COMMUNITY COMPOSITION AND ANNUAL SURVIVAL OF LOWLAND TROPICAL FOREST BIRDS ON THE OSA PENINSULA, COSTA RICA

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Resumen. – Composición de la comunidad y la supervivencia anual de las aves de los bosques tropicales de tierras bajas en la Peninsula de Osa, Costa Rica. – La deforestación tropical ha dado lugar a muchos paisajes donde los bosques existen en forma de parches de diferente tamaño pero a la vez, estos están conectados dentro de un paisaje dominado por humanos. Entender las implicaciones de estos paisajes para la dinámica de la biodiversidad y la población es hoy en día un gran reto para la biología de la conservación tropical. Hemos examinado la composición de la comunidad y la supervivencia anual de las aves en un paisaje parcialmente deforestadas en la Península de Osa de Costa Rica, que es una región de alta biodiversidad y de creciente preocupación para su conservación. Nuestro estudio se basó en un estudio de siete años de redes de niebla en un terreno de 3 ha y un año entero de conteo de puntos. Estos recuentos se llevaron a cabo en dos tipos de hábitat: un paisaje fragmentado, con una mezcla de parches de bosque y áreas de agricultura abierta, y un parche de 100 ha de bosque maduro. La riqueza de especies estimada, tiende a ser mayor en el paisaje fragmentado (116 vs 89), probablemente porque este paisaje todavía cuenta con cubierta forestal moderada; lo cual da protección a las especies que toleran algo de deforestación, así como a las especies que prefieren hábitats más abiertos. En consecuencia, sólo 43 especies fueron detectadas en los hábitats fragmentados, mientras que en el bosque sólo fueron detectadas 22. El último resultado sugiere que algunas especies de bosque han sido capaces de sobrevivir en esta región parcialmente deforestadas, probablemente debido a la presencia de estos grandes parches de bosque y la conectividad entre ellos. Nuestro estudio también incluye un número moderado de *Habia atrimaxillaris*, en peligro de extinción que fue detectado principalmente en las zonas de mayor cubierta forestal. Para ocho Passerines comunes, la supervivencia anual aparente de las aves adultas oscilaron entre un mínimo de 0.35 ± 0.07 (SD) para *Mionectes oleagineus* hasta un máximo de 0.81 ± 0.11 para *Thamnophilus bridgesi* con un promedio de 0.63 ± 0.05 en todas las especies. Esta tasa media es similar a otros estudios que han estimado la supervivencia de aves utilizando técnicas de redes de niebla, marcado y recaptura en otros lugares del trópico. Nuestro estudio proporciona una de las primeras evaluaciones de la composición de la comunidad aviar y la supervivencia en los paisajes rurales de la Península de Osa. Los objetivos de conservación necesitaran considerar este tipo de paisaje y se encuentran en discusión estudios adicionales que pudieran incrementar el conocimiento de la región.

Abstract. – Tropical deforestation has resulted in many landscapes where forests exist as patches of varying size and connectivity within a human-dominated landscape. Understanding the implications of these landscapes for biodiversity and population dynamics is now a major challenge for tropical conservation biology. We examined community composition and annual survival of birds in a partially deforested landscape on the Osa Peninsula of Costa Rica, which is a region of high biodiversity and

increasing conservation concern. Our study was based on seven years of mist-netting surveys on a 3 ha plot and a single year of point counts. These counts were conducted in two habitat types: a fragmented landscape with a mix of forest patches and open agricultural areas, and an approximately 100 ha patch of mature forest. Estimated species richness tended to be higher in the fragmented landscape (116 vs 89), likely because this landscape still contains moderate forest cover thus supporting species that tolerate some deforestation as well as species that prefer more open habitats. Accordingly, 43 species were only detected in the fragmented habitats while 22 were only detected in forest. The latter result suggests that some forest specialists have been able to persist in this partially deforested region, likely because of the presence of larger forest patches and connectivity between them. Our surveys also included moderate numbers of the endangered Black-cheeked Ant-Tanager (*Habia atrimaxillaris*), which was primarily detected in areas of greater forest cover. For eight common passerines, apparent annual survival of adults ranged from a low of 0.35 $\pm$ 0.07 (SD) for Ochre-bellied Flycatchers (*Mionectes oleagineus*) to a high of 0.81 $\pm$ 0.11 for Black-hooded Antshrikes (*Thamnophilus bridgesi*) with an average of 0.63 $\pm$ 0.05 across all species. This average rate is similar to other studies that have estimated survival with mist-net mark-recapture techniques elsewhere in the tropics. Our study provides one of the first assessments of avian community composition and survival in countryside landscapes on the Osa Peninsula. Conservation goals will increasingly need to consider such landscapes and we discuss additional studies that could further our knowledge in the region. *Accepted 4 August 2011.*

INTRODUCTION

The Neotropics contain a vast diversity of species and habitats, including approximately forty percent of the global avifauna (Collar *et al.* 1997). Despite the importance of tropical forests for the maintenance of biodiversity and ecosystem services, unprecedented levels of deforestation threaten many tropical forest communities (Malhi *et al.* 2008, Wright 2005). A common scenario in many regions today is that tropical forests exist as a fragmented patchwork with stands of varying size and age embedded within a human-dominated agricultural landscape (Daily 1997, Laurance & Bierregard 1997, Daily *et al.* 2001). How populations respond to these changes can be quite variable depending on the taxa examined. Some bird groups appear to be particularly sensitive to fragmentation (e.g., understory insectivores) and are rarely found outside of large forested areas (Canaday 1996, Sekercioglu *et al.* 2002, Sigel *et al.* 2006), while others are less susceptible and able to use fragmented habitats to varying degrees depending on the size and connectivity

among forest fragments (Gascon *et al.* 1999, Daily *et al.* 2001, Uezu *et al.* 2005, Sekercioglu *et al.* 2007). Development in many tropical regions is expected to continue and we need further study on avian community structure in countryside landscapes, as well as the consequences of these landscapes for population dynamics.

