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Resource tracking and its conservation implications for an obligate frugivore (*Procnias tricarunculatus*, the three-wattled bellbird)

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ABSTRACT

In Monteverde, Costa Rica, the vulnerable Three-wattled Bellbird (*Procnias tricarunculatus*) feeds primarily upon the fruit of Lauraceae species during its reproductive and post-reproductive seasons. To understand and advance appropriate conservation measures, this study identified the bellbird's foraging challenges in its search for a temporally and spatially fluctuating resource. Although there are at least 96 species of Lauraceae found in the five life zones of Monteverde, the distinct distributions of tree species both among and within life zones require the bellbirds to track seasonal fruiting across the various zones. In this 6-year study, we monitored the fruiting of tree species and bellbird abundance in 24 study plots within its post-reproductive life zone, the Premontane Wet forest, to identify preferred bellbird food resources and how the fruiting of these species drives the spatial distribution of the bellbird. Our research revealed phenological patterns of annual, biennial, and triennial fruiting with high levels of fruiting synchrony within several identified key fruit species. Of critical conservation importance is that no single species of Lauraceae produced a consistent food supply for bellbirds each year. Therefore, even within life zones, the bellbird's survival depends on its mobility to search for and obtain fruit, as well as the availability of fruits of multiple tree species. The conservation implications include focused attention on multiple core areas within given life zones, protection of existing forest and remnant trees, and forest restoration with plantings of multiple tree species. We suspect that other tropical frugivorous species face similar conservation challenges.

Abstract in Spanish is available with online material.

Key words: Frugivory; Lauraceae; Monteverde; *Myrcianthes* 'black fruit'; *Nectandra salicina*; *Ocotea floribunda*; *Ocotea monteverdensis*; phenology.

Obligate frugivorous birds face temporal and spatial foraging challenges that highlight the need for landscape level conservation (Terborgh & Winter 1980, Price *et al.* 1999, Guindon 2000, Gomes *et al.* 2008, Tobias *et al.* 2013). The vulnerable (IUCN 2016a) Three-wattled Bellbird (*Procnias tricarunculatus*) of Central America epitomizes these challenges. Efforts to conserve frugivorous birds, such as the bellbird, and the integrity of their ecological functions in tropical regions, where food resource identification is problematic and phenological data are limited (Garcia & Ortiz-Pulido 2004), are hampered by an incomplete understanding of the spatial and temporal complexity of fruit availability (Wheelwright *et al.* 1984, Levey 1988, Loiselle & Blake 1991, Kinnaird *et al.* 1996, Garcia & Ortiz-Pulido 2004, Chapman *et al.* 2005, Berens *et al.* 2014, Chaser *et al.* 2014). The identification of core areas, where intense use of resources occurs in small subregions within a frugivore's home range, can help clarify some of this complexity (Asensio *et al.* 2014); however, clear understanding of responses by frugivorous vertebrates to shifting resource availability, especially in fragmented landscapes, will aid in identifying appropriate habitat for protection (Loiselle & Blake 1991, Rey 1995, Moegenburg & Levey 2003, Garcia & Ortiz-Pulido 2004, Martinez & Garcia 2015). The need to correlate community–wide frugivore census data with fruit availability across regions within landscapes has been identified (Levey 1988, Sargent 1990, Rey 1995, Moegenburg & Levey 2003, Carlo *et al.* 2007, Prasad & Sukumar 2010). Knowledge of alternative food resources for frugivores when the customary or preferred fruits are not available is also valuable information for effective conservation measures (Terborgh 1986, Kannan & James 1999).

As obligate frugivore specialists important for seed dispersal (Wenny & Levey 1998, Wenny 2000), bellbirds exhibit a high degree of migratory flexibility in their search for an assortment of fruit species. The bellbird population of Monteverde, Costa Rica migrates to both the Caribbean and Pacific coastal areas each year and spends 6 to 8 months (February-September) in the Tilarán Mountains, where they track the ripening fruit of certain tree species through four to five distinct Holdridge life zones (Holdridge 1967) on both sides of the continental divide (Powell & Bjork 2004). This study focuses on one of those life zones, the Premontane Wet Life Zone on the Pacific side of Monteverde, which provides the principal habitat for bellbirds during their post-reproductive period in June through September, before they migrate out of the Monteverde region.

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Within the Premontane Wet Life Zone, the bellbird must compensate for varied spatial and temporal distribution of fruits. Of particular concern is that this life zone is fragmented and restricted in size in Monteverde (Wheelwright 1983, Harvey *et al.* 2000, Powell & Bjork 2004) and has almost been eliminated in Costa Rica (Sánchez-Azofeifa *et al.* 2001). Because of this extensive loss of habitat and because the size of the available fruit crop varies greatly from year to year, it has been estimated that as many as 300 individual bellbirds may rely on no more than 20 ha of remaining, degraded forest fragments in certain years (Harvey *et al.* 2000). Bellbirds switch foraging areas in the pursuit of food between three distinct sub-zones, or core areas, within this life zone, with intermittent use of two sub-zones (the upper, wetter region of the Premontane Wet Life Zone and the lower, drier region), and consistent use of a transition sub-zone which is located between the two. The identification of food resources driving this behavior has not been researched previous to this study.

Thirty-one fruit species have been identified in the bellbird's diet in the Monteverde Region with over half of the species in the Lauraceae family and several species lacking official or specific designations (Wheelwright 1985, Hamilton *et al.* 2003). The Lauraceae family is also of prime importance to other threatened frugivores, such as the Resplendent Quetzal (*Pharomachrus mocinno*) and the Black Guan (*Chamaepetes unicolor*) (Skutch 1969, Snow 1977, Wheelwright 1983, Guindon 2000, Haber et al. 2000, Powell & Bjork 2004, IUCN 2016b,c). In a seven-year study, Wheelwright (1986) revealed the high year-to-year differences in the average fruit crop produced by 22 bird-dispersed Lauraceae species in the montane forests of Monteverde.

