

Home-range size, habitat use, and reproduction of the Ivory-billed Woodcreeper (*Xiphorhynchus flavigaster*) in dry forest of western Mexico

Jorge H. Vega Rivera,^{1,4} Dalia Ayala,² and Carola A. Haas³

¹Estación de Biología Chamela, Instituto de Biología, UNAM, A.P. 21 San Patricio, Jalisco 48980, México

²Facultad de Ciencias, UNAM, Cd. Universitaria, México, D.F.

³Virginia Polytechnic Institute and State University, Department of Fisheries and Wildlife Sciences, Blacksburg, Virginia 24061 USA

Received 11 March 2002; accepted 19 July 2002

ABSTRACT. From March 1999 to August 2000, we used mist-netting, point counts, and radio-tracking to study habitat use, area requirements, and breeding of the Ivory-billed Woodcreeper *Xiphorhynchus flavigaster* in the tropical deciduous and semi-deciduous forest (arroyo forest) of the Chamela-Cuixmala Biosphere Reserve, western Mexico. The Ivory-billed Woodcreeper was a common, year-round resident. Breeding commenced at the end of the dry season (May) and continued during the rainy season through August. Our observations suggested that only the female builds the nest, incubates, and feeds nestlings. Ivory-billed Woodcreepers commonly foraged alone, but sometimes joined mixed-species flocks that passed through their territories, occasionally following army ant swarms. Home-range size varied from 6–36 ha, although most birds' home range was 15 ha or less. We did not find differences in home range size or mobility between the dry and rainy seasons, and we did not find a correlation between the size of the home range and the extent of semi-deciduous forest it included. We did not find evidence that suggested a greater use of semi-deciduous forest than of dry deciduous forest. We hypothesize that foraging habits and low competition could explain the lack of selection for semi-deciduous forest and the strong site fidelity exhibited by members of this species.

SINOPSIS. **Ámbito hogareño, uso del hábitat y reproducción de *Xiphorhynchus flavigaster* en el bosque tropical caducifolio del México occidental.**

Mediante el uso de redes de niebla, puntos de conteo y radiotelemetría, de Marzo 1999 a Agosto 2000 estudiamos el uso del hábitat, requerimientos de área y la reproducción del Trepatroncos bigotudo *Xiphorhynchus flavigaster* en el bosque tropical caducifolio y subcaducifolio (también conocido como bosque de arroyo) de la Reserva de la Biosfera de Chamela-Cuixmala, en el oeste de México. *X. flavigaster* es un residente permanente común en la Reserva. La reproducción comenzó al final de las secas (Mayo) y continuó durante la estación de lluvias hasta Agosto. Nuestras observaciones sugieren que sólo la hembra construye el nido, incuba los huevos y cuida y alimenta los pollos. *X. flavigaster* forrajea comúnmente solitario, pero algunas veces se une a parvadas mixtas de aves que pasan por su territorio, ocasionalmente siguiendo enjambres de hormigas soldado. El ámbito hogareño varió 6–36 ha, aunque en la mayoría de los individuos fue de 15 ha o menos. No encontramos diferencias en el tamaño del ámbito hogareño o en los patrones de movimiento entre las estaciones de secas y de lluvias; ni tampoco se encontró una correlación en el tamaño del ámbito hogareño y el porcentaje del ámbito hogareño cubierto con vegetación de arroyo. En el análisis de capturas, puntos de conteo y radiotelemetría, no encontramos evidencia sugiriendo un mayor uso de la vegetación de arroyo versus el bosque caducifolio. Basándose en nuestros resultados, planteamos la hipótesis que los hábitos alimenticios y la baja competencia podría explicar la carencia de selección del hábitat de arroyo y la fuerte fidelidad al sitio exhibida por miembros de esta especie en la Reserva.

Key words: Dendrocolaptidae, habitat selection, tropical dry forest, western Mexico, *Xiphorhynchus flavigaster*

In this study, we present information on habitat selection, activity patterns, and reproductive biology of the Ivory-billed Woodcreeper, *Xiphorhynchus flavigaster*. Of the 13 species of woodcreepers occurring in Mexico, the Ivory-billed Woodcreeper has the widest distribution (American Ornithologists' Union 1998). It is associated with wet and dry forests, secondary

growth, pine, and mangroves on both the Pacific and Atlantic slopes of Mexico and the Yucatan Peninsula (American Ornithologists' Union 1998). Despite it being a common species, there is little information on its general biology and habitat requirements; the scarce information available is dispersed in distributional bird guides and tropical community accounts (Skutch 1969, 1977; Binford 1989; Stiles and Skutch 1989; Howell and Webb 1995).

In western Mexico, the Ivory-billed Wood-

⁴Corresponding author. Email: jhvega@ibiologia.unam.mx

creeper is a common resident of tropical dry forest (Schaldach 1963). This forest system (also known as seasonal dry forest, tropical deciduous forest, tropical dry broadleaf forest, "selva baja caducifolia," or "bosque tropical caducifolio") is the predominant vegetation in the Pacific lowlands, where it forms an almost continuous corridor from southern Sonora to Chiapas, Mexico (Trejo and Dirzo 2000). Dry forest is a biologically important ecosystem that has received little attention in terms of research or conservation (Mooney et al. 1995). In spite of its high levels of endemism, dry forest is the least protected ecosystem in Mexico, although it is recognized as a global priority for protection (Murphy and Lugo 1986; Janzen 1988).

