

LONG-TERM OCCUPANCY OF HOME RANGES AND SHORT-TERM CHANGES
IN USE OF HABITAT BY CALIFORNIA TOWHEES (*PIPILO CRISSALIS*)

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ABSTRACT—California towhees (*Pipilo crissalis*) defend all-purpose, type-A territories throughout the year and are believed to remain on home ranges for successive breeding seasons. I present the first data regarding use of space by California towhees from a long-term study of a color-banded population. I examined individual site-fidelity to home ranges over 5 breeding seasons and combined this information with radiotelemetry data to assess sizes of home ranges and use of habitats. California towhees exhibited strong site-fidelity to breeding territories. All ($n = 31$) individuals located >10 times in a season were site-faithful across years for up to 4 years. Average size of home range was 0.83 ± 0.31 ha. Size of home range did not differ by sex, and paired birds occupied similar home ranges. All home ranges were composed of a variety of habitats, including open field, dense forest, and riparian areas. California towhees used habitat types differentially throughout the breeding season, and nested in a variety of plants. Prior to and following nesting, they were most often in open areas that provided good forage. While nesting, males and females were most often in dense vegetation. Because they defend type-A territories year-round, potentially for their entire lives, California towhees may benefit from settling on home ranges with high diversity of habitats that can meet fluctuating needs for resources.

RESUMEN—Los rascadores californianos (*Pipilo crissalis*) defienden territorios para todo uso, tipo-A, a través del año y se piensa que permanecen en su rango de hogar en épocas reproductivas sucesivas. Presento los primeros datos del uso del espacio por los rascadores californianos basados en un estudio de largo plazo de una población marcada con anillos de colores. Examiné la fidelidad al rango de hogar de individuos durante 5 épocas reproductivas y combiné esta información con datos de radioteleetría para evaluar el uso de hábitat y el tamaño del rango de hogar. Los rascadores californianos mostraron alta fidelidad a sus territorios reproductivos. Todos los individuos localizados >10 veces en una temporada ($n = 31$) mostraron fidelidad a su territorio por 4 años. El tamaño promedio del rango de hogar fue 0.83 ± 0.31 ha. El tamaño del rango de hogar no varió de acuerdo con el sexo y las parejas ocuparon rangos de hogar muy similares. Todos los rangos de hogar incluyeron una variedad de hábitats, incluyendo campos abiertos, bosques cerrados y zonas ribereñas. Los rascadores californianos utilizaron estas clases de hábitat de manera diferencial a través de la época reproductiva y anidaron en una variedad de plantas. Antes y después de anidar se encontraban más frecuentemente en áreas abiertas que proveían buen forrajeo. Mientras tenían huevos o crías, los machos y las hembras se encontraban más frecuentemente en vegetación densa. Dado que los rascadores de californianos defienden sus territorios tipo-A todo el año, posiblemente a lo largo de toda su vida, se pueden beneficiar eligiendo rangos de hogar con una alta diversidad de hábitat donde pueden satisfacer sus necesidades fluctuantes por recursos.

Ecologists have assumed that animals make informed choices when settling on territories, and therefore, patterns of occupation of territories should reflect optimal use of resources on a landscape (Fretwell and Lucas, 1970; Jones, 2001). Many birds live on type-A territories or home ranges that include all resources used by an individual, including mating, nesting, and feeding grounds (Nice, 1941). Birds of some

sedentary species defend type-A territories throughout the year over the course of their entire lives, living in the same small area for many years (Stuchbury and Morton, 2001). When this is the case, the initial choice of a home range becomes an important factor in overall lifetime reproductive success. Sedentary birds must choose home ranges carefully to meet long-term needs associated with survival and

reproduction that fluctuate over time and space (Orians and Wittenberger, 1991).

