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Biannual Cycles of the Cinnamon-bellied Flowerpiercer[1]

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ABSTRACT

Biannual cycles of reproduction and molt are rare in birds, with most species exhibiting a single annual cycle. We studied the breeding and molting phenology of the Cinnamon-bellied Flowerpiercer (*Diglossa baritula*), a nectar feeding passerine, in western Mexico. Monthly captures from December 1994 to May 1998 revealed clear biannual breeding and molting cycles. The two breeding seasons took place from January to April (dry season) and from July to October (rainy season). Their July to October breeding season coincided with the single breeding season exhibited by resident hummingbirds at our study site. Even though flowerpiercers and hummingbirds use the same food resources, hummingbirds only molt and breed once a year. Male flowerpiercers breed and molt flight feathers twice a year, whereas females appear to breed only once. A higher proportion of females bred in the rainy season (90%) than in the dry season (30%), and they underwent a complete molt only during the rainy season. Proportions of males in breeding condition during the dry and the rainy season were similar (86 and 92%). Some males (40%) showed an incomplete molt in the dry season, while most males (80%) underwent a complete molt in the rainy season. Differences in proportions of breeding and molting individuals between the dry and the rainy season suggest that the dry season cycle is limited by food availability. We hypothesize that *D. baritula* individuals use soft fruits in addition to flowers to fuel their breeding during the dry season.

RESUMEN

Los ciclos bianuales de reproducción y muda son raros en las aves. La mayoría de las especies presentan un ciclo anual único. En este trabajo estudiamos la fenología reproductiva y de muda de *Diglossa baritula*, un paseriforme nectarívoro, en el occidente de México. Los muestreos mensuales con redes de niebla (Diciembre 1994–Mayo 1998) mostraron que esta especie presenta ciclos bianuales de reproducción y muda. Las dos temporadas reproductivas ocurrieron en Enero-Abril (secas) y Julio-Octubre (lluvias). La temporada reproductiva de lluvias se traslapó con la temporada de reproducción única de los colibríes residentes en nuestra área de estudio. Aunque los colibríes y *D. baritula* utilizan los mismos recursos alimenticios, los colibríes se reproducen y mudan sólo una vez por año. Los machos de *D. baritula* se reprodujeron y mudaron plumas de vuelo dos veces por año, mientras que las hembras parecen hacerlo sólo una vez. Se reprodujeron más hembras en la temporada de lluvias (90%) que en la de secas (30%). Los porcentajes de machos en condición reproductiva fueron similares para las dos temporadas (secas 86% y lluvias 92%). Algunos machos (40%) mostraron una muda incompleta en la temporada de secas, mientras que la mayoría presentó una muda completa en la temporada de lluvias (80%). Las diferencias en las proporciones de individuos reproductivos/mudando entre la temporada seca y la temporada de lluvias sugieren que durante la temporada de secas la disponibilidad de recursos alimenticios es limitante. Conjeturamos que *D. baritula* combina flores y frutos blandos para satisfacer los requisitos energéticos de su reproducción durante la época seca.

Key words: biannual cycles; breeding phenology; Diglossa baritula; *Mexico; molt; nectar-eating birds.*

BIANNUAL CYCLES OF REPRODUCTION AND MOLT ARE RARE IN BIRDS. Most species have one breeding peak per year at a time often presumed to be in synchrony with the season of maximal food availability (Skutch 1950, Martin 1987, Poulin *et al.* 1992). In the Neotropics, most land birds breed and molt during the end of the dry season and the beginning of the rainy season when insect abundance and/or fruit production peak (Skutch 1950, Diamond 1974, Loiselle & Blake 1991, Poulin *et al.* 1992). Nectar-feeding birds also tend to show single breeding and molting peaks, but these peaks occur

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during the dry season when flower abundance is at a maximum (Skutch 1950, Stiles 1980). Worldwide, only a few species show irregular or continuous cycles in which breeding and molting occur throughout the year (Bates 1908; Miller 1959, 1961, 1962; Snow & Snow 1964; Tallman & Tallman 1997).

At high latitudes, annual cycles are controlled by day length and temperature, which presumably predict resource abundance (Lack 1950, Perrins 1970). In the tropics, timing of reproduction can be influenced by humidity (Thomson 1950, Voous 1950), rainfall (Keast 1968, Diamond 1974, Bancroft *et al.* 2000), insect abundance (Fogden 1972, Poulin *et al.* 1992), plant phenology (Skutch 1950, Stiles 1980, Bancroft *et al.* 2000), or a combination of all these factors (Thomson 1950, Perrins 1970, Young 1994). Biannual breeding is restricted to tropical and subtropical areas and has been associated with three possible sets of circumstances: (1) Many bird species in East Africa (Moreau 1950) and a few species in the Andes (Miller 1962, Moynihan 1979) show bimodal reproduction associated with relatively constant minimal temperature and bimodal rainfall; (2) *Phainopepla nitens* migrates elevationally and breeds in two elevational zones of the same region, presumably tracking the abundance of mistletoe fruits (Merriman 1896, Rand & Rand 1943, Chu & Walsberg 1999); and (3) *Tiaris olivacea*, an omnivorous Neotropical species, reproduces twice in response to the asynchronous availability of grass seeds and fleshy fruits (Skutch 1950, Stiles *et al.* 1989).