Dry forest presents a highly marked seasonality in precipitation and plant phenology (Mooney et al. 1995). In western Mexico, the dry season may last up to eight months (November to June). During this period, vegetation loses its leaves, creeks dry out, microclimatic conditions change (Bullock and Solis-Magallanes 1990), and food availability decreases (Janzen and Schoener 1968; Lister and Garcia 1992). Animals living in this forest ecosystem have to develop strategies to cope with the extreme seasonality (Ceballos 1995). In response to seasonal changes in resource abundance in the dry forest, many birds move altitudinally and horizontally to track food resources (Stiles 1983:508; Ornelas and Arizmendi 1995) and adopt a generalist feeding strategy (Poulin et al. 1993). During the dry season of western Mexico, birds move to forest along river edges and seasonally dry creeks where vegetation retains leaves throughout the year (Arizmendi et al. 1990; Berlanga 1991; Ornelas et al. 1993; Renton 2001).

We used radio telemetry to document the pattern of movements of the Ivory-billed Woodcreeper during the dry and rainy seasons, and to evaluate differences in habitat use between seasons. We hypothesized that the extreme seasonality of dry forest would generate changes in the Ivory-billed Woodcreeper's temporal distribution and habitat use patterns, similar to changes shown by other birds there. We predicted that home-range size would vary seasonally, with larger home ranges during the dry than the rainy season. We also predicted that scarcity of food resources during the dry season would cause the Ivory-billed Woodcreeper to

include arroyo habitat in their home range in a larger proportion than expected by chance. Finally, we expected reproduction to occur during the rainy season, when insect populations increase.

METHODS

We conducted the study in the Estacion de Biologia Chamela (3300 ha), which is part of the Chamela-Cuixmala Biosphere Reserve. The Reserve encompasses 13,142 ha, and represents one of the more protected areas of tropical dry forest in Mexico (Ceballos and Garcia 1995). It is located on the coast of Jalisco, Mexico, between 19°22' and 19°35'N and 104°56' and 105°03'W (Fig. 1). The Reserve has pronounced dry and rainy seasons; annual rainfall averaged 798 mm (1977–1999) and was concentrated from late June to October. The mean annual temperature was 24°C with an average daily minimum temperature of 16°C (1978–1986; Bullock 1986). The Reserve has a hilly topography with lowland and rolling hills, ranging from sea level to 584 m elevation. Creeks do not contain surface water during the dry season.

Within the Reserve, we defined two types of habitats: dry deciduous forest and semideciduous forest. Dry deciduous forest is the dominant vegetation, 5–12 m tall, with trees branching at a low height and a well-developed understory of shrubs. Common species in dry forest are *Cordia alliodora*, *Croton pseudoniveus*, *Lonchocarpus lanceolatus*, *Trichilia trifolia*, *Thouinia parvidentata*, *Caesalpinia eriostachys*, and *Rhandia thurberi* (Lott et al. 1987). Semideciduous forest extends along arroyo floodplains forming strips 30–40 m wide between the dry hillsides. Hereafter, we refer to this habitat as "arroyo forest." This forest averages 20 m tall, but some trees can be 30 m tall. Density of trees is lower and trees with diameter at breast height (dbh) of 30 cm or more are common. Some species common to arroyo forest are *Astronium graveolens*, *Brosimum alicastrum*, *Couepia polyandra*, *Cynometra oaxacana*, *Tabebuia donnell-smithii*, and *Thouinidium decandrum* (Lott et al. 1987).

Mist-netting and point counts. From March 1999 to August 2000, we conducted monthly point counts and mist netting at four sites along two existing trails (2 m wide and 3

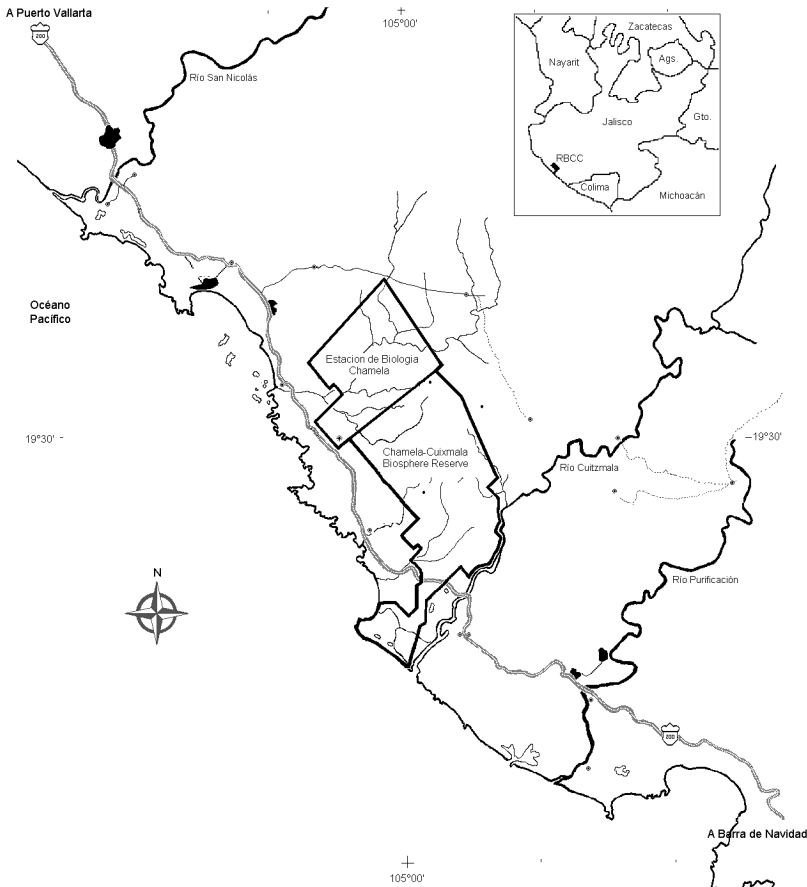


Fig. 1. Location of the Chamela-Cuixmala Biosphere Reserve, Jalisco, Mexico.

km long) dominated by dry deciduous forest and in semideciduous forest bordering two creeks. The four sites were separated from each other by approximately 1 km, and were characteristic of mature forest of the Chamela-Cuixmala Biosphere Reserve and of the region in general. We conducted additional mist-netting and point counts from February to July 2001.