Costa Rica is recognized as a country with exceptional biodiversity and while there is a considerable network of protected areas, there has also been notable deforestation over the past few decades. In 1991 for example, 29% of the land cover of Costa Rica was closed forest and only about 30% of this amount was protected by conservation policies (Sanchez-Azofeifa *et al.* 2001). Most landscapes outside of protected areas are managed for human activities and forests have become increasingly fragmented. Costa Rica has a relatively rich history of bird study compared to other tropical countries with numerous studies on avian community structure (e.g., Young *et al.* 1998, Blake & Loiselle 2001, Sigel *et al.* 2006) and demography (e.g., Ruiz-Gutiérrez *et al.* 2008, Young *et al.* 2008, Woltmann &

Sherry 2011). Many of these studies have been conducted in more pristine regions of Costa Rica, but there has recently been a greater emphasis on understanding avian use of partially disturbed countryside habitats (Daily *et al.* 2001, Matlock *et al.* 2002, Sekercioglu *et al.* 2007). Approximately 75 percent of the country's native landbirds have been shown to use deforested areas as long as forest patches with canopy trees are maintained (Stiles 1985).

The bird communities of the Osa Peninsula along the southwest Pacific Coast of Costa Rica have received little study, in part due to the remote nature of the region. Although only 1093 km², the Osa Peninsula has exceptional species diversity, high endemism and contains one of the largest intact regions of lowland rainforest in Mesoamerica (Barrantes *et al.* 1999). Approximately 375 bird species are believed to inhabit the Osa Peninsula for at least part of the annual cycle (Barrantes *et al.* 1999). Corcovado National Park (CNP) covers approximately 39% of the peninsula and protects large tracts of mature tropical forest. Considerable development and forest fragmentation has occurred outside of the park to the east and north in recent decades (Sanchez-Azofeifa *et al.* 2002). Our objectives in this study were two-fold. First, we report on the bird communities in a fragmented region of the Osa Peninsula approximately 10 km northwest of CNP. This region still contains larger tracts of forest but is becoming increasingly fragmented, primarily for agriculture. Our aims were to provide a baseline for comparisons with the bird communities of CNP as well as future comparisons outside of the park as habitat fragmentation continues. This component of our study included a comparison of the bird communities using larger stands of forested habitat with those using a more fragmented area with small patches of forest interspersed amongst open agricultural areas. We then use

data from 8 years of mist-netting on a single study plot to provide information on annual survival of species detected in countryside landscapes of the Osa Peninsula.

METHODS

Study area. The study was conducted during late March through late April of 2002 through 2008. The Osa Peninsula consists of three major life zones; tropical wet forest, premontane wet forest and tropical moist forest (Holdridge 1967). Annual temperatures and rainfall on the peninsula average 27°C and 5500 mm, respectively, with a dry season from December through April and a wet season from May through November. Our study area (08°41'N, 83°41'W) was located ~ 10 km north of Corcovado National Park and ~ 5 km west of the town of Drake Bay. Average elevation on the study area was about 25 m a.s.l..

Point counts. Our objective with point counts was to examine species representation in order to document the bird community of countryside habitats outside of Corcovado National Park. While the methods we used allow us to estimate community composition, we were unable to estimate species density. Point counts were conducted in 2008 by a single observer (SW) who had several years of experience identifying the bird community in the region by sight and sound. The point counts were conducted over two 1 km long transects. The 'forest' transect extended through a large patch of older secondary forest and primary forest to the southwest of the mist-net study area. Although this forested patch was large relative to the local area (~ 100 ha of nearly continuous forest), it would still be considered fragmented relative to the much larger continuous forests of CNP. The 'fragment' transect extended through a landscape containing patches or strips of smaller

and younger secondary forest, interspersed with open agricultural areas. Forest cover within 100 m of the centre of the point count circle was always greater than 90% on the forest counts (mean = 96%, SD = 4.3, n = 15) and less than 80% on the fragment counts (mean = 63%, SD = 13.7, n = 12).

All point counts were conducted between 06:00 h and 09:00 h from 13–27 April 2008. Because of difficulties in identifying birds at long distances in tropical forests, we only set a fixed radius of 40 m and noted all individuals by species that were detected within this radius over a 10 min period. Prior to initiating each count, the observer waited 5 minutes to avoid any bias associated with disturbing individuals upon entering the count area. Each count location was surveyed two to three times during the two week period. Fly-overs were included in the count if they passed over the 40 m radius circle but were only included in the appendix species list and not the habitat analyses because they would not necessarily have used that habitat. Point count data was summed across counts within a habitat to provide total species, number of individuals detected, and the proportion of the total detections represented by each species.