California towhees (*Pipilo crissalis*) occupy a variety of local environments in the western United States, including urban, agricultural, and undisturbed areas, with the main habitat requirements of the species being patches of dense vegetation used for cover and open spaces for foraging (Grinnell and Miller, 1944; Kunzmann et al., 2002). California towhees defend type-A territories that typically contain multiple types of habitat (Nice, 1941; Kunzmann et al., 2002). Reported sizes of territories are 0.24–0.8 ha (Kunzmann et al., 2002). Purcell and Verner (1998) estimated density of pairs in one population to be as low as 4.38 territories/30 ha, allowing for home ranges of ≤ 6.85 ha/pair (although it is unlikely that pairs use all available space within the landscape). None of these studies, however, used a marked population or radiotelemetry, so existing estimates of use of space are likely to be imprecise (Sibley, 2000). In this study, I used radiotelemetry to measure size of home range and use of habitat by California towhees throughout the breeding season.

Additionally, it is unclear whether or not California towhees remain on the same territory for successive years. They do defend territories year-round, and individual birds remain in breeding areas for successive breeding seasons, but previous studies have not examined fine-scale patterns of site-fidelity (Purcell and Verner, 1998; Kunzmann et al., 2002). I assessed long-term site-fidelity of color-banded California towhees over 5 breeding seasons and collected observations of territorial defensive behaviors.

MATERIALS AND METHODS—Research was conducted in June–July 2002 and March–July 2003–2006 at the Hastings Natural History Reservation, Carmel Valley, Monterey County, California. The study area comprised ca. 60 ha surrounding two creek drainages. Habitat in the area is predominantly oak woodland and chaparral, with areas of oak forest over dense understory vegetation (Griffin, 1990).

Adult California towhees were trapped in potter traps baited with cracked corn. Upon first capture, I determined sex of individuals based on presence or absence of a brood patch (females only) or cloacal protuberance (males only), and banded each bird with a unique combination of three colored bands and one metal leg band (United States Fish and Wildlife Service). Throughout the study, individuals were resighted opportunistically and behavioral descriptions were recorded. Nests were located through visual searches and, when possible, chicks were banded from

the nest at 7 days of age. All locations of trapping, resighting, and nesting were noted and then transformed into GIS coordinates by mapping locations onto an aerial photograph of the study site (resolution = 1.6 pixels/m) using the program ArcView GIS (Version 3.2; ESRI Industries, Redlands, California). Plants used as nest sites were identified to species and heights of nests were either measured or estimated using a visual reference of known size. Mated pairs of birds were identified as individuals attending a nest together or jointly occupying and defending a single territory.

During focal-animal watches, including 218 h of observations during 31 May 2003–17 May 2006, 41 individual California towhees were observed intensively. At each watch, an observer would note location, habitat, behavior, and vocalizations of the focal animal every 2 min. All interactions with conspecifics were noted. All locations were transformed into GIS coordinates in ArcView GIS as described above.

I fitted eight breeding California towhees with radiotransmitters to monitor patterns in use of space during 15 April–15 July 2003. Four individuals retained radiotransmitters throughout the breeding period, and four others were followed for only parts of the breeding season. Radiotransmitters weighed 1.62 g each (Model BD-2; Holohil Systems Ltd., Carp, Ontario, Canada), and were attached to birds using a harness method described by Rappole and Tipton (1991). California towhees wearing radiotransmitters were located 5 times every 2 days, once each within the following time intervals: 0500–0800, 1100–1400, and 1700–2000 h on day 1, and 0800–1100 and 1400–1700 h on day 2. For all recorded locations, observers either visually identified the individual ($n = 230$) or triangulated location ($n = 580$). Locations from radiotracking were converted into GIS data as described above.

All radiotracked individuals occupied a large patch of habitat comprised of a single field that measured 500 m long and ≤ 80 m wide, bordered on one side by an ca. 20-m wide strip of riparian vegetation along a creek and on the other side by a large swath of oak forest with poison oak understory and a road at the edge of the forest (Fig. 1). Birds were trapped and marked initially on the southwestern edge of the field.

All eight radiotracked birds included in analyses were paired with color-banded mates during the observation period, and six were paired with radiotracked individuals (comprising three complete radiotracked pairs). The sample included four males and four females. I located nests for six radiotracked birds with initiation of nests during 7–24 May.

