's Thrushes and other species. Therefore, evidence is not strong that juveniles were forced into alternate vegetation types due to intraspecific competition.

Our results that juveniles use vegetation types different than nesting adults concur with findings for the Wood Thrush (Anders et al. 1998, Vega Rivera et al. 1998, Fink 2003, but see Lang et al. 2002). However, alternate vegetation types used by juvenile Swainson's Thrushes were not early successional as with Wood Thrushes, rather they used coastal scrub and mixed-hardwood forest. In addition, our results corroborate the importance of alternate vegetation types adjacent to riparian forests for riparian nesting species in the West (Szaro and Jakle 1985). Szaro and Jakle (1985) found that riparian-associate birds used desert washes and upland desert-scrub vegetation types adjacent to riparian breeding areas.

Although we did not quantify moth or caterpillar use, we believe that their presence influenced thrush use of mixed-hardwood forests. One juvenile that used mixed hardwoods early in the season was observed foraging on moths that were congregating around California bay and coast live oak trees. Use of mixed hardwoods later in the season occurred in areas of irruptive caterpillar outbreaks and with an abundance of caterpillar frass on the ground and shrubs. Elsewhere, Swainson's Thrushes are known to forage on saddled prominent caterpillars (*Heterocampa guttivitta*, Holmes et al. 1986) and spruce budworm moths (*Choristoneura fumiferana*, Stanwood 1913, Langelier and Garton 1986), and are more abundant when these caterpillars and moths are present (Crawford and Titterington 1979, Holmes et al. 1986).

Our data did not support other hypotheses about the distribution of postfledging Swainson's Thrush juveniles, including the socialization hypothesis and the migration hypothesis. We tracked juvenile Swainson's Thrushes to sites with more than one radio-marked juvenile; these areas also were used by adult thrushes and by other species. These findings are similar to patterns described for juvenile Wood Thrush (Anders et al. 1998, Vega Rivera et al. 1998, Fink 2003) and we believe that population-level core areas are akin to the juvenile dispersal sites mentioned by Vega Rivera et al. (1998). Although juvenile Swainson's Thrushes used areas with many conspecifics, we believe that they occurred together because they were primarily attracted to those sites due to abundant food resources rather than the presence of other thrushes (socialization hypothesis). Lastly, the majority of juvenile thrushes (70%) remained in the natal watershed for 54 ± 1 day post-fledging;

therefore we found no evidence for gradual movements southward (migration commencement hypothesis).

RESOURCE SELECTION MODELING

The optimal foraging hypothesis was most strongly supported by our modeling efforts and revealed the importance of fruiting plants to juvenile Swainson's Thrushes during the postfledging period. The ''fruit'' model described the variability in our data better than other models, lending support to the optimal foraging hypothesis. A similar model, the *post-hoc* ''fruit and cover'' model also gave support to the cover hypothesis, in addition to supporting the optimal foraging hypothesis. We found no anecdotal evidence to support other hypotheses (prospecting for breeding sites, migration commencement, intraspecific competition, or socialization) that might explain juvenile habitat use or resource selection during the postfledging period.

The fruiting-shrub crop size was the most important variable, based on its relative importance and large effect size, when considering all variables in the set of models. The probability that a juvenile Swainson's Thrush would use a site increased with the presence of ripe fruit, especially when a species displayed a large number of ripe berries. Therefore, our findings also support the theory that fruiting shrubs display numerous and conspicuously colored fruits to attract frugivores for seed dispersal (Snow 1971), although this study was not designed to test this hypothesis. Other researchers have found a positive relationship between crop size and visitation or fruit removal by avian frugivores (Murray 1987, Sargent 1990, Sallabanks 1992), but ours is the first study to demonstrate selection of an abundant food resource by juvenile thrushes during the postfledging period.

Fruit was available to Swainson's Thrushes throughout the breeding season and was clearly important to juveniles during the postfledging period. Previous data from eastern North America indicated that peak fruit availability occurred during fall migration (Thompson and Willson 1979). However, in southeastern North America peak fruit availability occurred during the postfledging and winter periods; moreover, fruit was removed faster during the breeding season than winter (McCarty et al. 2002). Other studies also suggest that fruit may be more important to temperate-breeding birds than previously thought (Norment and Fuller 1997, Hampe 2001).

Used sites in coastal scrub had the greatest mean number of ripe fruit, while used sites in mixed hardwoods had the least; used sites in coastal scrub had 10% tree cover, while used sites in mixed hardwoods had 69% tree cover. These findings fit the ecology of fruiting shrubs. Fruiting shrubs are larger, have larger fruit crops and fruit earlier in areas with a more open canopy (Levey 1988a, 1988b). In addition, Levey (1988b) found that frugivores were most abundant in secondary forest where crop sizes were larger than in primary forest. Swainson's Thrush juveniles were also found in mixed hardwoods where there was not much fruit on average, they used oak moth caterpillars in this vegetation type as well as fruiting-shrub thickets.

In forest vegetation types, juvenile Swainson's Thrushes used sites that had less tree cover than random sites. This is contrary to findings for nesting Swainson's Thrushes where a high percentage of canopy cover is an important factor in nest-site selection (Evans Mack and Yong 2000). However, our results are similar to those for juvenile Wood Thrushes that used early-successional vegetation types, likely in part, because of the presence of ripe fruit (Anders et al. 1998, Vega Rivera et al. 1998, Fink 2003). On average, sites used by juvenile Swainson's Thrushes in riparian vegetation also had greater shrub cover and more fruit than random sites.

CONSERVATION IMPLICATIONS

This study clearly demonstrated that during the postfledging period juvenile Swainson's Thrushes used additional vegetation types different from those used by nesting adults. These vegetation types were not early successional, but sites did have less tree cover, more shrub cover, and more fruit than random sites. Therefore, when we think of vegetation types important to breeding Swainson's Thrushes we also need to include these alternate vegetation types adjacent to riparian nesting areas. Land management aimed solely at improving nest success will not necessarily protect resources important to juveniles but by understanding juvenile habitat requirements and resource selection, we can incorporate their needs into conservation plans, protecting vegetation types and resources for all stages of the breeding season.

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