At each site, every month we placed 12 mist nets (12×2.5 m, and 36 mm mesh size) in a line, each separated by 100 m. The overall distance along which mist nets were placed within a site was 1.1 km. Nets were opened at sunrise and checked hourly for 5 h, for three consecutive days. Each bird caught was banded with numbered aluminum bands and processed for body weight (0.1 g with a 50-g Pesola spring scale), bill and tarsus lengths (0.05 mm using

dial calipers) and unflattened wing cord length (0.5 mm using a flat-ended 15-cm ruler).

We established 12 point counts along the same line as the nets but extending twice as far (2.2 km). Point count stations were 200 m distant from each other. Point counts at each site were done after the monthly round of mist-netting in the four sites was complete. Starting at sunrise and for 3 hours thereafter, we recorded each bird seen or heard during a 12-min period within a 25-m circle (Hutto et al. 1986).

Radio tracking. From February to August 2000, we radio-marked eight individuals. Radio-transmitters (Wildlife Materials Inc., 1.8 g, average life of >80 d, and range of detection 800–1000 m) were attached using a leg back-pack-harness (Rappole and Tipton 1991).

Transmitters comprised <5% of the adult's body weight when attached, and had no observable effect on behavior of radio-tagged birds as compared to those without transmitters.

We located woodcreepers once every two days using hand-held 3-element Yagi antennas and portable receivers (TRX-1000S, Wildlife Materials Inc.). We pinpointed locations by approaching each bird. Birds sometimes responded to the observer's presence by moving before observed. Nevertheless, we made every effort to record the bird's initial position, occasionally based on the strength of the radio signal when the bird was close but obscured by vegetation. We marked the site where the bird was first observed, and took the geographical location using a Garmin GPS receiver or we referenced it (by annotating compass direction and distance) to a previously marked position if one was within 40 m. A minimum of 20 fixes were obtained for each location, which were averaged, and entered as a coverage into a GIS-database that included topography, roads, trails, and water drainages. Once a bird was located, we recorded habitat use (dry or arroyo forest) as well as information on foraging substrate (main trunk and secondary branches, dead trees and branches, bromeliads, and vine tangles), and whether it was alone or with a conspecific. Birds that initially moved in response to our approach resumed foraging almost immediately, making it possible to collect data on foraging behavior.

Analysis of movements. For each bird, we calculated home range size defined as the minimum area in which an animal has a specified probability of being located (Worton 1995). We calculated 50 and 95% Kernel home range estimators, hereafter referred to as a bird's core area and home range, respectively. Smoothing parameters were determined by least squares cross-validation and grid size was selected automatically using routines of Animal Movements Extension Program for Arc View (Hooge and Eichenlaub 1997). We also calculated minimum convex polygon (MCP) estimates of home range size because this technique is well-known, would allow our results to be more easily compared to those of other studies, and would allow figures (illustrating the boundaries of the entire occupied area) to be easily interpreted by the reader. Kernel estimators are non-parametric techniques that have proved

useful for analyzing home range data with respect to space use patterns and are thought to provide smaller, more precise estimates than MCP because MCP estimates often include rarely or unused areas. In addition, the MCP method tends to require a greater number of locations than the Kernel method for accurate home range estimation (Kenward 2001). We considered consecutive locations for a given bird as independent because they were separated by more than 24 h, a sufficient time for the animal to move between any two points in the area (White and Garrott 1990). We also calculated the average distance between consecutive locations and used it as an index of mobility for an individual.

Habitat selection. We were interested in both population and individual patterns of habitat use. Therefore, for the entire marked population we determined selection of forest type by plotting radio-locations from all birds on the GIS forest type coverage (use) and recording the habitat for each location (arroyo forest vs. dry forest). These were then compared against the area covered by the two habitats (availability). For this purpose, we defined boundaries of the study area as the 95% Kernel home range generated using radio-locations from all birds. Arroyo forest was delimited by a 20 m buffer zone generated along existing creeks. We used a χ^2 test of goodness of fit for the null hypothesis that usage occurs in proportion to availability, considering both habitats simultaneously (Neu et al. 1974). To ascertain individual patterns of habitat use, we compared the observed number of radio-locations occurring in each habitat type to what would be expected based upon the proportion of each habitat that occurred within each home range (Neu et al. 1974).

To lower the probability of making a Type II error, in all statistical tests a probability of 0.1 or less was accepted as significant, but we report actual *P* values for descriptive purposes. All values are reported as means \pm SD.

RESULTS

Ivory-billed Woodcreepers were caught during each one of the 18 months of sampling. However, monthly distribution of captures ($N = 150$) was not uniform (*G*-test for goodness-of-fit to a uniform distribution: $G = 14.1$, *P*

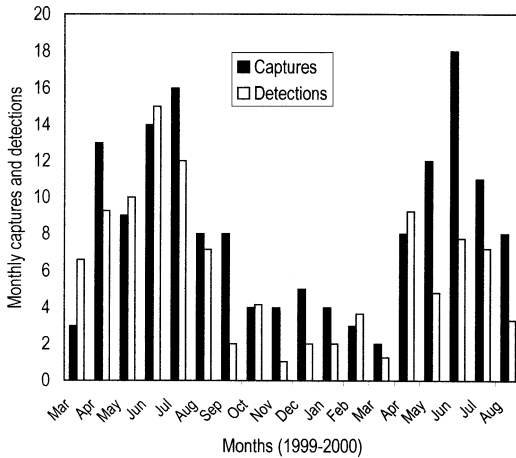


Fig. 2. Monthly detections and captures of the Ivory-billed Woodcreeper in the Chamela-Cuixmala Biosphere Reserve, Jalisco, Mexico.