With these results in mind, we investigated the flowering and fruiting phenology of the tree species potentially used by the bellbird in the Premontane Wet Life Zone, the potential preference of bellbirds for specific species of fruit, and the use of alternative fruit when preferred food resources were lacking. A more thorough understanding of the patterns of habitat use by bellbirds will inform the efforts of several organizations in the Bellbird Biological Corridor that are working on the protection of critical habitat for the long-term survival of the bellbird and other threatened species (Corredor Biologica 2017, Monteverde Institute 2017).

METHODS

STUDY SITE.—We established 24 tree plots (50 m × 20 m) between the elevations of 1200 and 1450 m asl in the Premontane Wet Life Zone in Monteverde, Costa Rica. Plot size was chosen to be large enough to include several fruiting trees yet small enough to allow observers to record presence of birds in or near the plots while sampling within plots. Eight plots were established in each of the following sub-zones: Premontane Wet Lower (PMW-L) (10°18′45″ N, 84°50′29″ W), Premontane Wet Upper (PMW-U) (10°17′51″ N, 84°48′47″ W), and a transition sub-zone between the two (TRA) (10°18′45″ N, 84°49′08″ W) (Fig. 1). The locations of the plots corresponded to distinct bellbird foraging areas known to be used during the months of June through September through regional census data from 1997 to 2004 (Fig. S1). The census data have also shown that bellbirds use remnant forest fragments and isolated trees in the TRA sub-zone consistently, while the use of the PMW-L and PMW-U sub-zones varies from year to year (Figs S1 and 1).

The Premontane Wet Life Zone in Costa Rica has been described as occurring between 800–1450 m asl and receives 2000–4000 mm of annual precipitation with a mean annual temperature of 17–24°C (Hartshorn 1983). In the vicinity of Monteverde, this broad zone exhibits a steep moisture gradient with elevation, and it has been classified as 'Premontane Moist Life Zone' below 1200 m, and as 'Premontane Wet Life Zone', between 1200 m and 1450 m in other studies (Guindon 1997, Haber *et al.* 2000). Within this Premontane Wet Life Zone, the evergreen forest hosts a moderate epiphyte abundance and diversity and experiences an average dry season of three months (0–5 months possible) (Bolaños & Watson 1993). Lauraceae is the dominant tree family in the remaining mature forest patches (Haber 2000, Haber *et al.* 2000). Using recent aerial photography, ground verification, and GIS analysis, we estimate that only 330 hectares (3.3 km^2) of this mature forest remains within the 30 square kilometers of this life zone surrounding Monteverde. Most of this remaining mature forest consists of unprotected, highly degraded fragments (Guindon 1997, Powell & Bjork 2004, Harvey *et al.* 2008).

TREES SELECTED FOR STUDY.—Sixteen tree species which produce fruit while bellbirds are found in the Premontane Wet Life Zone were identified and tagged in the 24 tree plots (Appendix S1). Species included all members of the Lauraceae family found in our study sites (13 species) as well as three other species in the Myrtaceae, Flacourtaceae, and Symplocaceae families that are known to be eaten by bellbirds (Wheelwright *et al.* 1984,., Hamilton *et al.* 2003). Other fruit producing species were noted, if present in or near the study plots, such as trees in the families Moraceae, Rosaceae, Verbenaceae, and Melastomataceae, which produced fruits principally outside of June-September of our 6-year study period. There were between four and 13 tagged trees per plot (mean = 8.2) and from three to 12 of these were in the family Lauraceae (mean = 7.0).

Our results are restricted to the seven tree species that produced sufficient fruit during June through September in at least some years of our study to warrant analysis; these species include one in the family Myrtaceae (*Myrcianthes* new species 'black fruit') and six in the family Lauraceae (*Beilschmiedia brenesii, Nectandra salicina, Ocotea floribunda, Ocotea monteverdensis, Ocotea* new species 'los llanos', *Ocotea whitei*). These six Lauraceae species comprised 80% of the tagged Lauraceae trees in the study. Two of the Lauraceae species are on the IUCN red list, one as 'near threatened' and the other as critically endangered (*N. salicina* and *O. monteverdensis* respectively; Rohwer 1998, Joslin *et al.* 2013), and two are undescribed species (*Ocotea* new species 'los llanos' and *Myrcianthes* new species 'black fruit'; Setzer *et al.* 1999, 2006, Tropicos.org 2017). Each tree was classified into one of four crown classes

