

Changes in the apparent survival of a tropical bird in response to the El Niño Southern Oscillation in mature and young forest in Costa Rica

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Abstract The effects of habitat alteration and climatic instability have resulted in the loss of bird populations throughout the globe. Tropical birds in particular may be sensitive to climate and habitat change because of their niche specialization, often sedentary nature, and unique life-cycle phenologies. Despite the potential influence of habitat and climatic interactions on tropical birds, we lack comparisons of avian demographics from variably aged forests subject to different climatic phenomena. Here, we measured relationships between forest type and climatic perturbations on White-collared Manakin (*Manacus candei*), a frugivorous tropical bird, by using 12 years of capture data in young and mature forests in northeastern Costa Rica. We used Cormack–Jolly–Seber models and an analysis of deviance to contrast the influence of the El Niño Southern Oscillation (ENSO) on manakin survival. We found that ENSO had little effect on manakin survival in mature forests. Conversely, in young forests, ENSO explained 79 % of the variation where dry El Niño events

negatively influenced manakin survival. We believe mature forest mitigated negative effects of dry El Niño periods and can serve as refugia for some species by buffering birds from climatic instability. Our results represent the first published documentation that ENSO influences the survival of a resident Neotropical landbird.

Keywords El Niño Southern Oscillation · ENSO · Frugivore · SOI · Tropical bird

Introduction

Rampant replacement of mature tropical rainforest by regenerating young forest can alter regional hydrology (Salat and Vose 1984), ecosystem services (Foley et al. 2007), species composition (Gascon and Lovejoy 1998), and increase susceptibility to drought and forest fire (Laurance and Williamson 2001). In addition to the detrimental effects of forest clearing, climatic events associated with the El Niño Southern Oscillation cycle (ENSO) can alter tropical precipitation patterns thereby changing water availability, fire regimes and plant communities (Holmgren et al. 2001). Climatic changes associated with ENSO may also affect population-level dynamics of wildlife. For example, ENSO has been correlated with demographic fluctuations of seabirds and migrant landbird populations in temperate and tropical latitudes (e.g., Timmermann et al. 1999; Gergis and Fowler 2009; Sillett et al. 2000; Nott et al. 2002; Butler and Taylor 2005; Wolfe and Ralph 2009). Additionally, the timing of avian lifecycle events may also be affected by ENSO. For example, in Costa Rica, a dry signal associated with El Niño was found to influence the fecundity of Spotted Antbirds (*Hylophylax naevioides*) where individuals delayed the onset of nesting (Styrsky and Brawn 2011).

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Thus, determining the resilience of New World tropical ecosystems to retain functionality in light of the synergistic effects of ENSO and forest conversion is critical given projected increases in climatic variability and forest clearing (Travis 2003).

In the Neotropics, one way that ENSO may affect landbirds is by altering precipitation patterns and the subsequent abundance of fruit and insect food resources relied upon by birds, hence leading to changes in bird behavior (Wolfe and Ralph 2009; Styrsky and Brawn 2011) and survival (Nott et al. 2002). The severity of ENSO's impact on landbirds is probably influenced by differences in resource stability between young and mature tropical forests. For example, early-successional tropical forests typically have a less complex canopy and are often fragmented relative to homogenous mature forest (e.g., Pena-Claros 2003; Wright et al. 1999; Wolfe et al. 2014a) and are, therefore, more susceptible to the drying effects of wind and sun exposure leading to depression of fruit production (Brown and Lugo 1990). During dry periods, tall multi-layered mature forest canopies may serve as understory moisture refugia, thereby providing more predictable and stable fruit resources for birds. Conversely, young-tropical forests may yield more fruit relative to mature forest during wet periods due to increased sunlight penetration through a relatively more porous canopy (Martin 1985; Wolfe et al. 2014a). Capture data from Costa Rica supports this assertion where Red-capped Manakin (*Pipra mentalis*), a frugivorous bird, was captured more often in second growth and primary forest during wet and dry seasons, respectively (Blake and Loiselle 2002). Differences in capture rates across seasons and forest types probably reflect individual birds tracking fruit resources. Given that El Niño is associated with dryer and La Niña with wetter seasonality in the Caribbean (Ropelewski and Halpert 1987; Styrsky and Brawn 2011; Gouirand et al. 2014), we believe the demographics of frugivorous birds are similarly affected by ENSO and forest structure in the Caribbean.