Detailed descriptions of biannual breeding and molting cycles using data from recaptured individuals are available only for one Neotropical species (*Zonotrichia capensis*; Miller 1959, 1961, 1962). Here we provide the first description of biannual breeding in the Cinnamon-bellied Flowerpiercer at a high elevation site in western Mexico and compare the frequency and timing of breeding and molting of males and females. We also compare the phenology of Cinammon-bellied Flowerpiercers with those of a sympatric resident hummingbird (*Lampornis amethystinus*) and several passerine species and discuss the factors that might allow flowerpiercers to have biannual cycles.

METHODS

STUDY SITE.—We studied Cinnammon-bellied Flowerpiercers at Las Joyas Research Station (19°35′N, 104°16′W) in the Sierra de Manantlán Biosphere Reserve, Jalisco, Mexico. The station occupies 1245 ha of rugged mountains and ravines spanning elevations from 1560 to 2220 m (Jardel 1991). Mean annual rainfall is *ca* 1700 mm. The site experiences a pronounced rainy season from June to September, but sporadic rains and fog from October to February make the winter relatively wet. A dry season with almost no precipitation extends from March to May (Saldaña-Acosta & Jardel 1991). Four dominant vegetation types can be found in the study area: pine forest, pine–oak forest, cloud forest, and secondary scrub (Cuevas 1994). Of 221 species of birds reported for the area, 43 percent (96) breed at the station. Las Joyas also has one of the most diverse communities of nectarivorous birds in the Neotropics (22 spp.; Ornelas & Arizmendi 1995, Santana C. 2000).

The Cinnamon-bellied Flowerpiercer (*Diglossa baritula*) is a small nectarivorous tanager that specializes in robbing hummingbird-pollinated flowers (Skutch 1954, Burns 1997). They range from Honduras to west–central Mexico (Isler & Isler 1999). Males are territorial and pair with only one female. Both the male and the female share the defense of the nesting territory and the feeding of the young (Skutch 1954). In this sense, they are monogamous; it is unknown if they conduct extra-pair copulations. In the mountains of western Mexico, *D. baritula* feeds primarily on hummingbird-pollinated flowers with tubular corollas (*Salvia* spp., *Fuchsia* spp., and *Lobelia* spp.; Arizmendi *et al.* 1996, Arizmendi 2001) during the fall and winter. As the availability of these floral resources decreases in spring and summer, they shift their feeding to soft fruits such as blackberries (*Rubus* spp.), melastome berries (*Leandra subseriata*), and to a lesser extent, nectar of less common flowering species (*Byttneria catalpifolia*, *Circium jaliscoana*, *Ipomea* spp.; JES, pers. obs.; Arizmendi 1994, 2001). As is the case with other nectarivorous birds, *D. baritula* complements its nectar diet by eating insects regularly (JES, pers. obs.; Skutch 1954, Isler & Isler 1999).

DATA COLLECTION AND ANALYSIS.—As part of a long-term bird monitoring program, we recorded breeding status and molt of all birds caught in mist nets. Bird captures were conducted at seven mist-netting stations that were monitored from December 1994 to March 1998. With the exception of one month (March 1997) when sampling was cancelled, nets were opened once a month. Banding sites were distributed in three habitat types: mature cloud forest and pine forest (2 sites each), and secondary vegetation (3 sites). Each mist-netting site consisted of

10 to 15 standard mist nets (12 × 2.6 m with a 30 mm mesh) and was sampled for two consecutive days each month. We sampled for a total of 35,150 net hours. The number and location of nets at each site was kept constant throughout the study.

Each bird captured in a mist net was banded with a numbered aluminum band and its age, sex, breeding condition (presence of an enlarged cloacal protuberance or vascularized brood patch), fat accumulation, and molt status were determined (Pyle *et al.* 1987, Ralph *et al.* 1993). In passerines, age and sex are determined using plumage characteristics (Peterson & Chalif 1973, Howell & Web 1995) and patterns of skull ossification. Based on recaptures, we determined that the skull of *D. baritula* takes from four to six months to ossify. Age and sex of hummingbirds were determined using patterns of bill striation (Ortiz-Crespo 1972) and plumage (JES & IRT, pers. obs.). Only birds that showed primary or secondary feathers missing or in sheath in a symmetrical fashion were used for the analysis of molt.

Patterns of fat accumulation were scored a little differently than by Ralph *et al.* (1993), using only four categories (0–3). A zero indicated absence of visible fat. A score of one indicated an incomplete layer of fat in the furcula. A score of two was used when the furcula had a complete layer of fat. Finally, a score of three indicated fat extending above the furcula with fat deposits in other areas of the body.

Patterns of breeding phenology were obtained by determining the monthly percentage of adult males presenting enlarged cloacal protuberances and adult females showing vascularized brood patches. The presence of an enlarged cloacal protuberance in males is correlated with higher levels of testosterone and sperm production and indicates that the birds are ready to copulate (King 1974, Tuttle *et al.* 1996, Wingfield *et al.* 1992). Cloacal protuberances tend to be larger during the nest building and egg laying stages of the breeding season and can be used as an indirect indicator of male breeding activity (Nakamura 1998, Lombardo 2001). Vascularized brood patches occur in females that are incubating eggs, and at a population level can be used to estimate the number of nesting pairs (Steel & Hinde 1963, White & Hinde 1968).