= 0.07), with the lowest capture rate occurring from October to March. A similar pattern was suggested by point-count data ($G = 29.5$, $P < 0.001$, Fig. 2).

Although birds were monitored using telemetry during only 2–6 mo, our data from mist-netting suggest that at least some birds remain in the same area throughout the year. Nineteen birds were recaptured 1–6 times from March 1999 to July 2001. For these birds, average maximum distance between captures was 470 ± 420 m (range 100–1600 m). All recaptures, except one, were within rather than between mist-net arrays. Three of the radio-tagged birds were caught in the same area a year before they were radio-tagged. For instance, one of these birds, radio-tracked from February to June 2000, was previously caught in October and December of 1999 and again in August 2000 (see Fig. 3).

Home range. We radio-tracked eight individuals, six during the dry season and three during the rainy season. One of these birds was a female monitored during both the dry and rainy seasons. Home range varied from 5.5–36.3 ha (14.9 ± 9.6 ha) and core area varied from 0.8–5.8 ha (2.0 ± 1.6 ha; Table 1). There were no significant differences in average home-range size (Wilcoxon test, $W = 30$, $P > 0.9$) between the dry (15.2 ± 10.9 ha) and the rainy seasons (14.3 ± 8.4 ha). Mobility also did not vary between the dry (162 ± 52 m) and rainy (123 ± 82 m) seasons ($W = 33$, $P = 0.52$).

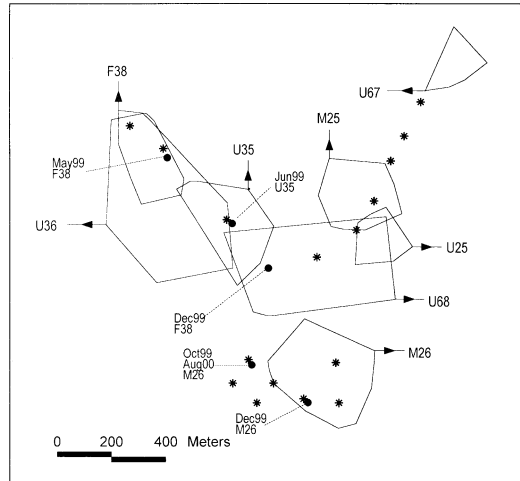


Fig. 3. Home range (95% minimum convex polygon) of Ivory-billed Woodcreepers radio-tracked from February to August 2000 in the Chamela-Cuixmala Biosphere Reserve, Jalisco, Mexico. Polygon ID's represent the sex (Male, Female and Unknown); black dots represent previous captures of radio-tagged birds; each asterisk represents a capture of a non-radio-tagged individual in the same period.

Core area represented 12–24% ($17 \pm 5\%$) of the home range during the dry season, and 11–18% ($15 \pm 5\%$) during the rainy season.

There was some overlapping among home ranges (Fig. 3); however, in all cases date of occurrence for these birds was separated by >2 d. During radio-tracking (i.e., February–August), we captured 15 additional birds in the same area covered by radio-tagged birds. These birds are indicated by an asterisk (Fig. 3).

Habitat and resource selection. For the area defined by the 95% Kernel home range using radio-locations from all birds, 75% was dry deciduous forest and 25% was arroyo forest. Within this area, 73% of radio-locations were in dry deciduous forest and 27% were in arroyo forest. According to these data, the Ivory-billed Woodcreeper used dry deciduous and arroyo forest in proportion to their availability ($\chi^2_1 = 0.64$, $P = 0.42$). In the analysis of habitat selection within each bird's home range, three birds from the dry season showed a greater use of arroyo forest than expected, one bird from the rainy season showed greater use of dry forest than expected, and five birds showed no preference (Table 2). We also analyzed the relation between the amount of arroyo forest and

Table 1. Home-range size of Ivory-billed Woodcreepers radio-tracked from February to August 2000, in the Chamela-Cuixmala Biosphere Reserve, Jalisco, Mexico.

I.D. ^a	Months radio-tracked	No. positions	95% Kernel home range (ha)	50% Kernel home range (ha)	95% MCP (ha) ^b
Dry season					
F35 ^c	March–May	37	9.7	1.3	13.8
M25	February–May	45	10.5	1.3	7.7
M26	February–June	34	14.1	0.9	8.3
U25	February–May	44	5.5	1.0	3.7
U35	March–May	33	15.2	2.4	9.1
U36	March–May	33	36.3	5.8	24.3
Rainy season					
F68	June–August	24	7.1	0.8	5.4
U67	June–July	13	12.2	2.13	6.7
U68	June–August	29	23.6	2.7	21.5

^a I.D. represents sex (M, male; F, female; U, unknown).

^b MCP: minimum convex polygon.

^c F35 and F68 are the same individual, followed in both the dry and rainy seasons. Her overall home range is represented in Fig. 2 as F38.

the size of the home range. We found a non-significant negative correlation between both variables ($r = -0.26$, $N = 9$, $P = 0.95$).