Based on potential relationships between climate, forest structure and fruit availability, we used 12 years of capture data from uneven-aged forests in northeastern Costa Rica to study potential synergistic effects of ENSO and forest type on White-collared Manakin (*Manacus candei*) survival (Φ). The ubiquity, non-migratory behavior and frugivorous diet of the manakin make it an ideal study species to measure the influence of ENSO on population-level demographics between young and mature forest. More specifically, our study tested the following hypotheses:

1. If fruit availability influences White-collared Manakin survival (Φ) and mature forest provides more stable fruit resources relative to young forest, then manakin

survival will be less variable in mature forest when compared to young forest, and, parenthetically,

2. If fruit availability influences White-collared Manakin survival (Φ) and ENSO influences fruit availability disproportionately in young relative to mature forest, then manakin survival will be more strongly influenced by ENSO in young forest.

Materials and methods

Since 1995, four mist-net capture stations (termed Caño Palma, CCC, Parque, and Aeropuerto) have been operated near the village of Tortuguero on the northeast coast of Costa Rica, in Limón Province (10°33'51"N, 83°31'7"W; see Online Resource 1). The study area is dominated by lowland, wet broadleaf tropical forest (Holdridge 1987) that is dissected by canals and rivers that flow east into the Caribbean Sea. The area receives an average rainfall of >5,000 mm per year, making it one of the wettest regions in the country. The majority of the forest lands surrounding the village are protected by the 170,000-ha Tortuguero National Park and Barra del Colorado National Wildlife Refuge.

During the course of the study, each capture station had 10–16 net sites (12 × 3 m, 36 mm mesh), totaling 46 net sites, which were opened 15 min prior to sunrise and operated at least once a week for 6 h throughout the year (Ralph et al. 1993); we used data from the months of August–May. No nets were moved during the course of the study. Stations were at least 2 km apart and nets within each station were usually 40–70 m apart. Stations were located in coastal scrub, primary forest, and mature and young second growth forest.

To eliminate dispersing young from the analysis and reduce the likelihood of transient individuals influencing our results, we only used adult White-collared Manakin capture data from 1995 through 2007. Adult birds were identified by fully ossified skulls and the absence of molt limits (Wolfe et al. 2009, 2010). Although White-collared Manakins do not commonly occur in remote mature forest patches, they do occupy different forest types along the Caribbean coast of Costa Rica (Stiles and Skutch 1989) and can, therefore, be regularly captured in a diversity of forested habitats in our study area. Previous studies in Costa Rica have also captured modest numbers of White-collared Manakins in mature second growth forest (Blake and Loiselle 2002).

Habitat at each station was classified by establishing 15 × 15 m vegetation plots centered at each net site (Online Resource 2). Within each vegetation plot, the following measurements were taken: tree diameter at breast height (DBH), canopy closure, canopy height, soil

Table 1 Twenty Cormack–Jolly–Seber models used in the mark–recapture analysis of White-crowned Manakins (*Manacus candei*) captured between 1995 and 2007 in Tortuguero, Costa Rica

| Model | ΔQAICc | W_i | K |
|---------------------------------------|----------------------|-------|-----|
| Φ (mature(.), young-SOI) p(t) | 0.00 | 0.52 | 15 |
| Φ (mature-SOI, young-SOI) p(t) | 0.77 | 0.35 | 16 |
| Φ (mature(.), young-SOI) p(g*t) | 3.63 | 0.09 | 27 |
| Φ (mature-SOI, young-SOI) p(g*t) | 5.27 | 0.04 | 28 |
| Φ (mature-(t), young-SOI) p(t) | 15.03 | 0.00 | 26 |
| Φ (mature-SOI, young(t)) p(g*t) | 15.70 | 0.00 | 37 |
| Φ (mature-SOI, young-SOI) p(g) | 19.84 | 0.00 | 6 |
| Φ (mature-(t), young-SOI) p(g*t) | 20.05 | 0.00 | 37 |
| Φ (mature(.), young-SOI) p(.) | 20.84 | 0.00 | 4 |
| Φ (mature-SOI, young-SOI) p(.) | 22.05 | 0.00 | 5 |
| Φ (t) p(t) | 25.37 | 0.00 | 23 |
| Φ (g*t) p(t) | 25.64 | 0.00 | 35 |
| Φ (g*t) p(g*t) | 30.60 | 0.00 | 46 |
| Φ (mature-(t), young-SOI) p(g) | 33.38 | 0.00 | 16 |
| Φ (g) p(g) | 34.78 | 0.00 | 4 |
| Φ (g) p(.) | 36.56 | 0.00 | 3 |
| Φ (.) p(.) | 39.12 | 0.00 | 2 |
| Φ (g*t) p(g) | 43.65 | 0.00 | 26 |
| Φ (t) p(.) | 43.89 | 0.00 | 13 |
| Φ (mature-SOI, young(.)) p(g*t) | 46.92 | 0.00 | 27 |