Molting phenology was obtained by determining the monthly percentage of birds with symmetrical flight feather molt accompanied by heavy body molt. To be sure that birds were undergoing a complete molt, we recorded areas of body molt and the progression of molting for primaries, secondaries, and rectrices, both on recaptured individuals and at the population level. Seasonal patterns of flower, fruit, and insect abundance for Las Joyas were obtained from the literature (Parada 1987, Rivera-Cervantes 1988, Moya-Raygoza *et al.* 1990, Arizmendi 1994, Ornelas & Arizmendi 1995, López-Vieyra & Rivera-Cervantes 1998, Arizmendi 2001). Humidity, rainfall, and temperature were recorded daily by station personnel at a local meteorological station.

We compared the seasonal distribution of molting and breeding in males and females using a Kolmogorov–Smirnov test. We present data as means ± SD. We set α at 0.05 for all our statistical analyses.

RESULTS

NUMBER OF CAPTURES.—In 42 months, we captured Cinnamon-bellied flowerpiercers 760 times (558 individuals, with 116 birds recaptured 1 or more times). Monthly numbers of *D. baritula* captures varied during the study from a minimum of 3 in January and May 1995, to 47 in December 1996. The average monthly capture rate was 16 birds (±10). Only six months had fewer than 9 captures (December 1994 [4], January [3], March [4], May [3], and August [4] 1995, and March 1998 [3]).

We captured similar numbers of females (245) and males (243). We were unable to determine the sex of 70 juveniles. The number of recaptures per sex was also similar (100 females and 102 males). Monthly captures of adult birds showed a sex ratio of 1.1 females per male (±0.63, $N = 40$), with the exception of December 1994 when we captured only males and October 1997 when we captured only females.

BREEDING PHENOLOGY.—Cinnamon-bellied Flowerpiercers exhibited a clear biannual breeding phenology (Fig. 1). Two distinct breeding seasons occurred: January–April (dry) and July–October (rainy). These two breeding seasons occurred just before and after the main breeding season for passerines in the study area (April–August; Santana C. 2000). The two breeding seasons were usually separated by a two-month period. During those months, captured birds did not exhibit vascularized brood patches or enlarged cloacas, and singing males were uncommon. Our recapture data do not allow us to determine whether individual birds produce only one, or more than one, clutch each breeding season.