Mist-netting. Mist-netting was conducted on a 3 ha study area that is typical of the habitat structure within the region: secondary forest (15–25 years of age) with two small open areas used for banana and pineapple plantations (each approximately 25 x 25 m). Habitats to the east of the study area contained a mix of secondary forest fragments and open, agricultural areas, while to the south and west was a larger expanse of secondary and primary forest. The study area bordered a small ecotourism lodge along the coast to the north, which also had a mix of open habitat and secondary forest fragments. The mist-nets (12 x 2.6 m, 36 mm mesh) were set at

ground level and with a few exceptions, extended in a north-south linear design through the study site. Twelve to fifteen mist-nets were opened each day at dawn and operated for approximately 6 h. All captured birds were identified, sexed and aged when possible, and fitted with a numbered aluminum band to allow individual recognition. We also measured wing length, mass, and breeding condition based on the presence of a brood patch or cloacal protuberance. Hummingbirds were only banded from 2004 through 2007 but data on recaptured individuals were recorded in 2008.

Species richness, diversity, and community similarity. Measures of species richness, diversity, and community similarity were calculated using ESTIMATES software (Colwell 2009). Species richness was calculated using the Abundance-based Coverage Estimator (ACE, Chao & Lee 1992, Chazdon *et al.* 1998). Species diversity was calculated using Shannon's Index (Magurran 2004), which provides a combined measure of the abundance and evenness among species in the different habitats. The index typically ranges between 1.5 and 5, with higher values of the index indicating greater diversity. To estimate similarity of the avian community between forest and fragment point count transects we used the Chao-Sorensen abundance based similarity index (Chao *et al.* 2005). Classical indices of similarity, such as the Sorensen and Jaccard indices, are highly sensitive to sample size especially if rare species are present. The Chao-Sorensen abundance based similarity is a probabilistic derivation of the Sorensen index that compensates for the presence of unseen, shared species among samples and helps to correct for the under-sampling bias of the classical approaches (Chao *et al.* 2005). Values of this index range between 0 (no shared species) and 1 (complete species overlap). Comparisons of richness, diversity, and similarity were

only conducted using the point count data because the mist-net study area was an intermediate habitat type that would be difficult to directly compare to either point count habitat. However, the mist-netting capture information was used to assist in documenting the bird community of the region, and abundance based on captures is presented in Appendix 1.

Survival analysis. We used Cormack-Jolly-Seber (CJS) models in program MARK (White & Burnham 1999) to estimate apparent annual survival and recapture for resident species based on our mist-net data. Eight species of passerines had sufficient numbers of captures and recaptures to provide an estimate of annual survival. Survival estimates based on mist-netting data include information from resident, after hatch year adults and hatch year birds, which often include transients that are only passing through the study area. Drawing estimates from the interval after first capture can be problematic because transient individuals may no longer be available for capture during subsequent intervals. Time-since-marking (TSM) models can account for this effect by allowing for a different survival estimate between the first period after initial capture (φ_1) and all subsequent periods (φ_2) (Pradel *et al.* 1997). Accordingly, we focus our interpretation of the survival estimates from the second group (φ_2). For the two manakin species, we only estimated survival rates for females because males had very low recapture rates (< 10%) likely because they were on leks during the period of study and therefore not available to be recaptured using systematic mist-netting. In their first year, juvenile manakins resemble adult females and so the data for these species were only included if they were known females at first capture based on the presence of a brood patch indicating breeding activity. With the exception of Orange-crowned (*Manacus aurantiacus*) and

Red-capped Manakin (*Pipra mentalis*), we had insufficient data to examine sex-specific survival rates.

For the TSM models, the recapture parameter was either assumed to be constant or allowed to vary depending on an index of low, medium or high effort each year based on the number of mist-netting hours. For each species, we used the median c-hat method to estimate over-dispersion of the data, and thus the model fit. The quasi Akaike's Information Criterion for small samples (QAICc) was used to evaluate support for the constant or effort based recapture estimate (Burnham & Anderson 2002). The top recapture model was then used to estimate survival.

RESULTS

Bird community–point counts. In 2008, we performed 63 point counts (33 in forest habitat, 30 in fragmented habitat) and recorded 1290 individuals with 569 individuals from 76 species recorded on forest counts and 721 individuals from 97 species recorded on the fragment counts (Table 1). Ninety-two percent of these individuals were identified to species (120 species in total). Fifteen of these species were Neotropical migrants and 105 were residents, austral migrants or elevational migrants within Central America.

The ACE measure of species richness was 89 in the forest habitat, 116 in the fragmented habitat and 134 for both habitats combined. The Shannon Index of species diversity was 3.75 ± 0.02 (SD among runs) for the forest habitat and 3.87 ± 0.02 for the fragmented habitat. Thus, our results showed slightly higher species richness and diversity in the fragmented habitat. Of the 120 observed species, 58 were present in both habitats and the Chao-Sorensen abundance based similarity index between the forest and fragment point counts was 0.73, thus indicating a moderate amount of overlap in the species community

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TABLE 1. Ten most commonly detected species from point count surveys in 2008 on the Osa Peninsula, Costa Rica located in fragmented or forest habitats. Values refer to the percent of total observations in that habitat represented by each species. See Appendix 1 for all species and scientific names.