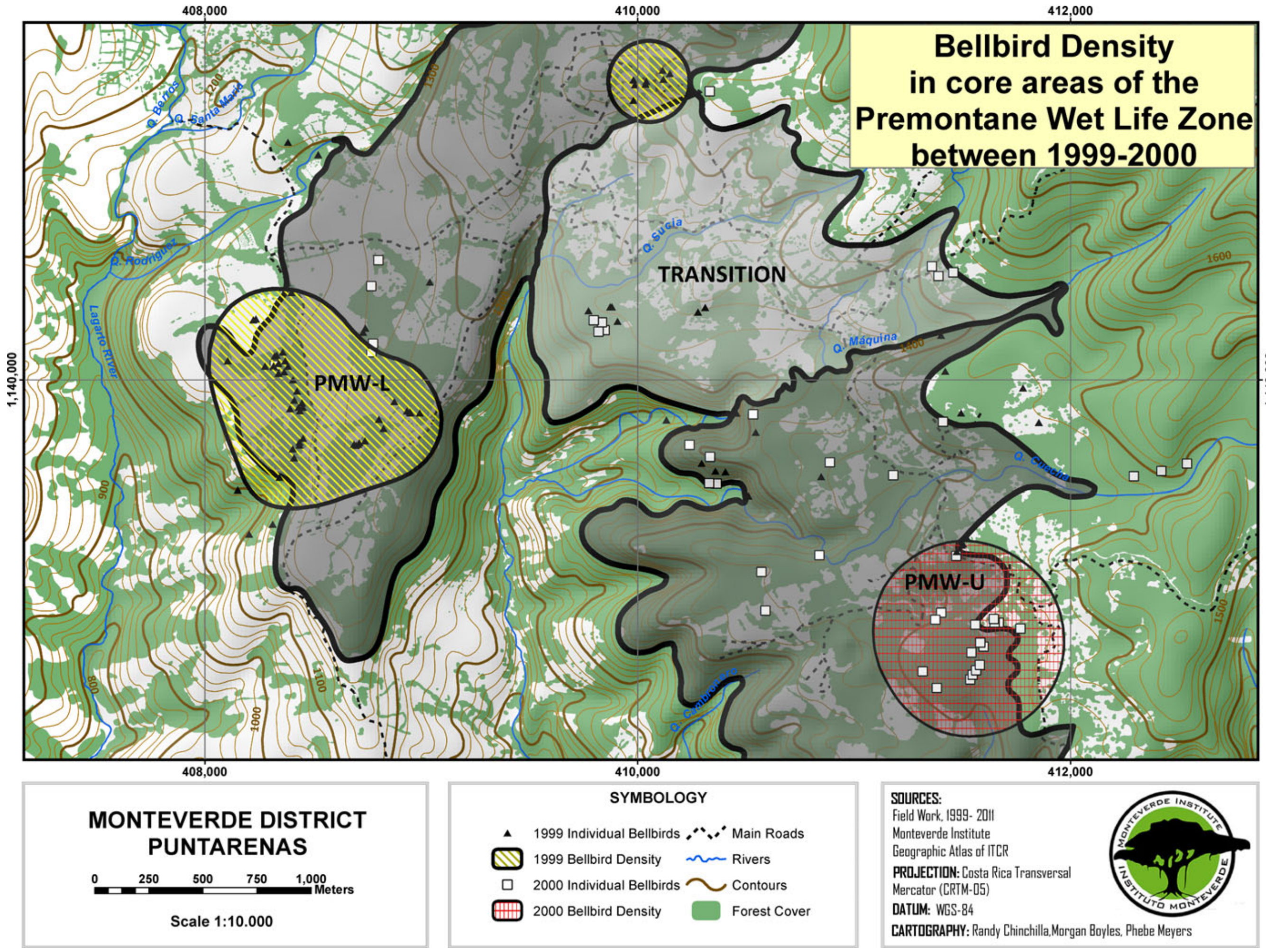

FIGURE 1. Identification of three sub-zones of the Premontane Wet Life Zone and the shifting use by bellbirds in the post-reproductive period in Monteverde, Costa Rica as they track fluctuating food resources. Diagonal hash marks in green represent habitat with high bellbird density during 1999; cross hash marks in red represent habitat with high bellbird density during 2000. Note: These two years were chosen to represent the year-to-year variability in habitat use by bellbirds, though similar temporal differences were observed throughout annual censuses from 1997–2004 (D. Hamilton unpubl. data). See Fig. S1 for more census data.

(dominant, co-dominant, intermediate, and suppressed) based on the system described by Smith (1962), and diameter at breast height (1.3 m above the ground; dbh), was measured. Additional information on these tree species, including the size of their fruit and use by frugivorous birds, can be found in Appendix S1 and Table S1 respectively.

DATA COLLECTION.—Data were collected for a total of 56 months from June, 2005 to September, 2010, encompassing 6 years of monthly data during the June through September period. For each tree species, the phenophases of flowering, small green fruit, large green fruit, and ripe fruit were recorded for all 56 months, and the phenology patterns were analyzed for 12- to 24-month phases. After 2005, data were collected every other month during the October to February period, when bad weather and lack of bellbird presence is typical; because fruit of these species develop slowly, it is unlikely that we missed any important fruiting patterns with this approach. For the few months lacking data, values were estimated using data from the previous and subsequent months.

Bellbirds and other large frugivorous birds were surveyed in each plot between the hours of 0700 to 1100 h for a 25-min period each month of the sampling period. Recorded bird data included species, sex, location in a specific tree, distance to nearest fruiting tree, and behavior (foraging, calling, interacting). Bellbirds outside of study plots, but within 20 m of plot edges, were also recorded.

Flowering for each tree was categorized as 'very few' (only on a few branches), 'scattered' (present at low levels throughout the tree), or 'full crown' (present along most branches in the canopy). Fruit quantity was estimated by multiplying the number of visible fruit in single binocular views, by the number of binocular views necessary to cover the entire canopy of the tree. This method was preferred over dbh correlations because of uneven flowering and fruit distribution in crown areas. Fruit was categorized by the quartile percentages of small green, large green, and black (ripe) fruit. To standardize fruiting level across a variety of tree species with different fruit sizes, maximum numbers of fruit, and crown distribution, we assigned a fruiting index to each tree for each month ranging from zero to three based on the fruit quantity estimate (described above) and ripeness (Table 1).

DATA ANALYSES: TREE DISTRIBUTION ACROSS SUB-ZONES.—For the seven tree species included in our data analysis, chi-square analysis was used to test whether they were distributed evenly among our plots in the three sub-zones, and the percentage of each species found in each sub-zone was graphed.

DATA ANALYSES: FLOWERING PHENOLOGY.—Values for graphing flowering phenology were determined on a monthly basis and are reported as the average percentage of trees in a given species that were flowering (either 'scattered' or 'full crown') in a given month across all years. For the sole known dioecious species in our study (*O. floribunda;* Little & Wadsworth 1964), only trees determined to be female were included in the calculation of the average percentage flowering.

DATA ANALYSES: FRUITING PHENOLOGY.—A monthly fruiting value for each tree species was calculated by summing the number of fruits in each size class (small green, large green and ripe) produced by all individuals across all years. These sums were then divided by the number of individuals of the species that fruited at some time in the study, and by the number of times that month of the year was observed (including extrapolated values), to provide a value for the average number of fruit per tree per month.

DATA ANALYSES: SYNCHRONY INDEX.—To quantify the tendency of individual trees within a species to produce (or not produce) fruit in the same year, we used a 'synchrony index' based on the method of Buide *et al.* (2002). In highly synchronous species, most of the trees either have a good crop year or have a poor year, resulting in high variability in total crop from year to year.

TABLE 1. *Summary of criteria for determining the fruiting index of individual trees based on number of fruit and stage of fruit development. Note: fruit that appears large green and unripe to observers may be edible to bellbirds.*

Fruiting index	Definition
0	No Fruit
1	<150 fruit, or, if equal to or >150 fruit, no visible ripe fruit present and <60% large green.
2	Number of fruit 150 to 299 with some visible ripe fruit present and/or ≥60% large green.
3	Number of fruit 300 or greater with some visible ripe fruit present and/or ≥60% large green.