Individual adult males developed enlarged cloa-

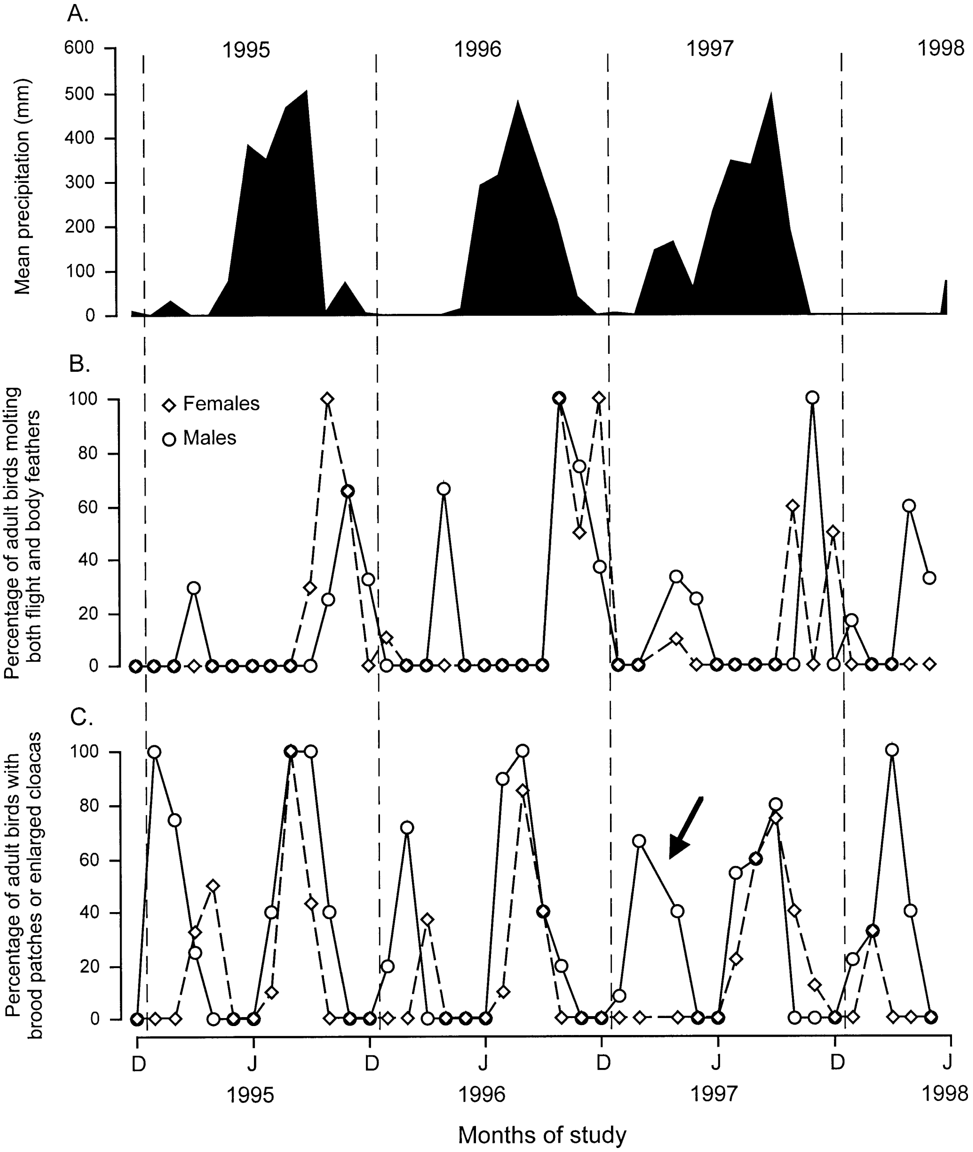

FIGURE 1. (C) Biannual breeding and (B) molting cycles of male and female individuals of *Diglossa baritula* in relation to (A) rainfall. Birds bred and molted during the dry season (January–April) and at the end of rainy season (July–October; panels C and B). The arrow in panel C points to the dry season of 1997 when no females with brood patches were captured. Monthly sample sizes averaged 16 birds (±10; see text for details on sample size). Dotted vertical lines separate calendar years (D = December, J = June).

cas twice a year, with no marked differences in the proportion of males captured in breeding condition during the dry (87% ± 18, $N = 165$) and the rainy season (92% ± 11, $N = 176$; Kolmogorov–Smirnov $\chi^2 = 2.03$, df = 2, $P > 0.72$). Of the 14 males recaptured in two consecutive breeding seasons, 64 percent (9) displayed enlarged cloacas during both seasons, and 2 birds recaptured in five consecutive breeding seasons showed enlarged cloacas in all five (spring 1996–spring 1998).

Individual females apparently developed vascularized brood patches only once a year. Only 1 recaptured female of a total 50 recaptured females had a brood patch during two consecutive breeding seasons. Of 13 females that were recaptured in three or more consecutive breeding seasons, 69 percent (9) had vascularized brood patches during two consecutive rainy seasons, but not in the intervening dry breeding season. The distributions of the proportions of captured females that exhibited vascularized brood patches differed between dry and rainy seasons (Kolmogorov–Smirnov $\chi^2 = 8.12$, df $= 2$, $P = 0.03$), with more females exhibiting vascularized brood patches in the rainy season (90% ± 12, $N = 173$) than in the dry season (30% ± 21, $N = 149$). Curiously, no females displaying vascularized brood patches were captured during the dry breeding season of 1997 (Fig. 1).

A few individuals (4 males and 3 females) captured as fledglings were recaptured the following breeding season showing enlarged cloacas or vascularized brood patches. Thus, *D. baritula* individuals appear to be able to reproduce only three to five months after fledging.

MOLTING PATTERNS.—Symmetrical flight feather molt also occurred in a biannual fashion, with molting peaks following breeding peaks by about one month (Fig. 1). Distributions of molting birds differed between seasons (Kolmogorov–Smirnov $\chi^2 = 12.45$, df $= 2$, $P < 0.01$), with fewer birds showing a symmetrical flight feather molt during the dry (19% ± 5, $N = 112$) than during the rainy season (77% ± 20, $N = 123$). This difference was due to male and female flowerpiercers showing different patterns of molting during the dry season.

While both sexes exhibited a complete molt after the rainy season breeding peak, only males exhibited symmetrical flight feather molt during the dry season. Males had an incomplete molt during the dry season in which they replaced some of their secondaries (secondaries 3, 4, and 5), the central rectrices, and most of their body feathers with the exception of their primary coverts. During the dry season, females exhibited heavy body molt without replacing flight feathers. We captured only one female with symmetrical flight feather molt during a dry season molting peak (secondaries 4 and 5, April 1997; Fig. 1).

The distribution of molting males differed between the dry and the rainy season (Kolmogorov–Smirnov $\chi^2 = 12.45$, df $= 2$, $P < 0.01$), with a smaller proportion of males molting flight feathers in the dry season (41% ± 17, $N = 64$) than in the rainy season (89% ± 19, $N = 83$, Fig. 1). Of 18 males that we recaptured in two consecutive molting peaks, 6 (33%) had a symmetrical flight feather molt in both seasons. These males molted secondaries 2, 3, and 4 two times in the same year, suggesting that males undergo an incomplete molt in the dry season and a complete molt in the rainy season (instead of an interrupted complete molt).

The pattern of flight feather replacement during the complete molt followed a sequence similar to the one exhibited by most passerines (Ginn & Melville 1983, Pyle 1997). Birds molted the primaries first, starting with primary 1 and replacing them sequentially toward primary 10. The secondaries were molted from secondary 1 inward, starting when the progression of molt for the primaries reached primaries 6 and 7. Tertials were usually molted synchronously with primary 9 and secondaries 3 and 4. The central tertial was molted first, followed by the inner and outer ones. The last flight feathers to be molted were secondaries 5 and 6. Body molt started at the crown and extended into the back and ventral areas. Contour feathers were replaced almost simultaneously all over the body, with the tail coverts usually being the last group of feathers to be molted.