Sizes of home range were estimated using the Animal Movement Extension in the program ArcView (Hooge and Eichenlaub, 2000). Home ranges for the eight radiotracked individuals were calculated by the 95%-kernel method using all radiotracking, resighting, and trapping locations for a single individual during the 2003 breeding season ($n = 17$ –145 locations). Home ranges for the five pairs that included at least one radiotracked individual were calculated by the 95%-kernel method using all radiotracking, resighting, and trapping locations for both individuals combined. I did not measure levels of aggression while collecting radiotracking data, so it is unknown to what

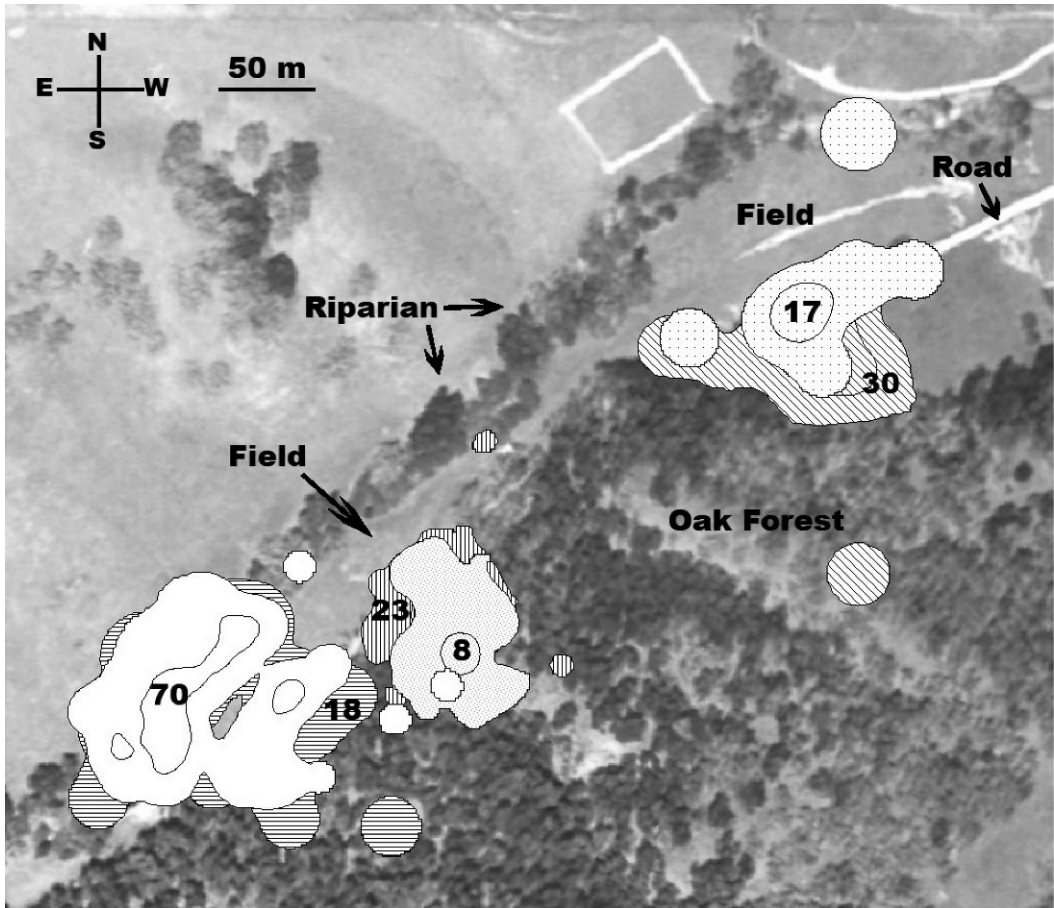


FIG. 1—Observation area, showing habitat types, and home ranges of six California towhees (*Pipilo crissalis*) wearing radiotransmitters at the Hastings Natural History Reservation, Carmel Valley, Monterey County, California, 15 April–15 July 2003. Home ranges were calculated using the 95%-kernel method including data on radiotracking, resighting, and trapping. Shapes of home ranges are labeled with identification number of the bird and are patterned differently for each individual. Mated pairs are as follows: 1) male 18 and female 70; 2) male 8 and female 23; 3) male 30 and female 17.

extent boundaries of home ranges were defended from conspecifics. Therefore, all kernels were treated as home ranges, rather than territories. Size of home ranges of males and females were compared using a two-tailed, unpaired Student's *t*-test. Unless otherwise stated, all values reported are means \pm SD. All statistical tests were performed using the software program JMP, version 5 (SAS Institute, Inc., Cary, North Carolina).