DATA ANALYSES: BELLBIRD ABUNDANCE AND FRUIT AVAILABILITY.—To document year-to-year variation in total bellbird numbers and in their use of different sub-zones during our study, we graphed the percentage of bellbirds encountered in each sub-zone and added an overlay of the total number of bellbirds encountered each year. We tested for significance among years in use of the sub-zones using chi-square analysis.

To test for relationships between bellbird abundance and total fruiting indices for the months of June through September, we used the statistical analysis software R to conduct Poisson repeated measures regression analyses; the repeated measures model accounts for the fact that within years, monthly data are not independent (R Core Team 2016). We did this analysis for bellbird abundance and total fruiting across all seven tree species in all three sub-zones, and we did two rounds of analyses for individual tree species within each of the three sub-zones. The first round of analyses included all six years of data. The second round of analyses excluded the years of 2007 and 2010 (both heavy fruiting years for the preferred *O. monteverdensis*) to identify other important fruiting species when preferred fruit was not available.

Tree species that produced fruit in fewer than 5 months in a given sub-zone across the entire study were excluded from these analyses for that sub-zone. For the first round of analyses, twelve tree species/sub-zone combinations were included; for the second round of analyses, ten tree species/sub-zone were included. To correct alpha for multiple comparisons, we used the Bonferroni correction (McDonald 2014) to determine statistical significance; this correction resulted in alphas of 0.0042 (=0.05/12) and 0.005 (=0.05/10) for analyses one and two respectively.

Poisson repeated measures multiple regression analyses were also used to test for the effect of fruiting of multiple tree species on bellbird abundance. As these analyses did not reveal any significant effects beyond those from the single species analyses, only the individual regression analysis results are reported.

RESULTS

TREE DISTRIBUTION.—The seven tree species analyzed in this study were not evenly distributed across our plots in the three sub-zones within the Premontane Wet Life Zone (Fig. 2; df = 12, $P < 0.0001$, $\chi^2 = 99.92$). For three species (*Ocotea* 'los llanos', *Myrcianthes* 'black fruit', *Nectandra salicina*), over 50 percent of individuals in our study were in the PMW-L sub-zone; for two species (*O. floribunda, O. whitei*), over 50 percent were in the TRA sub-zone. *Ocotea monteverdensis*, a species endemic to the Monteverde region of Costa Rica, was present almost exclusively in the PMW-U sub-zone. A distribution map for this species can be found in Fig. S2.

ANNUAL VARIATION IN SIZE OF FRUIT CROPS BY SPECIES.—The consistency of sufficient fruit crop sizes from year to year in the Premontane Wet life zone is a significant issue for the conservation of the bellbird. Table 2 rates each tree species with regard to the observed probability of its producing a large fruit crop—and that

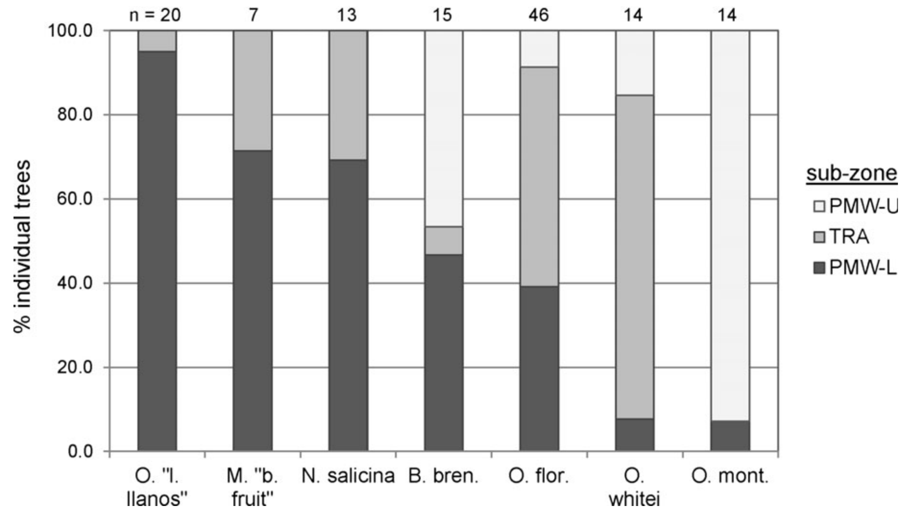

FIGURE 2. Distribution of the seven tree species showing the percentage of individuals for each tree species found in each of the three sub-zones. Species are presented left to right in descending order of abundance in the Premontane Wet Lower sub-zone (PMW-L).

of producing a poor fruit crop (defined as a percentage of the mean crop size for each species for the 5–6-year study period). All seven species had a 50 percent or lower probability of 'good crop' years with the lowest probability being 1 in 6 for *Myrcianthes* 'black fruit'.

Ocotea monteverdensis and *O. whitei* were particularly likely to have 'poor crop years', in part because individuals take 18–20 months to complete the flower-to-mature-fruit cycle and therefore 'skip' 1 or 2 years. Wheelwright (1986) found very similar seasonal patterns of flowering and fruiting in *O. monteverdensis* (called *Nectandra hypoglauca* in his study), and heavy fruiting years tended to alternate with poor years.

In addition to low probabilities of producing significant fruit crops in consecutive years, three species—*O. monteverdensis, O. whitei* and *Myrcianthes* 'black fruit'—showed high flowering and fruiting synchrony, wherein individuals of these species have a very strong tendency to produce either large or very small crops in the a given year (Table 2). *Nectandra salicina* and *O. floribunda* showed low synchrony, resulting in a more even distribution of fruit from year to year.

The flowering and fruiting phenology of *O. monteverdensis* exemplifies this lack of yearly consistency in fruit production; this species produced significant fruit crops in only two of the six years in our study (2007 and 2010; Fig. 3). Details of flowering and fruiting phenology for the remaining species can be found in Fig. S3.