Point count (fragment)		Point count (forest)	
Swainson's Thrush	8.3	Swainson's Thrush	13.1
Cherrie's Tanager	8.0	Dot-winged Antwren	6.1
Bananaquit	6.5	Lesser Greenlet	5.4
Orange-chinned Parakeet	5.6	Chestnut-backed Antbird	5.2
Lesser Greenlet	4.7	White-shouldered Tanager	3.8
White-shouldered Tanager	4.2	Tawny-crowned Greenlet	3.8
Dot-winged Antwren	3.5	Orange-billed Sparrow	3.1
Eastern Kingbird	3.3	Blue-crowned Manakin	3.1
Red-legged Honeycreeper	3.0	Black-cheeked Ant Tanager	2.7
Rufous-tailed Hummingbird	2.6	Red-capped Manakin	2.5

between the two habitats. Twenty-two species were only detected on the forest counts, while 43 were only detected on fragment counts. Species commonly detected only in forest included Tawny-crowned Greenlet (*Hylophilus ochraceiceps*, n = 20), Blue-crowned Manakin (*Lepidothrix coronata* , n = 16), and Red-capped Manakin (n = 13) while species commonly detected only in the fragmented habitat include Cherrie's Tanager (*Rampho-celus costa-ricensis*, n = 53), Orange-chinned Parakeet (*Brotogeris jugularis*, n = 37), Rufous-tailed Hummingbird (*Amazilia tzacatl*, n = 17), and Variable Seedeater (*Sporophila corvina*, n = 14).

Bird community–mist-net surveys. Over the 2002–2008 period, we conducted 17,095 mist-net hours in mid-March to late-April and captured 4790 individuals of 122 species. This included 2511 individuals from 19 Neotropical migrant species although this sample was dominated by Swainson's Thrush (*Catharus ustulatus*), which represented 95% of Neotropical migrant captures. For residents, we captured 2279 individuals of 103 species. Relative to Neotropical migrants, there was far greater diversity in the resident captures with the 10 most common species representing 42% of captures and the 20 most common representing 63% of captures. Forty-two species captured by mist-netting were not detected on point counts, but because of the much greater sampling effort with mist-nets it is difficult to directly compare these two approaches. With both mist-netting and point count data combined a total of 160 species were recorded.

Annual survival. Survival rates were estimated for eight passerines using program MARK. There was little evidence of over-dispersion for any species with the highest c-hat = 1.20 for the Orange-billed Sparrow (*Arramon aurantiirostris*). Models with constant recapture had greater support for six species while including mist-netting effort improved support for the remaining two. Ochre-bellied Flycatchers appeared to have particularly low survival, estimated at 0.35 for resident adults (φ_2), while Black-hooded Antshrikes and Orange billed Sparrows had the highest annual survival rates [φ_2 = 0.81 and 0.77, respectively (Table 2)]. Among the remaining passerines, φ_2 ranged from 0.56 to 0.66. The recapture rate, p, averaged 0.54 with a range from 0.35 to 0.65 (Table 2).

TABLE 2. Annual apparent survival estimates of passerines on the Osa Peninsula, Costa Rica, 2002–2008. For apparent survival estimates, we show results for age 2^+ individuals (φ_2) using a time since marking model and a constant or effort based recapture model depending on which had greater model support (using $QAIC_c$ estimates). In each case, we show the mean $\pm$ SE with the 95% confidence interval in brackets below. n refers to the number of new individuals marked and r refers to the number of individuals recaptured at least once in a subsequent year. *Only female manakins were included in the analysis.

Species		n/r	Recapture model	Annual survival	Mean recapture rate
Ochre-bellied Flycatcher	*Mionectes oleagineus*	120/26	constant	0.35 + 0.07 (0.21–0.53)	0.63 + 0.15 (0.35–0.93)
Black-hooded Antshrike	*Thamnophilus bridgesi*	29/13	constant	0.81 + 0.11 (0.52–0.94)	0.37 + 0.10 (0.21–0.57)
Bicolored Antbird	*Gymnopithys leucaspis*	46/16	constant	0.66 + 0.12 (0.21–0.84)	0.65 + 0.14 (0.38–0.92)
Chestnut-backed Antbird	*Myrmeciza exsul*	52/18	constant	0.62 + 0.11 (0.40–0.80)	0.47 + 0.12 (0.23–0.70)
Wedge-billed Woodcreeper	*Glyphorynchus spirurus*	64/22	constant	0.66 + 0.09 (0.49–0.83)	0.65 + 0.12 (0.42–0.88)
Red-capped Manakin*	*Pipra mentalis*	74/18	effort	0.66 + 0.17 (0.30–0.90)	0.35 + 0.13 (0.10–0.61)
Orange-collared Manakin*	*Manacus aurantiacus*	62/16	constant	0.56 + 0.12 (0.33 - 0.77)	0.66 + 0.14 (0.39–0.93)
Orange-billed Sparrow	*Arremon aurantiirostris*	99/24	effort	0.77 + 0.09 (0.55–0.90)	0.55 + 0.12 (0.32–0.78)

DISCUSSION

Avian community. Our point count and mist-net surveys detected 160 species in a countryside landscape on the northwest portion of the Osa Peninsula. The vast majority of these species were resident landbirds, while a smaller number (n = 24) were confirmed Neotropical migrants that were overwintering, or passing through the Osa Peninsula during spring migration. The most numerous species recorded at this time of year (March/April) was the Swainson's Thrush, which dominated mist-net captures (49% of individuals from all species, 95% of Neotropical migrant individuals) and was the most commonly detected species on point counts in both forest and fragmented habitats. We previously showed that this region is a key spring migratory stopover area for the Swainson's Thrush that ulti-

mately breed in west and central regions of the boreal forest of Canada (Wilson *et al.* 2008a, b).