The occurrence of the first complete molt seemed to depend on the season of hatching. Nine juvenile birds (3 males and 6 females) that hatched in the dry season had their first complete molt in the next rainy season molting peak (4–6 months old); however, 12 juveniles (5 males and 7 females) born in the rainy season molted a full year later during the next rainy season molting peak. We found many cases of both males ($N = 12$) and females ($N = 16$) in immature plumage showing either enlarged cloacas or vascularized brood patches. Females did not molt while displaying vascularized brood patches, and only 3 males (2%, $N = 176$) overlapped molting and breeding activity during the rainy season breeding/molting peak.

BODY MASS AND FAT ACCUMULATION PATTERNS.—Fat accumulation did not show clear biannual patterns (Fig. 2). The amount of fat reserves varied greatly among individual birds. Birds, however, tended to show higher fat scores after molting, with the fat accumulation peaks occurring about one month after the molting peaks (Fig. 2). Although the highest average fat scores were found on females, patterns of fat accumulation did not differ between the sexes (Kolmogorov–Smirnov $\chi^2 = 3.2$, df $= 2$, $P = 0.403$; Fig. 2). Fat accumulation patterns in 1997 were different from those in 1995 and 1996. The dry season peak of fat accumulation was shifted from April to June (Fig. 2). This coincided with the only dry season in which no females were found with brood patches (Fig. 1).

ANNUAL CYCLES OF OTHER BIRDS IN THE STUDY AREA.—Passerine birds in the study area bred from

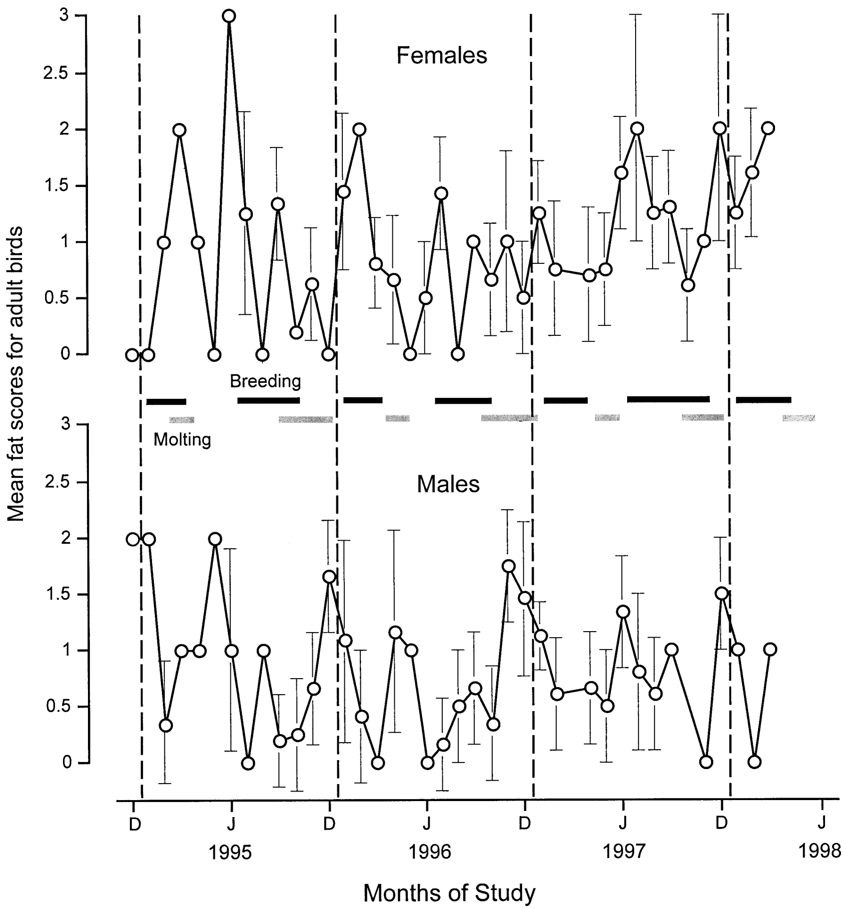

FIGURE 2. Fat accumulation in *Diglossa* did not show clear bimodal patterns. Adult males tended to accumulate fat after molting (lower panel), but this was not clear for adult females (upper panel). Points are mean values of fat scores and error bars are the standard deviation. Horizontal bars represent the period when more than 20 percent of the adult population exhibited complete molt (gray) or cloacal protuberances/vascularized brood patches (black). Dotted vertical lines separate calendar years (D = December, J = June). Sample sizes are the same as in Figure 1.

the end of the dry season (May) through the first half of the rainy season (July–August; JES & ESC, pers. obs.; Santana C. 2000, Carrillo 2001). Their breeding peaks were synchronous with the rainy season and did not overlap with any of the two breeding peaks of *D. baritula.* The breeding season of frugivorous–insectivorous birds (*Catharus occidentalis*, *C. frantzii*, *C. aurantiirostris*, and *Turdus assimilis*, exemplified in Fig. 3 by *C. occidentalis*; Carrillo 2001) and of the most abundant insectivorous species (*Basileuterus belli* and *Myioborus miniatus*) peaked during the months of highest insect abundance in the area (June–July; ESC, pers. obs.; Rivera-Cervantes 1988, Moya-Raygoza *et al.* 1990, López-Vieyra & Rivera-Cervantes 1998).