EFFECTS OF TREE SIZE AND CANOPY POSITION ON FRUIT PRODUCTION.—When trees were divided among diameter and canopy position classes, sample size did not allow for formal

TABLE 2. *Characterization of phenological characteristics of seven principal tree species. A 'good crop year' is one where the total annual productivity is at least 15 percent more than the mean for the six years of the study; in a 'poor year,' productivity is < 60 percent of the mean. Synchrony index (based on method of Buide* et al. *2002) portrays the tendency of most of the individual trees of a species to produce similar crop sizes in a given year. In highly synchronous species (index >0.70), most of the trees either have a good crop year or have a poor year, resulting in high variability in total crop from year to year. Note: Synchrony index for* Ocotea monteverdensis *based on a separate random sample of 40 individuals evaluated with aerial photography in a major crop year. Co-dominant crowns form the canopy, receiving full light from above but little from the sides; intermediate trees receive sparse direct light from above and none from the sides; suppressed crowns are entirely below the canopy, receiving no direct light. Note: All* Myrcianthes *trees in study were co-dominants of at least 61 cm diameter.*

Species	Problity. of 'good crop year'	Problity. of 'poor crop year'	Length: flower-fruit cycle (mos.)	Trees flowering in peak month (%)	Synchrony index	Minim. tree diam. to fruit (cm)	Lowest crown class to fruit
Beilschmiedia brenesii (*n* = 15)	1 in 3	1 in 3	12	9	Med. (0.458)	18	Suppressed
Nectandra salicina (*n* = 13)	1 in 3	1 in 2	12	48	Low (0.344)	23	Intermediate
Ocotea floribunda (*n* = 41)	1 in 2	1 in 3	12	37	Med. (0.456)	23	Intermediate
O. 'los llanos' (*n* = 20)	1 in 2	1 in 2	12	50	Med. (0.575)	26	Intermediate
O. monteverdensis (*n* = 14)	1 in 3	2 in 3	18	95	V. high (0.800)	24	Co-dominant
Ocotea whitei (*n* = 14)	1 in 3	2 in 3	20	31	V. high (0.822)	32	Intermediate
Myrcianthes 'black fruit' (*n* = 7)	1 in 6	2 in 3	8	84	V. high (0.827)	61	Co-dominant

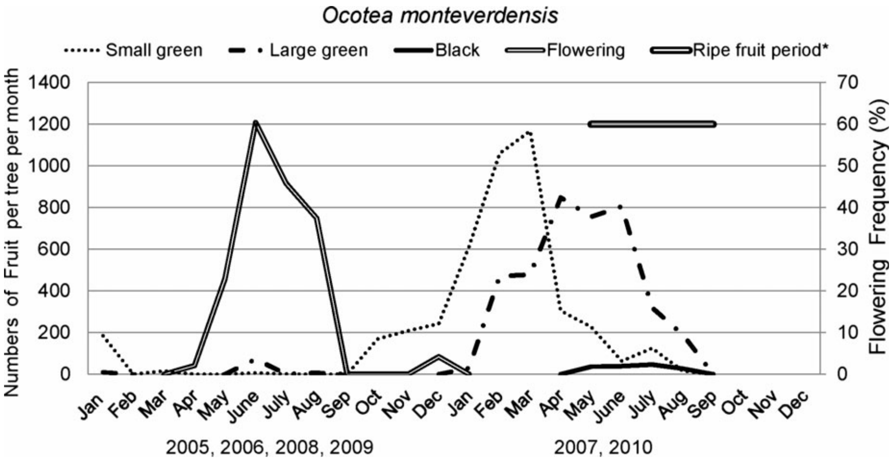

FIGURE 3. Phenology of flowering and fruiting in *Ocotea monteverdensis.* Mean values per month of the year for the entire study period shown for flowering, small green fruit, large green fruit, and large black (mature) fruit. Flowering observations recorded as the percentage of trees that flowered ('full crown' or 'scattered') in a given month of the year averaged across the entire study. For the occasional months when observations were not made, values were extrapolated by averaging the preceding month and following month. Fruiting is reported by month of year as the average number of fruit in a given size class per tree per month observed, using all individuals that fruited at least one time during the study. A 24-month cycle is depicted; the years when flowering predominated are separated from the years when fruiting predominated.

analysis of the effects of those factors on fruiting. Nonetheless, there were a few notable patterns. For example, it appears that *O. monteverdensis* is much more likely to produce fruit when trees are large (>50 cm dbh) and occupy dominant or co-dominant canopy positions; two species (*B. brenesii* and *N. salicina*) produce fruit even when of small stature (<30 cm dbh) and in sub-canopy positions (Fig. S4).

FRUITING AND BELLBIRD ABUNDANCE.—Temporal variation in the use by bellbirds of the three sub-zones among years was statistically significant (df = 10, $P = 0.014$, $\chi^2 = 22.15$), a pattern demonstrated by the TRA sub-zone in which the percent of bellbirds found in our study ranged from over 80% in 2008 to <20% in 2010 (Fig. 4).

Regression analysis revealed that for the months of June through September, there was a significant relationship across all plots between monthly bellbird abundance (tallied by sub-zone) and total fruiting of the seven tree species combined (df = 53, $P = 0.0001$, $R^2 = 0.18$; Fig. 5); when sub-zones were analyzed separately, the relationship was significant for two of the three sub-zones (df = 17; $P = 0.023$ and 0.0004 for PMW-L and PMW-U respectively). Strong effects at low and high fruiting levels are apparent and indicate that the year-to-year and month-to-month variation in the number of bellbirds found in each sub-zone appears to be driven by total fruit availability (Fig. 5), though the relatively low R^2 value does suggest that factors other than fruiting may be influencing bellbird abundance. In nine out of eleven month/sub-zone combinations with no fruiting, no bellbirds were recorded and only one or two bellbirds were recorded in the remaining two month/sub-zone combinations with no fruiting. Conversely, the month/sub-zone combination with the greatest total fruiting (fruiting index of 43 in PMW-U in