Estimated species richness and diversity was slightly higher in the fragmented habitat relative to the larger forest patch. This is opposite to the pattern often observed in tropical bird communities, where species richness declines as fragment size decreases, and as the patches become more isolated from larger areas of continuous forest (Gascon *et al.* 1999, Daily *et al.* 2001, Uezu *et al.* 2005). Our findings of higher richness in the fragmented habitats is likely due to the fact that this landscape still had moderate forest cover (mean = 63% cover around point count stations) and larger forest patches were often present near smaller fragments. As a result, this landscape was still selected by forest species that tolerate low to moderate levels of deforestation as well

as species that prefer more disturbed, open habitats. Forty three species were only detected on the fragment transect counts, and because much of the Osa Peninsula historically consisted of continuous forest, abundance of these species have almost certainly increased in the region as fragmentation has increased.

Twenty two species were never detected on counts in the fragmented landscape, including some, such as Blue-crowned Manakin and Red-capped Manakin, that were quite common in the forested habitats. Roberts (2007) also showed that the Red-capped Manakin abundance declined as forest patch size and the amount of forest cover on the landscape decreased in the Sarapiqui region of northeast, Costa Rica. The endangered Black-cheeked Ant-Tanager (IUCN 2009) was also frequently detected on our surveys and was disproportionately observed in the forest habitat, although a few individuals were detected in the fragments. Overall, these results suggest that forest specialists are still present in moderate abundance in larger forest patches (in this case 100 ha), even though the overall landscape is partially deforested. However, it is also possible that the maintenance of stable populations for some of these species requires dispersal from larger areas of continuous forest, a possibility that warrants further study. In the case of the Black-cheeked Ant-Tanager, Corcovado National Park likely provides a stronghold for the global population, however, efforts to maintain large patches of mature forest, as well as the connectivity between forest patches outside of Corcovado, would greatly facilitate conservation efforts for this endangered species.

Although recorded species richness was higher in the fragmented landscape, the species richness of forest habitats in the region may have been underestimated for two reasons. First, our ability to detect individuals was likely lower on the forest counts because of reduced visibility and greater canopy height. This effect would most influence our ability to detect upper canopy and secretive understory species. Additional studies using mist-netting and canopy point counts across a greater range of forest structure would be a useful complement to our study. Second, at only ~100 ha, our study forest patch had likely lost species that require larger forest tracts (e.g., Robinson 1999, Sigel *et al.* 2006, Stouffer *et al.* 2011), and thus likely under-represents the bird communities in large, continuous forests of the Osa Peninsula. Other studies in Costa Rica and elsewhere, have shown that understory insectivores are particularly sensitive to fragmentation (Canaday 1996, Sekecioglu *et al.* 2002), and at La Selva, even the maintenance of a large protected area of older forest (1611 ha) could not prevent the local extinction of some members of this guild (Sigel *et al.* 2006). Several understory insectivores, e.g., Chestnut-backed Antbird (*Myrmeciza exsul*), Black-faced Ant Thrush (*Formicarius analis*), and Streak-chested Antpitta (*Hylopezus perspicillatus*), were still reasonably common in the forest habitat in our study, but a number of other species that are expected to occur in the lowlands of the Osa Peninsula (Stiles & Skutch 1985) were rarely or never detected in our area. Other bird groups that disappear quickly in fragmented areas include large forest raptors and some members of the Cracidae family (Thiollay 2005). Neither group is easily surveyed by point counts due to their low abundance, but targeted surveys in forest patches of varying size would help address the consequences of local deforestation on the Osa Peninsula for these taxa.

Annual survival. Our survival estimates were based on a 7 year data set for seven passerine species, and across these species, the average survival of adults was 0.63 with a standard

deviation of 0.14. Our samples sizes were small for most species, resulting in wide confidence intervals, but the survival rates we observed were comparable to several studies from across the Neotropics that also used mist-net mark-recapture: 0.59 in eastern Ecuador (30 species, Blake & Loiselle 2008), 0.68 in Peru (14 species, Francis *et al.* 1999), 0.56 in Panama (25 species, Karr *et al.* 1990), and 0.65 in Trinidad (17 species, Johnston *et al.* 1997). Studies that use mark-resighting methodology often report higher apparent survival rates, including 0.79 for Ruddy-capped Nightingale Thrush (*Catharus frantzii*) in southern Mexico (Rangel-Salazar *et al.* 2008), 0.74–0.97 for White-ruffed Manakin (*Corapipo altera*) at Las Cruces, Costa Rica (Ruiz-Gutiérrez *et al.* 2008), 0.79 and 0.80 for male and female Chestnut-backed Antbirds respectively, at La Selva, Costa Rica (Woltmann & Sherry 2011), and 0.82–0.85 for Dusky Antbirds (*Cercomacra tyrannina*) in Panama (Morton & Stutchbury 2000). In our case, only the Black-hooded Antshrike and Orange-billed Sparrow had survival rates in the 0.70–0.85 range, while most other species were in the 0.55–0.65 range. Ochre-bellied Flycatchers had a particularly low survival estimate at 0.35 ± 0.07. Blake and Loiselle (2008) reported very similar rates for this species in Ecuador (0.32 ± 0.09), but a considerably higher rate of 0.62 ± 0.07 was observed in Trinidad (Johnston *et al.* 1997). These studies also estimated survival using mist-net mark-recapture but because mist-netting appears to underestimate annual survival for some species, it would be useful to measure rates for these species using mark-resight methods.