During 18 months of mist netting, we caught 45 individuals in the dry forest and 46 in the arroyo forest (considering only first captures). Similarly, there was no difference in average monthly captures (dry deciduous forest, 3.9 ± 2.3 ; arroyo forest, 4.4 ± 4.1 ; $W = 340$,

$P > 0.5$) and proportion of birds recaptured (dry deciduous forest, 0.37; arroyo forest, 0.42; $Z = 0.61$, $P > 0.5$). Testing of the null hypothesis of independence between season and habitat revealed no significant differences for the number of captures ($G = 2.55$, $P = 0.28$) and individuals observed/heard ($G = 0.38$, $P > 0.5$). Regarding sex and age classes, we caught eight females in dry deciduous forest

Table 2. Test of the null hypothesis that Ivory-billed Woodcreepers used habitat (arroyo forest vs. dry forest) in proportion to its occurrence within the 95% Kernel home range, in the Chamela-Cuixmala Biosphere Reserve, Jalisco, Mexico.

I.D. ^a	Percentage of arroyo forest within 95% Kernel HR (positions in arroyo forest/total positions)	χ^2	Preference
Dry season			
F35 ^b	17 (8/37)	0.56	NS ($P = 0.45$)
M25	22 (7/45)	1.09	NS ($P = 0.30$)
M26	19 (11/34)	3.93	arroyo forest ($P = 0.05$)
U25	48 (28/44)	4.31	arroyo forest ($P = 0.04$)
U35	23 (14/33)	8.02	arroyo forest ($P = 0.005$)
U36	22 (8/33)	0.09	NS ($P > 0.5$)
Rainy season			
F68	21 (7/24)	0.96	NS ($P = 0.33$)
U67	31 (2/13)	1.48	NS ($P = 0.22$)
U68	25 (2/29)	5.07	dry forest ($P = 0.02$)

^a I.D. represents sex (M, male; F, female; U, unknown).

^b F35 and F68 are the same individual (see Table 1).

and 17 in arroyo forest, as well as 12 immature birds in the dry deciduous forest and four in arroyo forest.

Our measure of body condition was mass divided by wing chord length. We did not find differences in body condition for individuals captured in dry deciduous forest (0.43 ± 0.03) versus arroyo forest (0.44 ± 0.04 ; $W = 1603$, $P = 0.21$). Seasonally, body condition was slightly lower during the dry season (median = 0.42) than the rainy season (median = 0.43; Kruskal Wallis test, $H = 5.41$, $P = 0.07$).

Ivory-billed Woodcreepers were observed ($N = 117$) using 65 tree species as foraging substrate; the most frequently used species (20% of all observations) were *Caesalpinia eriostachys* (17 observations) and *Spondias purpurea* (6). The rest of the species were used three or fewer times. The dbh of used trees (all species combined) varied from 5 to 80 cm, but most observations were on trees 10–40 cm dbh (66%). Woodcreepers foraged mainly on the trunk (70% of the observations), but were also observed foraging on snags and dead branches (10%), bromeliads (12%), and vine tangles (8%).

Observation of the Ivory-billed Woodcreeper foraging at army ant swarms was rare. Of seven birds radio-tracked, two were observed foraging at army ant swarms in five of 48 observations and two of 46 observations, respectively. The birds stayed close to the ground, perched on small branches and fallen logs from where they jumped to catch insects flushed by the ants. Among the birds observed at army ant swarms were the Dusky-capped Flycatcher (*Myiarchus tuberculifer*), Nutting's Flycatcher (*M. nuttingi*), Brown-crested Flycatcher (*M. tyrannulus*), Bright-rumped Attila (*Attila spadiceus*), Streak-backed Oriole (*Icterus pustulatus*), Red-crowned Ant-Tanager (*Habia rubica*), and Groove-billed Ani (*Crotophaga sulcirostris*). On seven occasions during point counts, we observed woodcreepers joining mixed species flocks. Regular resident birds participating in these flocks were Yellow-winged Caciques (*Cacicus melanicterus*), San Blas Jays (*Cyanocorax sanblasianus*), Yellow Grosbeaks (*Pheucticus chrysopleus*), Golden-cheeked Woodpeckers (*Melanerpes chrysogenys*), *Myiarchus* sp., Rose-throated Becards (*Pachyramphus aglaiae*), and Tropical Parulas (*Parula pitiayumi*). During the dry season, these flocks were joined by migratory species such as the

Nashville Warbler (*Vermivora ruficapilla*), Blue-grey Gnatcatcher (*Poliophtila caerulea*), and Black-and-White Warbler (*Mniotilta varia*). We observed only one individual of the Ivory-billed Woodcreeper attending these flocks, although we do not discard the possibility that other individuals were present.

Reproduction. During both years, captures of females with brood patch occurred in June (13 females), July (17) and August (7). We caught only two birds presumed to be adult males (sex confirmed by association with known females). Immature birds ($N = 17$) were caught from August to November. We found four nests in June and early July. Nests were natural cavities in the main trunk of trees (22–43 cm dbh) of *Psidium sartorianum* (two nests), *Caesalpinia eriostachys* (one nest), and *C. coriaria* (one nest). Nest entrance was 0.5–2.0 m from the ground, and cavity depth was 40–70 cm. We did not have information on the availability of natural cavities for the Ivory-billed Woodcreeper, but in the Chamela-Cuixmala Reserve the species of trees used for nesting are common in both the dry deciduous and arroyo forests (Lott et al. 1987). However, it is worth mentioning that a female with three eggs was expelled from one nest by Africanized honey bees (*Apis mellifera*).

Nest preparation, incubation, and care of nestlings were carried out by the female only. We never observed a change-over by the pair, or any other behavior that suggested that more than one bird was participating. We could clearly see into only two nests, both with three white eggs; one of these nests fledged three young. Measurements of these three young 1–2 days before they left the nest were tarsus 25, 23, 23 mm, culmen 15, 15, 15 mm, wing chord 66, 69, 69 mm, and mass 45, 46, 48 g. For comparison, average measurements of 87 adults banded in the study area were tarsus 23.1 ± 0.8 mm, culmen 30.3 ± 1.9 mm, wing chord 102.9 ± 6.2 mm, and mass 44.5 ± 4.2 g. The plumage of the nestlings resembled that of adults but was darker. Another nest appeared to contain at least two young, based on the calls we heard from the nest (snake-like hissing). From the observation of the one accessible nest, we calculated that incubation lasted about 15 d and nestlings remained in the nest 18–21 d.