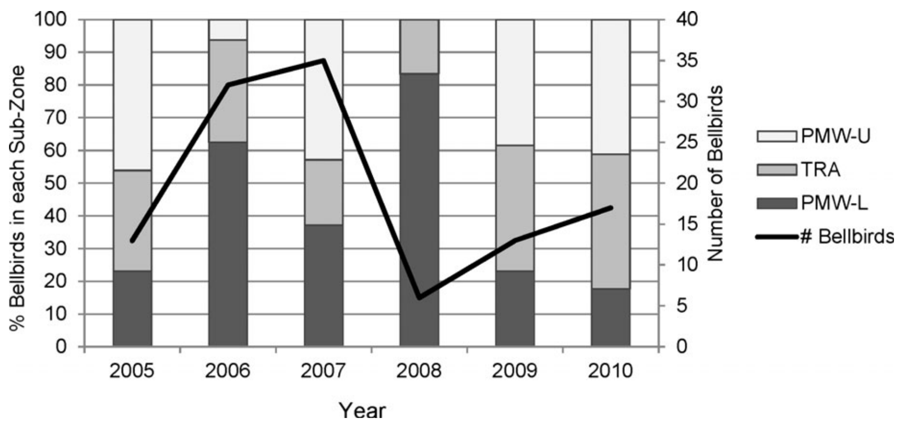

FIGURE 4. Total number of bellbirds encountered per year in study (black line) and the percent found in each region each year. Differences in use of sub-zones among years is statistically significant (df = 10, $P = 0.014$, $\chi^2 = 22.15$).

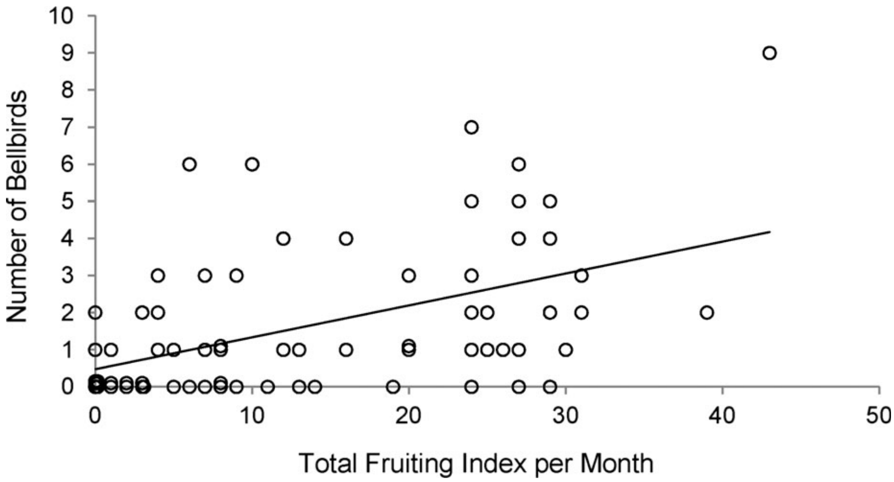

FIGURE 5. Relationship between the number of bellbirds and total fruiting of the seven tree species in the Premontane Wet Life Zone. Each data point represents one month in one sub-zone (df = 53, $P = 0.0001$, $R^2 = 0.18$; Poisson repeated measures regression analysis). A small random 'jitter' was added when data points overlap to allow visualization.

June of 2007) corresponded to a bellbird count of nine, the highest for any month/sub-zone combination.

Four tree species showed significance when testing for relationships between fruit availability and bellbird abundance: *O. monteverdensis, N. salicina, O.* 'los llanos', and *B. brenesii* (Table 3). However, when adjusted for multiple comparisons, only *O. monteverdensis* in the PMW-U sub-zone resulted in a significant relationship (Bonferonni corrected alpha = 0.0042; $P = 0.0013$). The scatterplot showing bellbird abundance vs. the fruiting index of *O. monteverdensis* does show a fair amount of variability (Fig. 6A, $R^2 = 0.25$), yet further investigation supports the importance of this species. In ten of the 11 months when the fruiting index for *O. monteverdensis* was zero, no bellbirds were recorded in this sub-zone; the one exception occurred in June of 2006 when only two bellbirds were recorded. In contrast, in June of 2007, the month with the highest number of bellbirds recorded (nine, as mentioned above), the fruiting index for *O. monteverdensis* was 30, the greatest for any month (Fig. 6A).

To determine what tree species might be important in producing alternative fruit, a second round of regression analyses was performed excluding the data from the two heavy fruit years for *O. monteverdensis*—2007 and 2010. These analyses revealed positive trends of bellbird abundance with fruit availability for the following three additional tree species sub-zone combinations: *Nectandra salicina* and *Myrcianthes* 'black fruit' in the PMW-L sub-zone and *O. floribunda* in the TRA sub-zone (Fig. 6B–D), though the *P*-values were not statistically significant when corrected for multiple comparisons (Table 3).

DISCUSSION

CONCERN REGARDING THE DECLINE of the endemic and vulnerable Three-wattled Bellbird of Central America has focused on the reduction of its habitat on the Pacific slope of several Central American countries (Guindon 2000, Hamilton *et al.* 2003, Powell & Bjork 2004, Saranathan *et al.* 2007, Allen *et al.* 2008). Of particular importance is the loss and alteration of forest in the Premontane Wet and Premontane Moist Life Zones (Powell & Bjork 1994, 2004, Harvey *et al.* 2000). To further clarify the effect of habitat loss on the bellbird, we undertook this study to gain insight into how food resources affect the annual variation in bellbird distribution and abundance in three sub-zones of the Premontane Wet Life Zone. A greater understanding of dietary selection and fruit availability—in particular its distribution, phenology and production—is critical for effective conservation measures.

Of the seven species of fruit that bellbirds have been observed frequently eating in the Premontane Wet Life Zone during the June–September post-reproductive period, *O. monteverdensis* showed a significant positive relationship of total fruit availability with bellbird abundance. *Ocotea monteverdensis* is known to be of particular importance in the diet of other threatened bird species such as the Resplendent Quetzal and Black Guan, as well as bellbirds while they are in Monteverde. This corresponds to Guindon (1997), wherein large frugivores were observed feeding at fruiting *O. monteverdensis* trees at 7.5 times the frequency predicted simply by the percentage of Lauraceae fruit available on trees studied.