To examine habitat preferences, I plotted each radiotracking location for all paired, radiotracked individuals in ArcView and used the aerial image to categorize type of habitat at each location. The following habitats were designated: 1) oak forest, 2) road, 3) edge, 4) edge of creek, and 5) field (Fig. 1). All points within 5 m of the edge of the creek were categorized as edge-of-creek locations. Edges included vegetated islands isolated within open fields, as well as areas of riparian and forest habitat <5 m from the

field. Habitat preference was calculated as percentage of time California towhees spent in a particular type of habitat. I calculated overall habitat preference by including all radiotracking locations for all eight individuals. Because habitat preferences appeared to change with breeding behavior, I also calculated habitat preference during the following periods for the six individuals with nest data: 1) pre-nesting, including all locations recorded prior to nest initiation, 2) nesting, the period between clutch initiation and chick fledging, and 3) post-nesting, after chicks fledged or the nest failed.

Site-fidelity to home ranges across years was assessed for 45 California towhees that were paired (with one or more partners) in multiple years. Data for radiotracking, resighting, trapping, and focal-animal watching for each breeding season were plotted in ArcView for each individual (mean number of locations was 65

TABLE 1—Size of home ranges for eight radiotracked California towhees (*Pipilo crissalis*) at the Hastings Natural History Reservation, Carmel Valley, Monterey County, California, 15 April–15 July 2003. Data for locations came from radiotracking, trapping, and resighting of individuals. All home ranges were calculated with the 95%-kernel method using the Animal Movement Extension in the program ArcView.

Identity of bird	Sex	Mate	Number of observations	Size of home range (ha)
23	Male	8	145	0.46
8	Female	23	51	0.47
17	Female	30	17	0.61
30	Male	17	137	0.82
6	Male	32	91	0.86
22	Female	76	55	0.91
70	Female	18	110	1.17
18	Male	70	36	1.31

± 94). Individuals were considered site-faithful when distributions of localities overlapped between years.

RESULTS—The average size of home range for eight California towhees was 0.83 ± 0.31 ha (Table 1). Pairs of California towhees had home ranges that averaged 0.86 ± 0.23 ha, only slightly larger than average size of individual home ranges. Size of home ranges did not differ significantly by sex ($t_6 = 0.31, P = 0.76$); home ranges of females averaged 0.79 ± 0.31 ha and home ranges of males averaged 0.86 ± 0.35 ha. Mated pairs had home ranges that were similar in size and location (Fig. 1, Table 1). Although home ranges of the three pairs shown in Fig. 1 were almost entirely spatially segregated, neighboring California towhees regularly were observed to use shared areas in addition to their exclusive-use territories. Both males and females actively defended territories by jointly or singly chasing, fighting with, and displaying aggressively to intruders of both sexes.

Breeding home ranges included a variety of habitat types. California towhees were located most often in dense vegetation and infrequently in open areas. Radiotracked birds were in oak forest during 62% of observations, in edge vegetation during 23% of observations, along the creek during 7% of observations, in the road during 4% of observations, and in open field during 4% of observations. All eight subjects were observed in every type of habitat, and they all crossed the field to make use of resources in the riparian zone and in the dense oak forest (Fig. 1).

Use of habitat varied with breeding behavior. Collectively, prior to nesting, birds spent 53% of

their time in oak forest and the remaining time in habitats near open fields. During nesting, birds were located in oak forest 89% of the time (Fig. 2). Post-nesting, birds spent only 17% of their time in deep, forested areas, instead favoring more open habitats including fields and edges of fields (Fig. 2). Individually, all four birds that were radiotracked throughout the breeding period, including three males, showed this tendency to use forest vegetation more often while breeding.