DISCUSSION

It has been well documented that strong seasonality of dry tropical forest has important repercussions on the life-history strategies of vertebrates living in this environment (Beck and Lowe 1991; Valenzuela and Ceballos 2000). For birds, Stiles (1983:508) wrote that in the dry forest of Costa Rica, "a number of bird species move to riparian situations during the dry season, then reoccupy the dry forest with the rain." In western Mexico, a response to seasonality consisting mainly in a greater use of arroyo forest during the driest months of the year has been documented for parrots (Renton 2001), and hummingbirds (Arizmendi and Ornelas 1990), and suggested for frugivorous birds (Berlanga 1991) and for the community of terrestrial birds in general (Ornelas et al. 1993). In this study, a main objective was to determine the importance of the arroyo forest as a refuge for the Ivory-billed Woodcreeper during the driest months of the year. We predicted that scarcity of food resources during the dry period would cause the Ivory-billed Woodcreeper to wander over a larger area and to select for arroyo forest.

We did not find statistical differences in home range size or mobility between the dry and rainy seasons. Most birds' home range was 15 ha or less; only two birds had larger home ranges. These birds were not observed in company of a partner, had not been captured before, and were not recaptured after they were radio-tagged, which suggests that they could have been floaters. The only other species studied that is comparable in size to the Ivory-billed Woodcreeper is the Plain-brown Woodcreeper (*Dendrocincla fuliginosa*) on Barro Colorado Island (Willis 1972). In that system, females had an average home range of 36 ha, and males maintained larger but non-exclusive home ranges overlapping with female territories.

Our data did not show a clear pattern of greater use of arroyo forest versus dry deciduous forest by the Ivory-billed Woodcreeper, and we did not find a correlation between the size of the home range and the amount of arroyo forest included in that home range. Analysis of habitat selection on pooled data suggested that both habitats were used in proportion to their availability. However, when individual home ranges were analyzed, three of six birds moni-

tored during the dry season showed a greater use of arroyo forest. Similarly, we did not find differences between dry deciduous forest and arroyo forest in total captures, monthly captures, or recapture rates. Thus, number of individuals captured in either habitat was independent of the season. Body condition of individuals captured was also similar in both habitats.

There could be several explanations for the lack of selection for arroyo forest. Although the Ivory-billed Woodcreeper is one of several species in the Reserve that feeds on insects, its foraging habits are linked to particular types of insects. Despite the marked seasonality of the dry forest, it could be that the abundance and distribution of the resources used by Ivory-billed Woodcreepers did not exhibit strong seasonal changes. For instance, Karr (1976) mentioned that insects are more stable and seasonally predictable than fruits, and that the bird species that forage on the bark of trees exploit a substrate that remains constant in size through the year. Accordingly, Lister and Garcia (1992) found that seasonal variation in arthropod biomass in the Chamela-Cuixmala Reserve was the largest recorded for a tropical habitat, but these fluctuations were less pronounced for arthropods living on the bark of trees. Similarly, in the dry forest of Costa Rica, Janzen and Schoener (1968) reported that during the dry season, zones adjacent to river bottom forest had greater biomass, abundance, and diversity of insects, compared to dry hillside forest. However, the proportion of larger insects was greater on dry hillside forest.

Another factor that might explain the lack of selection for arroyo forest is the fact that the Ivory-billed Woodcreeper is apparently the only Woodcreeper found in the Reserve, and therefore competition for resources could be low. Arizmendi et al. (1990) reported the White-striped Woodcreeper (*Lepidocolaptes leucogaster*) in the Reserve, but during two years of work in the area we have not seen this species. Reduced competition could also explain the relatively broad use of resources by this species in the Reserve. We found Ivory-billed Woodcreepers foraging on 65 species of trees ranging from 5 to 80 cm dbh, over main trunk and branches, dead trees and branches, bromeliads, vine tangles, and at army ant swarms. In contrast to our finding that most foraging occurred

on trunks, Stiles and Skutch (1989) mentioned that this species forages mostly on limbs in the canopy and less frequently on trunks in Costa Rica. In a study of woodcreepers in southeast Brazil, three species differed in the percentage of time they foraged on trunks, 70.8%, 86%, and 92.4% (Brooke 1983). In other studies, where more than one species of woodcreeper co-exists, the diet, type of substrate, and space utilized differed among these species (Willis 1966, 1982; Brooke 1983; Chapman and Rosenberg 1991; Puebla 2001).

Many species of woodcreepers typically join mixed-species foraging flocks and forage at army ant swarms. Some species, especially of the genus *Dendrocolaptes*, are considered obligate army ant followers (Willis and Oniki 1978). Our observations suggest that in the Reserve, the Ivory-billed Woodcreeper forages opportunistically with army ants and joins mixed-species flocks whenever they pass through its territory. In a previous work at our study area, Hutto (1994) reported that the Ivory-billed Woodcreeper was recorded in nine of 57 mixed-species flocks. However, he did not mention whether any of these flocks were foraging at army ant swarms.