Our results show that *O. monteverdensis* only produces significant fruit crops every two to three years, as occurred in the years 2007 and 2010 of the study period. This lack of consecutive-year fruit production by *O. monteverdensis* underscores the importance of alternative fruit species for the bellbird. We identified three alternative species *(O. floribunda, N. salicina*, and M. 'black fruit'), that are particularly important for bellbirds in the months and years when there is little fruiting of *O. monteverdensis,* by the positive trends between bellbird abundance and their fruit availability (Fig. 6B–D). One of the other alternative species, *M.* 'black fruit',

TABLE 3. *Summary of results from repeated measures Poisson regressions of bellbird abundance vs. the total fruiting index for each tree species in each sub-zone. The number of months when each species produced fruit is represented by n; if a tree species produced fruit during fewer than five months in a given sub-zone, no analysis was performed. When a species was not present within a particular sub-zone, n.p. (not present) is presented for n. For the First Analysis, 24 months were included in the analyses (6 years × 4 months–June through Sept.); for the Second Analysis (excluding the two years with a heavy* Ocotea monteverdensis *crop), 16 months were included in the analyses.*

		First analysis, df = 17			Second Analysis, df = 11		
Species	Sub-zone	n	P	R^2	n	P	R^2
Beilschmiedia brenesii	PMW-L	9	0.57	0.009	3	–	–
	TRA	3	–	–	0	–	–
	PMW-U	15	0.015*	0.15	11	0.15	0.10
Nectandra salicina	PMW-L	18	0.0208*	0.22	11	0.023*	0.33
	TRA	10	0.55	0.01	2	–	–
	PMW-U	n.p.	–	–	n.p.	–	–
Ocotea floribunda	PMW-L	16	0.26	0.05	11	0.099	0.19
	TRA	19	0.16	0.07	12	0.027*	0.33
	PMW-U	9	0.90	0.0007	6	0.18	0.52
Ocotea 'los llanos'	PMW-L	11	0.046*	0.06	9	0.16	0.06
	TRA	0	–	–	0	–	–
	PMW-U	n.p.	–	–	n.p.	–	–
Ocotea monteverdensis	PMW-L	0	–	–	0	–	–
	TRA	n.p.	–	–	n.p.	–	–
	PMW-U	14	0.0013**	0.25	8	0.052	0.21
Ocotea whitei	PMW-L	1	–	–	1	–	–
	TRA	10	0.95	0.0001	7	0.21	0.14
	PMW-U	n.p.	–	–	n.p.	–	–
Myrcianthes 'black fruit'	PMW-L	10	0.092	0.08	8	0.036*	0.22
	TRA	5	0.94	0.0002	5	0.89	0.001
	PMW-U	n.p.	–	–	n.p.	–	–

(*) = $P < 0.05$; (**) = $P < 0.05$ when corrected for multiple comparisons; the Bonferroni corrected values are 0.0042 (=0.05/12) and 0.005 (=0.05/10) for the two analyses respectively.

also did not produce fruit each year. Individuals of these species were highly synchronous within the population resulting in '*monteverdensis* years' (2007, 2010) and 'black fruit years' (2006, 2008). The other two alternative fruit species, *N. salicina* and *O. floribunda*, produced fruit in each year of the study but not in adequate quantities for sufficient food each year. Therefore, all four of these species together provide food for the bellbird, while the fruit production of any single species is not sufficient over the long term.

These four species of trees are primarily spatially distinct between the upper and lower sub-zone areas, with the exception of *O. floribunda*. *Ocotea monteverdensis* is mostly found in the PMW-U sub-zone, *O. floribunda* is principally located in the TRA sub-zone, and *N. salicina* and *M.* 'black fruit' in the PMW-L (Fig. 2). Human alteration of these forests has occurred, which could affect the distribution of these tree species, but we did not encounter any young *M.* 'black fruit' trees in the upper plots, nor any young *O. monteverdensis* in the lower plots, suggesting that this is a natural distribution of the species. Fruit production of these species was generally temporally distinct. The spatial and temporal differences among these species likely contribute to the separate core feeding areas for this frugivorous specialist, as observed over the years during the annual bellbird census (Fig. S1).

The use of multiple core foraging areas by bellbirds is likely a necessity as the bellbird depends upon a varied set of fruit species patchily distributed in the life zone. Since a single core area within the life zone would not produce a consistent food supply year after year, protection of a combination of biodiverse forest entities is necessary.

Of further consideration regarding the conservation of the bellbird is that two of its key food resources are species in jeopardy of extinction. Because of the restricted range of *O. monteverdensis* (Fig. S2), its small population size, and recent rates of deforestation, this tree species has been rated by the IUCN as 'critically endangered' (Joslin *et al.* 2013, IUCN 2016a). Our recent surveys from the air during flowering indicate that only about 750 mature trees remain. Similarly, *N. salicina*, due to its limited range and more recent habitat destruction for development, is considered 'near threatened' (Rohwer 1998, IUCN 2016d). Populations of both *O. floribunda* and *M.* 'black fruit' have also been greatly reduced in the Monteverde Region by forest clearing but have not been quantified to determine their actual status. The interdependence of these threatened seed-dispersing frugivores and their endangered food sources provides a good example of the cascading effects of forest degradation in a forest ecosystem of limited range with multiple mutualisms.

This study shows that there is a high risk of food insecurity for obligate, frugivorous specialists, such as the bellbird. Their 'feast or famine' food resources are limited, unevenly distributed in the landscape, lack consistent annual fruit production, and are highly synchronous in production among individuals within species. In addition to increased foraging time and risk for frugivores due to patchy distribution of food resources, there are challenges posed by the unknown long-term consequences of climate change, fragmentation, and other anthropogenic threats (Pounds *et al.* 1999, Hughes 2000, Rodenhouse *et al.* 2008), especially for avian species in tropical regions (Foden *et al.* 2013, Bregman *et al.* 2014).