Hummingbirds had a single breeding season that extended from the rainy season to the beginning of the dry season (September–January; JES & IRT, pers. obs.; Fig. 3). Juveniles from the three most abundant resident species (*Lampornis amethystinus*, *Hylocharis leucotis*, and *Colibri thalassinus*, exemplified in Fig. 3 by *L. amethystinus*) increased in abundance once a year, from the end of the rainy season to the beginning of the dry season (November–March), suggesting a single breeding season occurring synchronously with the rainy season flowering peak for the study area (August–December; Ornelas & Arizmendi 1995, Santana C. 2000). Observations of nesting *L. amethystinus* in December and January, *C. thalassinus* in November and December, and *H. leucotis* from September to December (JES & IRT, pers. obs.) corroborated

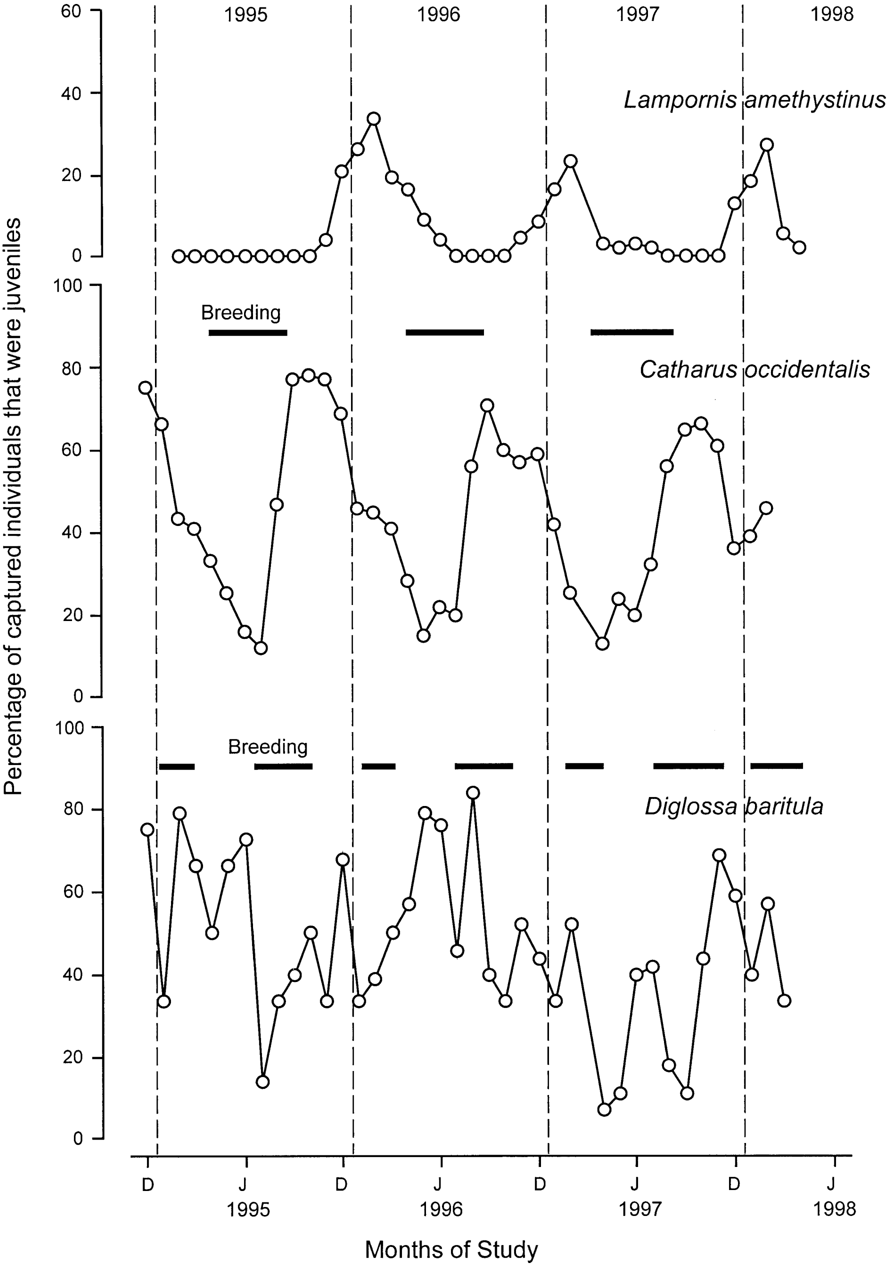

FIGURE 3. Abundance of juvenile hummingbirds (*Lampornis amethystinus*, top panel) and omnivorous passerines (*Catharus occidentalis*, center) peaked once a year, suggesting a single breeding season. *Diglossa baritula* (lower panel) juveniles did not show a clear pattern. Horizontal bars represent the time during which more than 20 percent of the adult population presented cloacal protuberances/vascularized brood patches. Because hummingbirds do not show distinctive cloacal protuberances/brood patches, no horizontal bars are used to indicate breeding in *L. amethystinus*. Dotted vertical lines separate calendar years (D = December, J = June). Numbers of captured juveniles varied dramatically during the year. Monthly sample sizes averaged 15 birds (±10) for *L. amethystinus*, 12 (±5) for *C. occidentalis*, and 9 (±5) for *D. baritula*.

our data from mist-net captures. The breeding season of resident hummingbirds overlapped with the rainy season breeding peak of *D. baritula* during September and October.