Females in breeding condition occurred in June–August, suggesting that reproductive activities started in May and probably earlier since males started singing in March. All nests and young were found during the rainy season, supporting our prediction that reproduction would coincide with the period of higher productivity of arthropods (Lister and Garcia 1992). We observed that only the female builds the nest, incubates, and feeds nestlings, a behavior that has been observed in another species in this genus, the Buff-throated Woodcreeper (*X. guttatus*; Skutch 1996), as well as for species in other genera in this family such as the Tawny-winged Woodcreeper (*Dendrocincla anabatina*; Skutch 1969, 1977; Stiles and Skutch 1989), the Plain-brown Woodcreeper (Willis 1972), and probably the Olivaceous Woodcreeper (*Sittastomus griseicapillus*; Skutch 1996). However, biparental care has been documented in two other genera, *Lepidocolaptes* and *Glyphorhynchus* (Skutch 1996).

Our data suggest that the Ivory-billed Woodcreeper is a permanent resident in the Reserve, with lower capture and detection rates occurring during the early dry season (November–

February). We believe that lower captures and detections during the post-rainy months do not reflect changes in behavior and strata shifts, but rather movements of some birds out of the study area with territory holders remaining.

Color-banded females of the Plain-brown Woodcreeper occupied the same territories for over 10 yr (Willis 1972). Mist-netting data suggested site fidelity for two other species of woodcreepers in Belize (Kricher and Davis 1998). In a study of four insectivorous passerines, including the Streak-headed Woodcreeper (*Lepidocolaptes souleyetii*), Lefebvre et al. (1992) implied that long-term territoriality functions primarily to ensure a breeding site for the following year, contrasting with temperate regions where the primary purpose of territoriality over the non-breeding season seems to be to ensure food resources. We do not have information on what factor is more important in the seasonal dry forest of Chamela-Cuixmala.

The Ivory-billed Woodcreeper is a species associated with the dry forest in the Pacific lowlands of Mexico, and is a common permanent resident in the Chamela-Cuixmala Reserve. However, the strong site fidelity exhibited by individuals of this species could make it vulnerable to the heavy changes in land use occurring through the Pacific lowlands, where the Chamela-Cuixmala Biosphere Reserve is the only area of this type of forest protected. At a national level, only 27% of the original cover of tropical dry forest (around 14% of the country) remained as intact forest by 1990, and less than 10% of the area covered with dry forest is under some type of protection (Trejo and Dirzo 2000).

ACKNOWLEDGMENTS

Funding for this project was provided by the Denver Zoological Foundation, Idea Wild, and Instituto de Biología, UNAM. Logistic support was provided by Estación de Biología Chamela, Instituto de Biología, UNAM. We are indebted to D. Curiel, I. Fariza, Manuel Lobato, K. Renton, and Talía Valdivia for assistance during field work. We thank C. Graham, K. Renton, and two anonymous reviewers for comments on the manuscript.

LITERATURE CITED

- AMERICAN ORNITHOLOGISTS' UNION. 1998. Check-list of North American birds. 7th ed. American Ornithologists' Union, Washington, D.C.
- ARIZMENDI, M. C., H. BERLANGA, L. M. MÁRQUEZ-VAL-