Although our knowledge on survival of tropical birds is improving, little is known regarding the degree to which the sexes differ in survival. For manakins, we only estimated survival for females, because males were on leks during the study periods, and thus would not be adequately surveyed with our methods. Apparent survival of female Orange-collared and Red-capped Manakins was 0.56 and 0.66 respectively, which is comparable to the average for the other passerines where both sexes were included. In eastern Ecuador, average adult survival across four manakin species (sexes combined) averaged 0.52 to 0.60 (Blake & Loiselle 2008). Blake & Loiselle (2002) reported higher survival of female over male Red-capped Manakins at La Selva, but no sex-specific differences for White-collared Manakins (*Manacus candei*). There were also no sex-specific differences in annual survival for White-ruffed Manakins at Las Cruces, Costa Rica (Ruiz-Gutiérrez *et al.* 2008), or Band-tailed Manakins in Bolivia (Pearce-Higgins *et al.* 2007).

Hummingbirds were commonly captured in our study, but the recapture rate was very low, and prevented a proper examination of survival. For the two most commonly captured hummingbirds (Charming Hummingbird *Amazilia decora*, Long-billed Hermit *Phaethornis superciliosus*), only 7% of individuals marked in one year were recaptured in a subsequent year. For comparison, the recapture rate for the five most common passerine species was 25%. Annual survival rates for hummingbirds are generally not well known, particularly in the tropics, and further study is needed. To our knowledge, most studies that have estimated survival of hummingbirds have used systematic mist-netting, but in our study, this method was inadequate due to the very low rates of recapture. Nectarivores typically have high movement in response to variable food sources, which may contribute to their low recapture rates (Parker *et al.* 2006). We also suspect that the agility of hummingbirds may allow for greater avoidance of nets, and this might contribute to a trap-shy response after first capture even if marked individuals are available for recapture within the study area.

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Future studies. To our knowledge, this is the first study of avian community composition on the Osa Peninsula since Orians' survey in the 1960s (Orians 1969), and the only study to measure survival rates of resident birds in the region. Our results provide much needed information that could be used to develop additional studies, and we suggest two areas in particular that would be valuable for future research. First, we recommend a study conducted over a broader spatial scale, to look at avian use of countryside habitats on the Osa Peninsula. This study could adopt a combination of ground and canopy based point counts, distance sampling, and mist-netting surveys to sample bird communities and densities along a gradient of fragmentation that ranged from the large and continuous forests of Corcovado National Park, down to the small forest fragments in the most deforested regions. Two types of demographic studies would be useful to further advance our knowledge of survival for the resident bird community. First, intensive color-marking for a few species would provide more detailed estimates of survival in relation to fragmentation, and if combined with visual re-sighting, would allow us to estimate seasonal movements, potentially including the degree to which species move among forest patches of varying size. In our study area, these projects would be feasible with the more common passerines, such as Ochre-bellied Flycatcher, Orange-billed Sparrow, Chestnut-backed Antbird, and potentially even Black-cheeked Ant-Tanager, which could provide very useful information for conservation efforts on this species. The only other demographic information collected on Black-cheeked Ant-Tanagers was by Sandoval & Gallo (2009), who provide nest records at a site on the eastern portion of the peninsula near Puerto Jimenez. Additional studies on survival of Neotropical hummingbirds would also be useful, because the very low recapture rates are concerning

and may lead to unreliable estimates of survival. Constant effort mist-netting appears to be a poor method for estimating annual survival of Neotropical hummingbirds, and alternative methods, such as target netting, should be considered.

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APPENDIX 1. Rank abundance of all captured or detected species (% of total) on the Osa Peninsula based on mist-netting (2002–2008) and point count surveys (2008). Mist-netting was primarily conducted in secondary forest habitats that were intermediate in age and structure to the forest (> 90% forest cover within 100 m of the plot centre) and fragmented (< 80% forest cover) habitats sampled by point counts. Status is defined as N for Neotropical migrants that breed in North America, R for residents (includes sedentary species, Austral migrants and elevational migrants), and B for species that could include individuals from either category. The status of black swifts are uncertain in this region.