Φ represents survival, p represents recapture probability, t represents time dependency, g represents group (mature and young forest), and SOI an El Niño Southern Oscillation metric which was employed as a time trend. Changes in QAICc relative to the top model are denoted by ΔQAICc , model QAICc weight is denoted by w_i , and the number of parameters is denoted by k . The top three models encompass 95 % of the QAICc weight and were subsequently averaged

moisture, tree density and vertical foliage density. All structural measurements were taken during the month of January, 2008. Although habitat measurements were taken 12 years after the start of the study, our measurements reflect the history of forest cutting (or lack thereof) and differences in vegetative structure at each station. Tree DBH was measured using a DBH tape (trees with a DBH under 5 cm were not measured), canopy height was measured using a laser range finder and canopy closure was measured using a spherical densiometer in four locations within the plot (Online resource 2). Soil moisture was measured by collecting and immediately weighing soil core samples (3 cm deep, 3-1/8" diameter \times 2"; c.8 \times c.5 cm) in four locations within the plot (Online resource 2), drying the samples to constant mass, and weighing them again to calculate percentage moisture. Each soil sample was collected at least 7 h after any precipitation event. Vertical foliage density was quantified following MacArthur and Horn (1969) by etching a 15-cell grid on the viewfinder of a 35-mm camera fitted with a

telephoto lens. The telephoto lens was standardized as a quasi-range-finder (i.e., when an object was in focus, a calibrated chart yielded the approximate distance). Thus, positioning the camera on a tripod and facing it straight up yielded a count of foliage intersecting the grid, at various heights: 0–3 m, 3–15 m and >15 m, which was used to estimate foliage density (for more information regarding habitat measurement data, see Wolfe et al. 2014a; Figd. S3–S6).

Importantly, no forest was cut at our study site after we began capturing birds in 1995. Associations between habitat structure parameters were analyzed by a principal components analysis (PCA) in program R (R Development Core Team 2010; Online Resource 3). The first and second principal components were used to generate an ordination to identify each net and station as being in either young or mature forest (see “Results”; Online Resource 4).

We used the Southern Oscillation Index (SOI) to measure the strength of ENSO phases (El Niño and La Niña collectively) in northeastern Costa Rica. SOI is calculated using sea level pressure differences between Tahiti and Darwin, Australia, and is administered by the National Oceanic and Atmospheric Administration (NOAA) to provide a long-term ENSO index for research purposes. Generally, SOI values above 1 and below -1 indicate La Niña (wet) and El Niño (dry) conditions, respectively, in our study area. Cormack–Jolly–Seber models in the program MARK were used to estimate apparent annual survival (Φ) (hereafter, survival is used instead of apparent survival) of White-collared Manakins (White and Burnham 1999). In total, 20 competitive candidate models were formulated a priori within program MARK’s design matrix where models varied by forest type and SOI values. More specifically, averaged annual SOI values were employed as time trends within models (Table 1). Models were formulated based on the most likely scenarios of ENSO influencing survival in mature and young forest; birds were not grouped by sex based on previous studies showing no substantial difference in survival between sex classes (Blake and Loiselle 2002). The data overdispersion factor (\hat{c}) was generated by taking the quotient of estimated deviance (using bootstrap goodness-of-fit, 1,000 iterations) and global model deviance (Cooch and White 2011). Models were ranked using corrected Akaike’s information criterion (AICc) that was subsequently adjusted to account for any over-dispersion using estimated \hat{c} to produce quasi-AICc (QAICc) values (Cooch and White 2011). The most competitive models encompassing 95 % of the QAICc weight (w_i) were averaged to account for model selection uncertainty. Finally, we conducted an analysis of deviance (ANODEV) in program MARK to determine what percentage of the variation associated with manakin survival in young and mature forest was explained by SOI.