Conservation actions should include planting a diverse mix of species and address the length of time to maturity for each of the key fruiting tree species for the bellbird. All four of the significant tree species are only common later in forest succession (Haber *et al.* 2000, W. Haber and C. Guindon, pers. comm.), and the key tree species *O. monteverdensis* may only bear fruit in significant quantity when it is a large, canopy tree. The active planting of mid- to late-successional Lauraceae species, as is being done in current reforestation efforts in Monteverde—should accelerate this succession process and help restore seed banks.

The complexity of frugivory in the tropics may be well represented by the case of the bellbird in Monteverde. The bellbird's

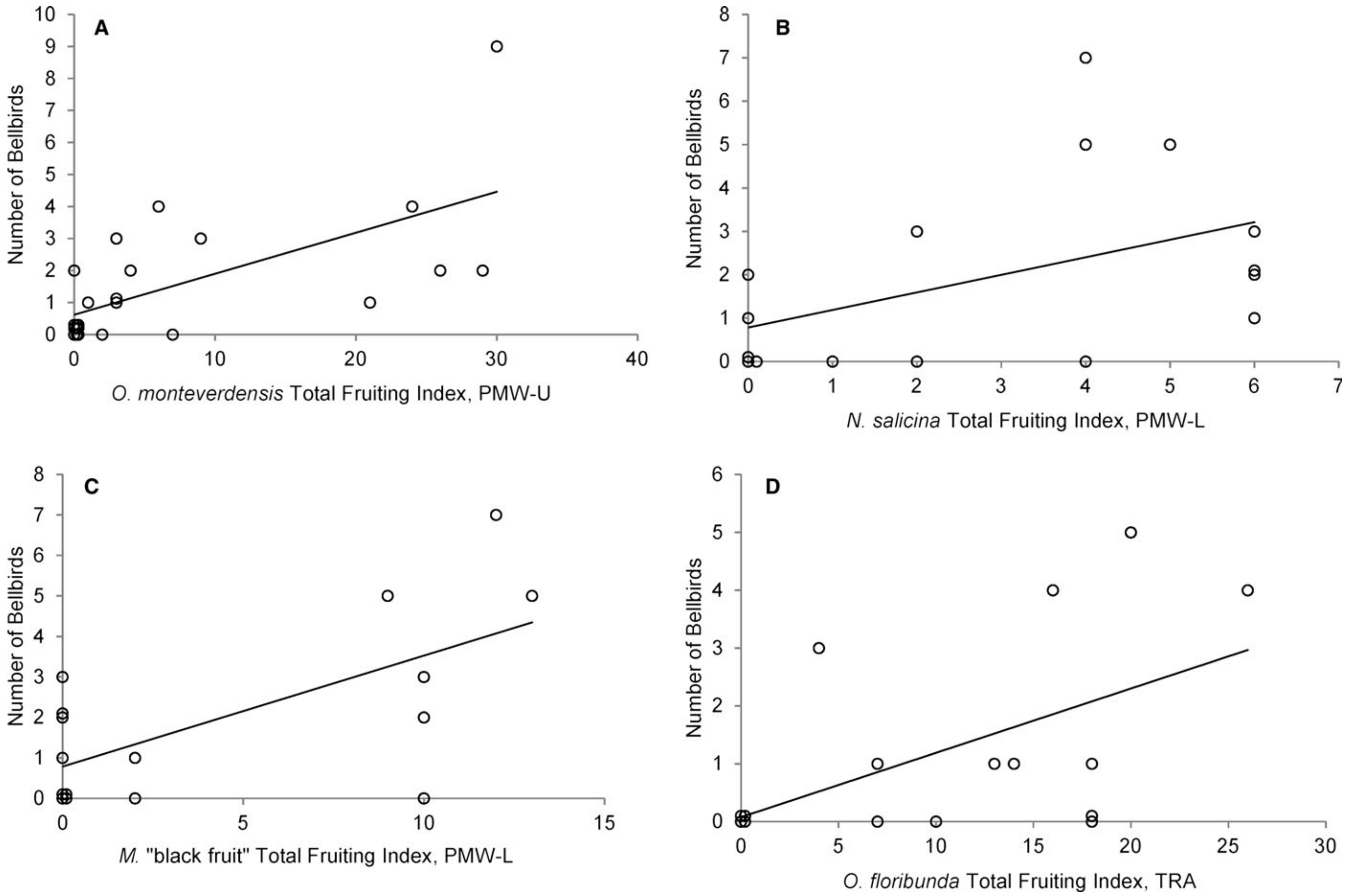

FIGURE 6. The number of bellbirds vs. total fruiting index for individual tree species in particular sub-zones. Except for *O. monteverdensis,* graphs and analyses exclude data from 2007 and 2010 (B, C, D). A small random 'jitter' was added when data points overlap to allow visualization. (A) *Ocotea monteverdensis* in PMW-U (df = 17, $P = 0.0013$, $R^2 = 0.25$); (B) *Nectandra salicina* in PMW-L (df = 11, $P = 0.023$, $R^2 = 0.33$), (C) *Myrcianthes* 'black fruit' in PMW-L (df = 11, $P = 0.036$, $R^2 = 0.22$), (D) *Ocotea floribunda* in TRA (df = 11, $P = 0.027$, $R^2 = 0.33$).

dependence on its ability to track fruit resources over large expanses of area due to the uneven spatio-temporal distribution of food resources highlights the intricate conservation considerations needed to enhance its survival. We do not believe that these conditions are exclusive to the bellbird and anticipate that other species in the tropics face these same challenges. Given the critical function of seed dispersal for forest succession, similar studies of other large frugivorous species would be beneficial in guiding conservation efforts.

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DATA AVAILABILITY

Data available from the Dryad Repository: https://doi.org/10.5061/dryad.v75c9 (Hamilton *et al.* 2017).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

APPENDIX S1. Descriptions of the seven principal species used in this study and list of additional species monitored.

FIGURE S1. Three-wattled Bellbird census data subset which shows the use of alternate regions of the Premontane Wet Life zone in different years.

FIGURE S2. *Ocotea monteverdensis* distribution map.

FIGURE S3. Phenology of flowering and fruiting in six principal species.

FIGURE S4. Effects of DBH and crown class on fruiting in seven species.

TABLE S1. *Characteristics of Lauraceae fruit by species in the study, including records of frugivorous birds eating fruit.*

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