- DELAMAR, L. NAVARIJO, AND J. F. ORNELAS. 1990. Avifauna de la región de Chamela, Jalisco. Cuadernos N°4, Instituto de Biología, Universidad Nacional Autónoma de México, México, D.F.
- , AND J. F. ORNELAS. 1990. Hummingbirds and their floral resources in a tropical dry forest in Mexico. *Biotropica* 22: 172–180.
- BECK, D. D., AND C. H. LOWE. 1991. Ecology of the beaded lizard, *Heloderma horridum*, in a tropical dry forest in Jalisco, Mexico. *Journal of Herpetology* 25: 395–406.
- BERLANGA, H. A. 1991. Las aves frugívoras de Chamela: su recurso vegetal y su papel en la dispersión de semillas. Tesis de Licenciatura. Universidad Nacional Autónoma de México, México, D.F.
- BINFORD, L. C. 1989. A distributional survey of the birds of the Mexican state of Oaxaca. *Ornithological Monographs No. 43*. American Ornithologists' Union, Washington D.C.
- BROOKE, M. DE L. 1983. Ecological segregation of woodcreepers (Dendrocolaptidae) in the state of Rio de Janeiro, Brazil. *Ibis* 125: 562–567.
- BULLOCK, S. H. 1986. Climate of Chamela, Jalisco, and trends in the south coastal region of Mexico. *Archives for Meteorology, Geophysics, and Bioclimatology* 36: 297–316.
- , AND A. SOLIS-MAGALLANES. 1990. Phenology of canopy trees of a tropical deciduous forest in Mexico. *Biotropica* 22: 22–35.
- CEBALLOS, G. A. 1995. Vertebrate diversity, ecology and conservation in Neotropical dry forest. In: *Seasonally dry tropical forest* (S. H. Bullock, H. A. Mooney, and E. Medina, eds.), pp. 195–220. Cambridge University Press, Cambridge, UK.
- , AND A. GARCIA. 1995. Conserving Neotropical biodiversity: the role of dry forest in western Mexico. *Conservation Biology* 9: 1349–1356.
- CHAPMAN, A., AND K. V. ROSENBERG. 1991. Diets of four sympatric Amazonian woodcreepers (Dendrocolaptidae). *Condor* 93: 904–915.
- HOOGE, P. N., AND B. EICHENLAUB. 1997. Animal Movements extension for ARC-VIEW. V. 1.1. Alaska Biological Science Center, U.S. Geological Survey, Anchorage, AK.
- HOWELL, S. N. G., AND S. WEBB. 1995. A guide to the birds of Mexico and northern Central America. Oxford University Press, New York.
- HUTTO, R. L. 1994. The composition and social organization of mixed-species flocks in a tropical deciduous forest in western Mexico. *Condor* 96: 105–118.
- , S. M. PLETSCHE, AND P. HENDRICKS. 1986. A fixed-radius point count method for nonbreeding and breeding season use. *Auk* 103: 593–602.
- JANZEN, D. H. 1988. Tropical dry forest: the most endangered major tropical ecosystem. In: *Biodiversity* (E. O. Wilson, ed.), pp. 130–137. National Academy Press, Washington, D.C.
- , AND T. W. SCHOENER. 1968. Differences in insect abundance and diversity between wetter and drier sites during a tropical dry season. *Ecology* 49: 96–110.
- KARR, J. R. 1976. Seasonality, resource availability and community diversity in tropical bird communities. *American Naturalist* 110: 973–994.
- KENWARD, R. E. 2001. Manual for wildlife radio tagging. Academic Press, San Diego, CA.
- KRICHER, J. C., AND W. E. DAVIS. 1998. Species richness and site fidelity among resident Neotropical birds. *Southwestern Naturalist* 43: 228–233.
- LEFEBVRE, G., B. POULIN, AND R. MCNEIL. 1992. Settlement period and function of long-term territory in tropical mangrove passerines. *Condor* 94: 83–92.
- LISTER, B. C., AND A. GARCIA. 1992. Seasonality, predation, and the behaviour of a tropical mainland anole. *Journal of Animal Ecology* 61: 717–733.
- LOTT, E. J., S. H. BULLOCK, AND J. A. SOLIS-MAGALLANES. 1987. Floristic diversity and structure of upland and arroyo forest in coastal Jalisco. *Biotropica* 19: 228–235.
- MOONEY, H. A., S. H. BULLOCK, AND E. MEDINA. 1995. Introduction. In: *Seasonally dry tropical forests* (S. H. Bullock, H. A. Mooney, and E. Medina, eds.), pp. 1–8. Cambridge University Press, Cambridge, UK.
- MURPHY, P. G., AND A. E. LUGO. 1986. Ecology of tropical dry forest. *Annual Review of Ecology and Systematics* 17: 67–88.
- NEU, C. W., C. R. BYERS, AND J. M. PEEK. 1974. A technique for analysis of utilization-availability data. *Journal of Wildlife Management* 38: 541–545.
- ORNELAS, J. F., AND M. C. ARIZMENDI. 1995. Altitudinal migration: implications for the conservation of the neotropical migrant avifauna of western Mexico. In: *Conservation of Neotropical migratory birds in Mexico* (M. H. Wilson, and S. A. Sader, eds.), pp. 312–325. Maine Agricultural and Forest Experiment Station, Miscellaneous Publication 727, Orono, ME.
- , ———, L. MARQUEZ-VALDERAMAR, L. NAVARIJO, AND H. BERLANGA. 1993. Variability profiles for line transect bird censuses in a tropical dry forest in Mexico. *Condor* 95: 422–441.
- POULIN, B., G. LEFEBVRE, AND R. MCNEIL. 1993. Variations in bird abundance in tropical arid and semi-arid habitats. *Ibis* 135: 432–441.
- PUEBLA, F. O. 2001. Aspectos ecológicos de la familia Dendrocolaptidae (Aves) en la localidad de Yaxchilan, Chiapas. Tesis de Maestría. Universidad Nacional Autónoma de México, México, D.F.
- RAPPOLE, J. H., AND A. R. TIPTON. 1991. New harness design for attachment of radio transmitters to small passerines. *Journal of Field Ornithology* 62: 335–337.
- RENTON, K. 2001. Parrot diet and resource availability: resource tracking by a parrot seed predator. *Condor* 103: 62–69.
- SCHALDACH, W. J. 1963. The avifauna of Colima and adjacent Jalisco, Mexico. *Proceedings of the Western Foundation of Vertebrate Zoology* 1: 1–100.
- SKUTCH, A. F. 1969. Life histories of Central American Birds. III. Pacific Coast Avifauna 35, Cooper Ornithological Society, Berkeley, CA.
- . 1977. A birdwatcher's adventures in tropical America. University Texas Press, Austin, TX.

- . 1996. Nesting of the Buff-throated Woodcreeper (*Xiphorhynchus guttatus*). *Auk* 113: 236–239.
- STILES, F. G. 1983. Birds. In: Costa Rican natural history (D. H. Janzen, ed.), pp. 502–530. University of Chicago Press, Chicago, IL.
- , AND A. F. SKUTCH. 1989. A guide to the birds of Costa Rica. Cornell University Press, Ithaca, NY.
- TREJO, I., AND R. DIRZO. 2000. Deforestation of seasonally dry forest: a national and local analysis in Mexico. *Biological Conservation* 94: 133–142.
- VALENZUELA, D., AND G. CEBALLOS. 2000. Habitat selection, home range, and activity of the white-nosed coati (*Nasua narica*) in a Mexican tropical dry forest. *Journal of Mammalogy* 81: 810–819.
- WHITE, G. C., AND R. A. GARROTT. 1990. Analysis of wildlife radio-tracking data. Academic Press, New York.
- WILLIS, E. O. 1966. Interspecific competition and the foraging behavior of Plain-brown Woodcreepers. *Ecology* 47: 667–672.
- . 1972. The behavior of Plain-brown Woodcreepers, *Dendrocincla fuliginosa*. *Wilson Bulletin* 84: 377–420.
- . 1982. The behavior of Black-Banded Woodcreepers (*Dendrocolaptes picumnus*). *Condor* 84: 272–285.
- , AND Y. ONIKI. 1978. Birds and army ants. *Annual Review of Ecology and Systematics* 9: 243–263.
- WORTON, B. J. 1995. Using Monte Carlo simulations to evaluate Kernel-based home range estimators. *Journal of Wildlife Management* 59: 794–800.