Species		Status	Mist-net	Point-count (forest)	Point-count (fragment)
Great Tinamou	*Tinamus major*	R		0.19	
Little Tinamou	*Crypturellus soui*	R			0.15
Black Vulture	*Coragyps atratus*	R			0.15
Yellow-headed Caracara	*Milvago chimachima*	R			0.60
Barred Forest Falcon	*Micrastur ruficollis*	R	0.04		
Double-toothed Kite	*Harpagus bidentatus*	R	0.02		
Tiny Hawk	*Accipiter superciliosus*	R	0.06		
Mangrove Black Hawk	*Buteogallus subtilus*	R			0.15
Broad-winged Hawk	*Buteo platypterus*	N			0.15
Roadside Hawk	*Buteo magnirostris*	R			0.15
Short-billed Pigeon	*Columba nigrirostris*	R		1.75	0.75
Ruddy Ground Dove	*Columbina talpacoti*	R	0.08		
Blue Ground Dove	*Claravis pretiosa*	R	0.02		
White-tipped Dove	*Leptotila verreauxi*	R	0.06		0.60
Gray-chested Dove	*Leptotila cassinii*	R	0.56	1.95	0.30
Ruddy Quail Dove	*Geotrygon montana*	R	0.27		
Scarlet Macaw	*Ara macao*	R		0.58	1.06
Orange-chinned Parakeet	*Brotogeris jugularis*	R			5.58
Red-lored Parrot	*Amazona autumnalis*	R		0.78	0.30
Mealy Parrot	*Amazona farinosa*	R		1.17	1.66
Squirrel Cuckoo	*Piaya cayana*	R		0.39	
Black Swift	*Cypseloides niger*	R			1.81
White-tipped Sicklebill	*Eutoxeres aquila*	R	0.02		
Bronzy Hermit	*Glaucis aenea*	R	0.23	0.39	0.30
Band-tailed Barbthroat	*Threnetes ruckeri*	R	1.06	0.39	
Long-billed Hermit	*Phaethornis superciliosus*	R	1.75	1.17	0.15
Stripe-throated Hermit	*Phaethornis longuemareus*	R	0.48	0.19	0.30
Scaly-breasted Hummingbird	*Phaeochroa cuvierii*	R			0.15
White-necked Jacobin	*Florisuga mellivora*	R	0.17	0.19	0.30
Violet-crowned Woodnymph	*Thalurania colombica*	R	0.90	0.58	
Blue-throated Goldentail	*Hylocharis eliciae*	R	1.38	0.58	0.60
Charming Hummingbird	*Amazilia decora*	R	2.17	2.14	1.06
Snowy-bellied Hummingbird	*Amazilia edward*	R	0.02		
Rufous-tailed Hummingbird	*Amazilia tzacatl*	R	0.98		2.56
Purple-crowned Fairy	*Heliothryx barroti*	R	0.02		0.15
Slaty-tailed Trogon	*Trogon massena*	R		0.78	0.30
Baird's Trogon	*Trogon bairdii*	R		0.58	0.15
Violaceous Trogon	*Trogon violaceus*	R			0.60

APPENDIX 1. Continuation.

Species		Status	Mist-net	Point-count (forest)	Point-count (fragment)
Black-throated Trogon	*Trogon rufus*	R	0.19	0.39	
American Pygmy Kingfisher	*Chloroceryle aenea*	R	0.10		
Green Kingfisher	*Chloroceryle americana*	R	0.15		
Blue-crowned Motmot	*Momotus momota*	R	0.15	0.39	0.30
Fiery-billed Aracari	*Pteroglossus frantzii*	R	0.04		
Chestnut-mandibled Toucan	*Ramphastos swainsoni*	R		0.78	0.30
Olivaceous Piculet	*Picumnus olivaceous*	R	0.19		0.15
Golden-naped Woodpecker	*Melanerpes chrysauchen*	R	0.04	1.36	0.30
Red-crowned Woodpecker	*Melanerpes rubricapillus*	R			0.15
Linneated Woodpecker	*Dryocopus lineatus*	R		0.19	
Rufous-tailed Jacamar	*Galbula ruficauda*	R	0.06		
White-necked Puffbird	*Notharcus macrorhyncos*	R	0.02		
White-whiskered Puffbird	*Malacoptila panamensis*	R	0.13		
Blue-crowned Manakin	*Lepidothrix coronata*	R	1.02	3.11	
Red-capped Manakin	*Pipra mentalis*	R	3.57	2.53	
Orange-collared Manakin	*Manacus aurantiacus*	R	2.67	0.39	0.60
Masked Tityra	*Tityra semifasciata*	R		0.39	
Thrush-like Schiffornis	*Schiffornis turdina*	R	0.25		
White-winged Becard	*Pachyramphus polychopterus*	R	0.02		
Rufous Piha	*Lipaugus unirufus*	R		0.19	0.15
Yellow-bellied Elaenia	*Elaenia flavogaster*	R			0.15
Yellow Tyrannulet	*Capsiempis flaveola*	R			0.30
Ochre-bellied Flycatcher	*Mionectes oleaginieus*	R	2.53	1.17	
Northern Bentbill	*Oncostoma cinereigulare*	R	0.46	1.56	1.21
Scale-crested Pygmy Tyrant	*Lophotriccus pileatus*	R	0.02		
Common Tody Flycatcher	*Todirostrum cinereum*	R			0.15
Eye-ringed Flatbill	*Rhynchocyclus brevirostris*	R	0.02		
Yellow-olive Flycatcher	*Tolmomyias sulphurescens*	R	0.06		
Golden-crowned Spadebill	*Platyrinchus coronatus*	R	0.40	0.97	
Sulphur-rumped Flycatcher	*Myiobius barbatus*	R	0.35	0.19	
Black-tailed Flycatcher	*Myiobius atricaudis*	R	0.04		
Ruddy-tailed Flycatcher	*Terenotriccus erythrurus*	R	0.25	0.19	
Western Wood Pewee	*Contopus sordidulus*	N		0.19	0.15
Yellow-bellied Flycatcher	*Empidonax flaviventris*	N	0.15	0.19	
Acadian Flycatcher	*Empidonax virescens*	N	0.02		
Willow Flycatcher	*Empidonax trailii*	N	0.13		
Alder Flycatcher	*Empidonax alnorum*	N	0.94		0.15
Traill's Flycatcher	*Empidonax* sp.	N		0.39	0.15
Piratic Flycatcher	*Legatus leucophaius*	R			0.45
Social Flycatcher	*Myiozetetes similis*	R			0.15
Gray-capped Flycatcher	*Myiozetetes granadensis*	R			0.15
Great Kiskadee	*Pitangus sulphuratus*	R		0.19	1.06
Sulphur-bellied Flycatcher	*Myiodynastes luteiventris*	R	0.02		0.45
Boat-billed Flycatcher	*Megarynchus pitangua*	R		0.19	1.36

APPENDIX 1. Continuation.