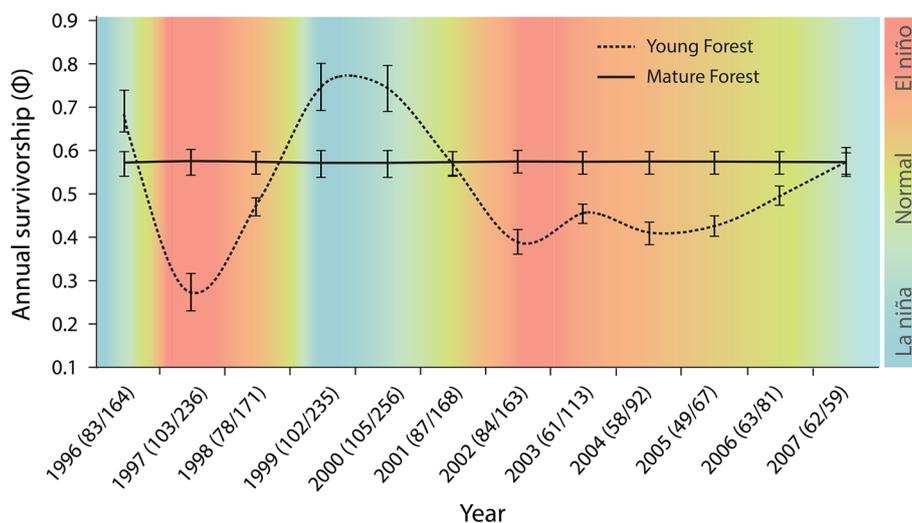


Fig. 1 White-collared Manakin (*Manacus candei*) apparent annual survival (Φ) derived from the averaged top three models encompassing 95 % of the QAICc weight (w_i); annual survival is grouped by young and mature forest with standard error bars. Values in parentheses after the date refer to the number of captures in mature and

young forest, respectively; captures during 1994, the first year of the study (53/126), are not shown. The Southern Oscillation Index (SOI), an El Niño Southern Oscillation metric, was added for comparative purposes. Data are from birds captured near Tortuguero, Costa Rica, from 1995 through 2007

Results

Based on our principal components analysis of habitat structure classification, we categorized each net site and station as being in either mature or young forest. The first principal component explained 41 % of the variation and indicated a strong positive association with mature forest characteristics (increased DBH, canopy height, canopy closure, soil moisture and foliage density >15 m) and a negative association with young forest characteristics (tree density, foliage density 0–3 m and foliage density 3–15 m; Online Resource 3). Based on the first principal components' high amount of variation explained and biologically meaningful loadings, we used the first principal component to separate 'mature' (positive values) from 'young' (negative values) forest types. In general, our young forest categorization was comprised of all nets in coastal scrub and second-growth forest that we estimated to be younger than 30 years, while our mature forest categorization included all nets in primary forest and second-growth forest older than 30 years. Additionally, young forest and mature forest nets were typically grouped by station (except for three young net sites associated with the predominantly mature Parque station; Online Resource 4). Because birds residing within a station were captured in multiple nets over the course of the study, and the vast majority of nets within a single station reflected the same habitat type, we classified each station as either young (AERO and CCC) or mature (PARQ and TORT) forest.