DISCUSSION

We found that in the mountains of west Mexico, Cinnamon-bellied Flowerpiercers had two distinct breeding seasons each year. These breeding seasons were asynchronous with those of insect- and fruit-eating species, and sexual differences were observed in the proportion of individuals that were in breeding condition or molting during the dry and the rainy seasons. While the same proportion of males exhibited cloacal protuberances in both of the breeding seasons, more females bred during the rainy season than during the dry season. In this discussion, we propose a hypothesis to explain these patterns. We begin by hypothesizing that the ability to feed on both flowers and soft fruits allows flowerpiercers to have a biannual pattern of reproduction. Then we compare the annual cycles of males and females. A third section compares the cycles of *D. baritula* with those of other passerine birds and hummingbirds. Finally, we propose a hypothesis to explain why Neotropical nectar-feeding birds tend to breed asynchronously with other birds.

WHY DO CINNAMON-BELLIED FLOWERPIERCERS SHOW BIANNUAL BREEDING? A HYPOTHESIS.—The biannual cycles of *D. baritula* were synchronized with the two main flowering peaks in the study area. The first breeding peak of *D. baritula* occurred at the end of the rainy season (July–August) and extended into October. These months corresponded with the season of abundant flowering for some hummingbird-pollinated plants (*Crucea coccinea*, *Fuchsia encliandra*, *F. fulgens*, and *Bomarea hirtella*; Ornelas & Arizmendi 1995, Arizmendi 2001). The second breeding peak occurred during the dry season (January–April); hummingbird flowers (*Salvia iodantha*) were abundant in February and became scarce in March and April (Arizmendi 2001). Other flowers (*F. encliandra*, *Ipomea* spp., and *C. jaliscoana*), melastome fruits (*L. subseriata*), and blackberries (*Rubus* spp.) became especially abundant after the flowering peak of *Salvia*. We hypothesize that Cinnamon-bellied Flowerpiercers were able to breed in the dry season by taking advantage of the abundance of soft fruits, using them as an important food resource in the absence of floral resuorces.

Although flowerpiercers are considered to be specialized nectar feeders, several species include fruits in their diets (Moynihan 1979, Isler & Isler 1999). *Diglossa baritula* preferred flowers over fruits in food selection trials but fed actively on fruits in the absence of flowers (JES, pers. obs.). When flowers were abundant, *D. baritula* spent 70–90 percent of its time feeding on nectar and hawked or gleaned for insects the remainder of the time (JES, pers. obs.). Proportion of time spent feeding on fruit increased markedly during the dry season and early part of the rainy season when flower abundance decreased and reached 40 percent of their foraging time by May. We observed *D. baritula* commonly feeding on fruits of three native (two *Rubus* spp. and *L. subseriata*) and two introduced species (*Prunus capulli* and *P. persica*). Blackberries were the most important component of *D. baritula*'s diet in March and April, when blackberry pulp was present in 65 to 80 percent of their feces (JES, pers. obs.). Cinnamon-bellied Flowerpiercers appear to rely on a combination of floral nectar and fruit to satisfy the energetic demands of breeding in the dry season.

Several severe freezing events that damaged the floral buds of *Rubus* spp. and *Salvia* spp. in December 1996 and January 1997 provided additional support for this hypothesis. This damage reduced the production of both flowers and fruits during the dry season of 1997 (JES & IRT, pers. obs.). The relative scarcity of these resources was accompanied by the absence of brood patches in *D. baritula* females and by a delay in the peak of fat accumulation during the dry season of 1997 (Figs. 1 and 2). The lack of nesting females during this breeding season preceded an apparent decrease in population size in our study area. In the fall of 1997, we captured 33 percent fewer individuals than during the same months in 1996 (JES & ESC, pers. obs.).

WHY DO MALE AND FEMALE FLOWERPIERCERS DIFFER IN THEIR BREEDING AND MOLTING CYCLES?—Males were in breeding condition and molted twice per year whereas females were in breeding condition and molted only once per year. These differences may have been due the combined effect of differences in the energetic costs of reproduction between the sexes and the seasonal availability of food resources. Reproductive costs include both physiological costs associated with the production of offspring and behavioral costs like territorial defense, mate guarding, incubation of eggs, and feeding young (Calow 1979, Jönsson *et al.* 1998). We hypothesize that the reproductive costs of female flowerpiercers are higher than those of males. Females invest energy and valuable nutrients in egg production (Nur 1988, Lindén & Møller 1989). In addition, only female flowerpiercers incubate the eggs, while other behavioral costs like territorial defense and feeding young are shared by both sexes (JES, pers. obs.; Skutch 1954). The hypothesis that females are more energy-/resource-limited than males was supported by our observation of frozen buds in 1997. In the months following the freezing of floral buds, no females bred, whereas males exhibited enlarged cloacal protuberances, molted, and built fat reserves (Fig. 1).