California towhees included in this study nested in a variety of habitats, including oak forest, edges of creeks, vegetation bordering open fields, and even ornamental shrubs planted around buildings (Table 2). Birds nested most often in coast live oak (*Quercus agrifolia*; $n = 17$ of 46) and poison oak (*Toxicodendron diversilobum*; $n = 11$ of 46), the predominant canopy and understory plants, respectively, in many areas of dense forest. Main criteria for nesting sites seemed to be dense cover immediately surrounding the nest, so that nests were well concealed in clumps of vegetation. Height of nest varied considerably (range 0.3–11.5 m), with a mean height of 3.1 ± 3.1 m and a median height of 1.45 m ($n = 46$).

California towhees were highly sedentary. All 31 individuals located >10 times in ≥ 1 season were site faithful across seasons. In total, 40 of 45 individuals were site-faithful to breeding home ranges across seasons and breeding attempts. Eight remained on a single home range for ≥ 4 years, 11 for ≥ 3 years, and 21 for ≥ 2 years. Some birds shifted boundaries of home ranges over time, but all continued to use at least a portion of their original ranges. Among 24 birds with >100

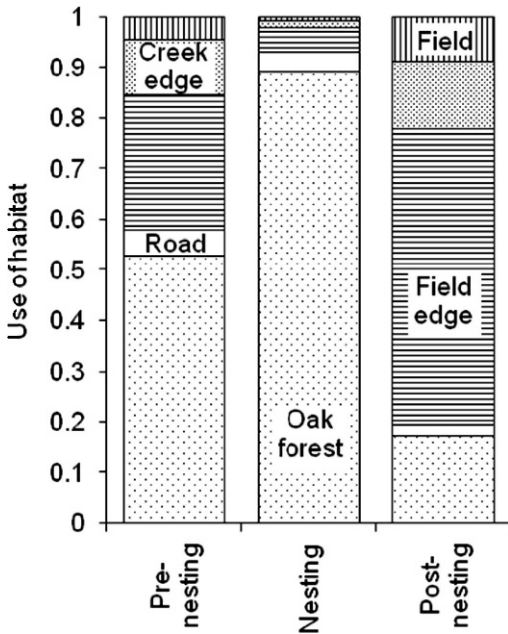


FIG. 2—Combined use of habitat according to breeding status by three male and three female California towhees (*Pipilo crissalis*) at the Hastings Natural History Reservation, Carmel Valley, Monterey County, California, 15 April–15 July 2003. Patterned areas within each bar represent the proportion of radiotracking locations for all individuals in each habitat during the appropriate breeding period.

locations across seasons, only three shifted their home ranges, all doing so soon after their mates disappeared (and presumably had died).

The five individuals that did not show site-fidelity were observed only an average of 4 ± 1.5 times/season, and the lack of site-fidelity may be due to small samples for spatial data, providing an incomplete picture of use of home range. One individual moved ca. 90 m to a new breeding home range when it lost its mate, apparently representing a real spatial shift. The other four individuals, however, were all observed to move <45 m between seasons, a distance well within the limits of a typical home range of California towhees (Fig. 1).

DISCUSSION—California towhees at the Hastings Natural History Reservation showed high site-fidelity to precise locations across breeding attempts and breeding seasons for up to 4 years, the maximum possible duration given the length of my study. Many individuals retained mates and neighbors from year to year. Among well-

TABLE 2—Species of plants in which California towhees (*Pipilo crissalis*) built nests at the Hastings Natural History Reservation, Carmel Valley, Monterey County, California, July 2002–July 2006.

Species of plant	Common name
<i>Pteridium aquilinum</i>	Western bracken fern
<i>Picea engelmannii</i>	Blue spruce
<i>Toxicodendron diversilobum</i>	Poison oak
<i>Artemisia californica</i>	Coastal sagebrush
<i>Artemisia douglasiana</i>	Mugwort
<i>Baccharis pilularis</i>	Coyote brush
<i>Lonicera interrupta</i>	Chaparral honeysuckle
Non-local <i>Lonicera</i>	Honeysuckle
<i>Sambucus mexicana</i>	Blue elderberry
<i>Arctostaphylos</i>	Manzanita
<i>Quercus agrifolia</i>	Coast live oak
<i>Quercus douglasii</i>	Blue oak
<i>Ribes californicum</i>	Hillside gooseberry
<i>Salvia mellifera</i>	Black sage
<i>Ceanothus cuneatus</i>	Buckbrush
<i>Cercocarpus betuloides</i>	California mountain-mahogany
<i>Rosa californica</i>	California wild rose
<i>Rubus ursinus</i>	Pacific blackberry
<i>Galium porrigens</i>	Bedstraw

observed individuals, boundaries of home ranges generally shifted little, unless an individual died or otherwise disappeared from the study site. Thus, home ranges (and territories) may be fixed in space for long periods relative to the lifespan of each individual. Given that California towhees defend type-A territories, the home range that an individual first settles on may end up providing all of the food, shelter, and reproductive resources that individual has access to for the rest of its lifetime.