In total, we captured 1,419 individual birds representing 1,931 total captures in young forest and 677 individual

birds representing 988 total captures in mature forest during the course of the study (1995 through 2007). The top three manakin survival models included 96 % of the QAICc weight (w_i) from the next most competitive model, suggesting that the top three models yielded superior explanatory power relative to all other candidate models. Additionally, our estimated \hat{c} value was 1.71, indicative of moderately-low data overdispersion. All three top models contained an El Niño Southern Oscillation metric (SOI) associated with manakin survival in young forest (Table 1). Conversely, two of the three top models did not associate SOI with survival in mature forest; all three top models were subsequently averaged to generate estimates of manakin survival. In general, we found remarkably stable survival in mature forests (Fig. 1) as exemplified by overlapping survival standard error values during the most dramatic El Niño and La Niña years (1997 and 1999), and little variation among all other years (Φ range 0.520–0.562). By contrast, manakin survival estimates from young forest were highly variable with non-overlapping standard errors during El Niño and La Niña years of 1997 and 1999 (Fig. 1; Online Resource 5), and relatively high variation among all other years (Φ range 0.270–0.750). However, by averaging the top three models, which included time-independent parameters associated with mature forest survival, associations between manakin survival in mature forest and ENSO may have been dampened. To examine the potential dampening effects of model averaging, we visualized the second most competitive model which had SOI associated with mature and young forest survival to illustrate that our findings are

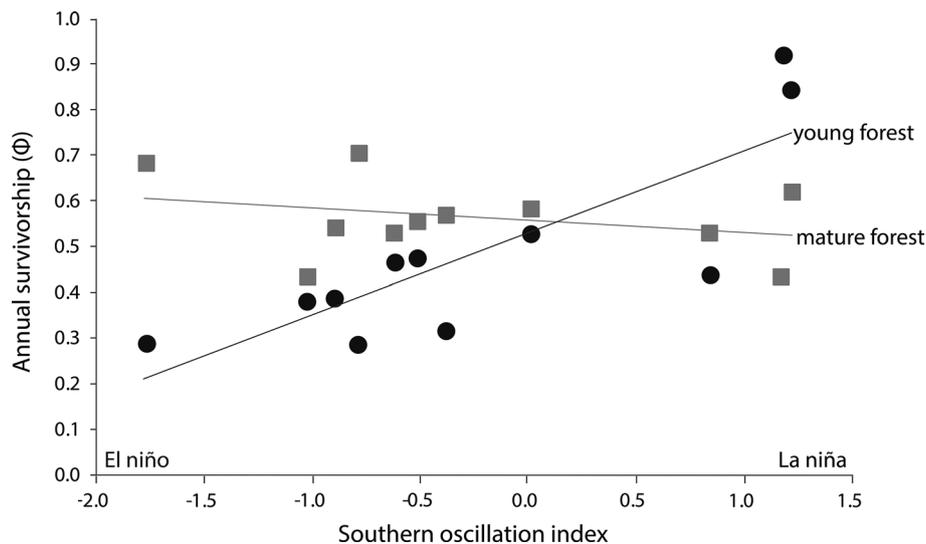


Fig. 2 Ordinary least squares regression between the Southern Oscillation Index (SOI), an El Niño Southern Oscillation metric, and annual survival estimates (Φ) of White-collared Manakins residing in young and mature forest. Estimates of survival were derived from a time-dependent (no SOI included) MARK model: $\Phi(g^*t) p(g^*t)$.

There is a positive correlation between young forest survival and SOI (Adj $R^2 = 0.65$, $p = 0.002$); conversely, no correlation was detected between mature forest survival and SOI (Adj $R^2 = 0.01$, $p = 0.35$). Data are from birds captured near Tortuguero, Costa Rica, from 1995 through 2007

robust and manakin survival is more stable in mature forest relative to young forest (see Online Resource 6). The ANODEV indicated that SOI explained 79 % of the variation among manakin survival in young forest, and only 1 % of the variation among manakin survival in mature forest.

To further explore and visualize relationships between manakin survival, forest type and ENSO, we used ordinary least squares (OLS) regression in program R to correlate SOI values with survival estimates derived from the time-dependent MARK model without an ENSO metric [$\Phi(g^*t) p(g^*t)$] (Fig. 2). We found significant positive relationships between young forest survival and SOI (Adj. $R^2 = 0.65$, $p = 0.002$); conversely, no correlation was detected between mature forest Φ and SOI (Adj. $R^2 = 0.01$, $p = 0.35$). Next, we employed an analysis of covariance (ANCOVA) in program R to test for differences between mature and young forest OLS models. The ANCOVA analysis yielded significant differences between manakin survival in young and mature forest ($p < 0.001$) where regression slopes for manakins in young forest were significantly steeper than slopes in mature forest.