Differences in the frequencies of adult birds that were in breeding condition or molting between the dry and the rainy season may be explained by differences in food abundance between these two seasons. The beginning of the rainy season breeding period of *D. baritula* overlapped with the months of higher rainfall (August, Fig. 1) and insect and flower abundance (June–August; Rivera-Cervantes 1988, Moya-Raygoza *et al.* 1990, López-Vieyra & Rivera-Cervantes 1998). High rainfall and warm temperatures from June to September were accompanied by both high insect and flower abundance. In contrast, the second half of the dry season breeding period occurred during the months in which hummingbird flowers became scarce (Ornelas & Arizmendi 1995, Arizmendi 2001) and insect abundance was low (January–March; Rivera-Cervantes 1988, Moya-Raygoza *et al.* 1990, López-Vieyra & Rivera-Cervantes 1998). In addition, high densities of migratory hummingbirds may have competed with resident nectar-feeding birds for floral resources during December–February (JES, pers. obs.; Calder & Contreras-Martínez 1995, Ornelas & Arizmendi 1995).

The differences in the proportions of males and females in breeding condition between the dry and the rainy season makes *D. baritula* a suitable candidate to have a complex mating system. If, as suggested by our data, males reproduce twice a year but individual females do it only once, we can expect males to switch partners. Additionally, depending on the length of the female breeding cycle, there could be potentially two populations of females: one breeding in the dry season and the other in the wet season. Unfortunately, our recapture data does not provide us with enough information to test these hypotheses. Future research on the mating system and the individual strategies of Cinnamon-bellied Flowerpiercers is needed to address these questions.

A COMPARISON BETWEEN CINNAMON-BELLIED FLOWERPIERCERS AND OTHER BIRDS.—Of all resident passerine birds at Las Joyas, only *D. baritula* has biannual breeding and molting cycles. Because *D. baritula* is the only primarily nectarivorous passerine in our study area, its reproductive season may be determined more by floral (and fruit) abundance than by insect abundance. The annual cycles of other nectar-feeding birds at Las Joyas were similar to those described for the highlands of Guatemala (Skutch 1950, 1954), Costa Rica (Stiles 1980), and other regions of Central America (Skutch 1950), where birds breed at the end of the rainy season and beginning of the dry season when flower abundance peaks. The end of the rainy season breeding period of *D. baritula* at Las Joyas coincided with the breeding season for resident hummingbirds; however, hummingbirds bred only once. Resident hummingbirds at Las Joyas seem to deal with the energy demands of breeding and molting by using the rainy season flowering peak to breed and the dry season floral peak to fuel their complete molt. Temporal separation of breeding and molting in hummingbirds that coincides with two blooming seasons has also been reported for the hummingbirds of La Selva, Costa Rica (Stiles 1980), and the island of Trinidad (Snow & Snow 1964).

CINNAMON-BELLIED FLOWERPIERCERS AND THE TIMING OF REPRODUCTION AND MOLT IN NEOTROPICAL BIRDS.—The biannual phenology of *D. baritula* at Las Joyas raises questions about the proximate and ultimate mechanisms that shape the temporal pattern of breeding and molting in tropical birds. Little is known about the circannual and endocrinological control of reproduction in birds with biannual reproduction (Miller 1959, 1962). The failure of females to breed in a year in which resources were scarce suggests that in *D. baritula* timing mechanisms may be regulated by the availability of critical resources (Wingfield *et al.* 1998, Gwinner 1996, Jacobs & Wingfield 2000). Cinnamon-bellied Flowerpiercers appear to be ideal organisms for investigating the interplay between endogenous controls and resource abundance on the timing of reproduction and molt in birds.

The biannual phenology of flowerpiercers also sheds some light on a vexing question about the ultimate evolutionary determinants of the timing of reproduction and molt in Neotropical birds. Why does reproduction by tropical hummingbirds occur out of phase with other sympatric non-nectarivorous species? Although the abundance of protein-rich insects is probably a crucial factor in the timing of reproduction for many bird species (Fogden 1972, Robbins 1981, Poulin *et al.* 1992), this does not seem to be the case in nectar-feeding birds (Skutch 1950, Stiles 1980). In these species, the abundance of energy-rich, but protein-poor, nectar seems to be the primary factor that determines the timing of reproduction. The reproductive timing of *D. baritula* at Las Joyas appears to depend on flower abundance in the rainy season and on the combined abundance of flowers and fruit in the dry season. None of these food resources is protein-rich. Like hummingbirds, Cinnamon-bellied Flowerpiercers seem to cue on the relative availability of energy to reproduce. Protein abundance does not seem to control the timing of their breeding and molting cycles, but appears to regulate breeding success, limiting the number of nesting females during the dry season. We hypothesize that energy availability limits the rate at which nectar-feeding birds can capture insects and provide protein to their developing young. Understanding the curious biannual phenology of *D. baritula* may help us understand both the proximate mechanisms and the ultimate causes underlying the timing of breeding and molting in tropical birds.

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