Data from radiotracking and observation fit classic descriptions of California towhees as birds of dense habitat that prefer vegetated edges with access to open fields for foraging (Kunzmann et al., 2002). Birds used a variety of habitats; all territories included every type of habitat present within the study area. Surprisingly, I detected a low proportion of radiotracking locations in the relatively large area of open field (Fig. 1). No radiotracked individual had a home range that included areas of open field to the north of the stream, although that habitat was unoccupied by conspecifics and contiguous with existing home ranges. Because of initial trapping at the forest-field edge by a road, home ranges were likely to contain these three habitats, but data from

radiotracking indicated that birds also went deep into dense oak forests and crossed open fields to use riparian areas. In fact, some home ranges included small areas in the riparian zone that were discontinuous with the rest of the home range, probably indicating that resources associated with water are particularly valuable.

California towhees frequently were seen in open habitat, presumably due to ease of observation, but this study suggests that they spent the majority of time in densely vegetated locations. This trend is particularly evident during the nesting period. Although many nests were situated in cover at the edge of open areas, all nests were placed in patches of locally dense vegetation that would provide protection from predators. California towhees nested in a variety of plants and placed nests at varying heights, indicating that there was no typical nest location for this species, and inspiring questions about the process of selecting a nest site. Prior to and following nesting, birds were most often at edges of fields, likely improving access to food. Adult birds consume mainly seeds and other vegetative matter, and even when feeding chicks they tend to forage in areas of open ground (Kunzmann et al., 2002). Nevertheless, they were rarely seen in truly open areas, and often foraged at edges of fields with overhanging vegetation.

Size of home ranges reported herein are slightly larger than previous estimates, and likely provide a more accurate measure of individual use of space than can be gained from purely observational studies. Spatial data indicate that California towhees maintain territories as pairs, rather than as individuals. Paired birds had overlapping home ranges and used the same range of habitats. Observational data indicate that pairs defended exclusive-use territories against neighbors and intruders, but also use areas of shared space, so neighboring pairs sometimes have access to the same environmental resources.

Sizes of home ranges were variable, with some being almost 200% larger than others, but all contained a variety of habitats. It is possible that smaller home ranges contained more densely packed resources and were, therefore, just as desirable as larger home ranges, but small size of home range also may reflect low quality of home range. Most striking was the observation that all individuals established home ranges that included a diversity of habitats, and then used habitats preferentially at different times. Other studies

have shown that avian species preferentially nest in areas of high diversity of habitats, but few have quantified changes in use of microhabitats within a single home range over time (Barbaro et al., 2008; Cohen and Lindell, 2005; Barg et al., 2006).

Breeding and behavioral data provide intriguing hints about factors driving the observed variation in use of resources, but further study would be informative in helping to determine the value of different habitat resources. Among California towhees, results suggest that value of a resource likely is context-dependent, causing the observed changes in use of habitat throughout the breeding season. For example, protection afforded by dense vegetation is apparently a much more important resource during nesting than at other times. These results reflect general patterns across many species of animals, for which high-quality breeding habitat is not high-quality foraging habitat (Myserud et al., 1999). Breeding sites and access to food are universal requirements for survival, but animals face trade-offs when these resources are not available from a single habitat (Myserud and Ims, 1998). Although my study did not explicitly examine quality of habitat, results indicate that diversity of habitat may be important to California towhees when selecting home ranges. If resource needs vary through time, but space use does not, then each individual will maximize fitness by choosing to live on a home range that provides diversity of resources. This principle may be generally applicable to any animals that maintain type-A territories, and particularly those that remain on these territories year-round throughout their lifetimes.

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