Discussion

Based on habitat classification and the inclusion of an El Niño Southern Oscillation (SOI) metric, our analysis yielded two important results: first, mature forest manakin survival was more stable (yet lower during wet La Niña years) when compared to populations in young

forest. Second, El Niño and its associated dry weather more strongly influenced young forest manakin survival relative to mature forest. Both of these findings support our two hypotheses that manakin survival in young forest was more variable and subject to climatically induced change. While only one of the three top candidate models contained an SOI metric associated with manakin survival in mature forest, we believe the association between SOI and mature forest demographics represents a small effect, if any, because the inclusion of an SOI metric only accounted for 1 % of the variation in mature forest survival, and estimates did not vary widely between major El Niño and La Niña events (1997 and 1999) (Fig. 1; Online Resource 6). Conversely, SOI accounted for 79 % of the variation among manakin survival in young forest coupled with widely varying estimates during major El Niño and La Niña events (1997 and 1999; Fig. 1). Based on these findings, our results represent the first published documentation that ENSO influences survival of a resident tropical landbird.

Because Cormack–Jolly–Seber models provide apparent survival estimates (often incapable of differentiating immigration and emigration from birth and death), changes in young forest survival in relation to ENSO may not represent accrued mortalities but local movements in and out of the area, although long movements appear to be rare for the species (Blake and Loiselle 2002). Either way, accrued mortalities or climatically induced dispersal represent biologically meaningful events. These findings are concordant with similar studies that documented differences in avian survival between degraded and pristine tropical forest

(Ruiz-Gutiérrez et al. 2008), and frugivore famine during dry periods associated with ENSO in Central America (Wright et al. 1999). Here, we unify previous findings and demonstrate that differences in manakin survival between forest types may be exacerbated by ENSO.

Ultimately, we believe that stable survival in mature forest probably resulted from climatic buffers associated with a larger and more complex canopy, coupled with an inherently moist understory. Conversely, ENSO in young forest may represent a climatically driven “boom/bust” scenario of manakin population dynamics at our study site. White-collared Manakins prefer second growth and are probably adapted to fluctuations in food resource availability unlike other manakin species that typically avoid young forest (Blake and Loiselle 2002). In general, our survival estimates from young forest were quite variable relative to previously published estimates, while mature forest estimates ($\Phi = 0.56$) were substantially lower than previously reported. For example, Blake and Loiselle (2002) estimated adult White-collared Manakin annual survival to be 0.75 in young second growth at La Selva, Costa Rica. Similarly, Johnston et al. (1997) found that adult female White-bearded Manakins (*Manacus manacus*) yielded similarly high estimates ($\Phi = 0.74$) in second growth forest in Trinidad. Differences between high survival in second growth in La Selva and Trinidad, and low survival in mature forest in Tortuguero may reflect landscape variation in survival (Wolfe et al. 2014b), more salubrious habitat at their respective study sites, or simply that *Manacus* spp. survival is typically higher in second growth during wet years despite being relatively more stable in mature forest.

Nonetheless, we believe that variation in manakin survival between forest types furthers our understanding of why certain species are sensitive to habitat alteration. For example, mature forest obligate species documented to be sensitive to forest loss may be incapable of persisting in regenerating forest where food resources are more subject to climatically induced variation (Sekercioglu et al. 2002). We suggest future studies directly measure associations between climate, food availability and subsequent changes in avian survival across variably aged forests. Such studies will provide insights into when bird communities in young forest approach the demographic stability of their mature forest counterparts (Powell et al. 2013).

The interactive effects of forest structure and climatic instability are obviously complex. Climatic refugia, such as mature tropical forest, may be important for many resident tropical bird species when considering the decreasing availability of mature forest coupled with increases in the severity of El Niño (Timmermann et al. 1999; Sillett et al. 2000; Gergis and Fowler 2009). Our results coupled with previous findings (e.g., Jetz et al. 2007) suggest that frugivorous

tropical bird survival is sensitive to the synergistic effects of habitat change and climatic variability.

Author contribution statement JDW and CJR conceived and designed the project design. PE facilitated data collection and provided editorial advice.

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