Species		Status	Mist-net	Point-count (forest)	Point-count (fragment)
Tropical Kingbird	*Tyrannus melancholicus*	R			0.15
Eastern Kingbird	*Tyrannus tyrannus*	N			3.32
Rufous Mourner	*Rhytipterna holerythra*	R	0.13		
Dusky-capped Flycatcher	*Myiarchus tuberculifer*	R	0.25	0.97	0.45
Great-crested Flycatcher	*Myiarchus crinitus*	N	0.13		0.90
Bright-rumped Attila	*Attila spadiceus*	R	0.58	1.36	0.30
Great Antshrike	*Taraba major*	R	0.02		
Black-hooded Antshrike	*Thamnophilus bridgesi*	R	0.65	2.14	1.36
Russet Antshrike	*Thamnistes anabatinus*	R	0.06		
Slaty Antwren	*Myrmotherula schisticolor*	R	0.23	0.19	
Dot-winged Antwren	*Microrhopias quixensis*	R	0.96	6.23	3.47
Chestnut-backed Antbird	*Myrmeciza exsul*	R	1.04	5.25	2.41
Bicolored Antbird	*Gymnopithys leucaspis*	R	0.92	0.19	0.15
Black-faced Ant-thrush	*Formicarius analis*	R	0.15	1.36	0.30
Streak-chested Antpitta	*Hylopezus perspicillatus*	R	0.06	1.36	0.15
Buff-throated Foliage Gleaner	*Automolus ochrolaemus*	R	0.31	0.39	
Ruddy Foliage Gleaner	*Automolus rubiginosus*	R	0.02		
Scaly-throated Leaftosser	*Sclerurus guatemalensis*	R	0.27		
Plain Xenops	*Xenops minutus*	R	0.67	0.78	0.60
Tawny-winged Woodcreeper	*Dendrocincla anabatina*	R	0.44	0.39	
Long-tailed Woodcreeper	*Deconychura longicauda*	R	0.17		
Wedge-billed Woodcreeper	*Glyphorynchus spirurus*	R	1.12	2.14	0.15
Northern Barred Woodcreeper	*Dendrocolaptes sanctithomae*	R	0.21		
Cocoa Woodcreeper	*Xiphorhynchus susurrans*	R	0.44	0.97	0.60
Black-striped Woodcreeper	*Xiphorhynchus lachrymosus*	R	0.04	0.19	0.30
Philadelphia Vireo	*Vireo philadelphicus*	N	0.02	0.58	0.30
Red-eyed Vireo	*Vireo olivaceus*	N	0.23		0.30
Yellow-green Vireo	*Vireo flavoviridis*	R	0.65	0.39	0.60
Tawny-crowned Greenlet	*Hylophilus ochraceiceps*	R	0.50	3.89	
Lesser Greenlet	*Hylophilus decurtatus*	R	0.15	5.45	4.68
Black-bellied Wren	*Thryothorus fasciatoventris*	R	0.08	0.58	0.90
Riverside Wren	*Thryothorus semibadius*	R	0.84	1.95	1.66
House Wren	*Troglodytes aedon*	R	0.17		0.75
Nightingale Wren	*Microcerculus philomela*	R	0.02		
Scaly-breasted Wren	*Microcerculus marginatus*	R	0.04	0.97	
Long-billed Gnatwren	*Ramphocaenus melanurus*	R	0.65	1.95	0.45
Tropical Gnatcatcher	*Polioptila plumbea*	R	0.10	2.33	2.41
Swainson's Thrush	*Catharus ustulatus*	N	49.6	13.23	8.30
Wood Thrush	*Hylocichla mustellina*	N	0.04		
Clay-colored Robin	*Turdus grayi*	R	0.15	0.19	0.90
Tennessee Warbler	*Vermivora peregrina*	N	0.08		
Chestnut-sided Warbler	*Dendroica pensylvanica*	N	0.35	0.39	0.60
Yellow Warbler	*Dendroica petechia*	N	0.02		
Prothonotary Warbler	*Protonotaria citrea*	N	0.02		

APPENDIX 1. Continuation.

Species		Status	Mist-net	Point-count (forest)	Point-count (fragment)
Worm-eating Warbler	*Helmitheros vermivorum*	N	0.02		
Northern Waterthrush	*Seiurus noveboracensis*	N	0.27		0.15
Kentucky Warbler	*Oporornis formosus*	N	0.15		
Mourning Warbler	*Oporornis philadelphia*	N	0.10		0.15
MacGillivray's Warbler	*Oporornis tolmiei*	N	0.02		
Buff-rumped Warbler	*Basileuterus fulvicauda*	R	0.04		
Bananaquit	*Coereba flaveola*	R	1.06	0.39	6.49
Gray-headed Tanager	*Eucometis penicillata*	R	0.96	0.78	0.15
White-throated Shrike Tanager	*Lanio leucothorax*	R	0.15	0.78	
White-shouldered Tanager	*Tachyphonus luctuosus*	R	0.63	3.89	4.22
Black-cheeked Ant-Tanager	*Habia atrimaxillaris*	R	1.13	2.72	0.45
Scarlet Tanager	*Piranga olivacea*	N			0.45
Summer Tanager	*Piranga rubra*	N	0.02		0.15
Cherrie's Tanager	*Ramphocelus costaricensis*	R	0.94		7.99
Blue-gray Tanager	*Thraupis episcopus*	R			0.30
Palm Tanager	*Thraupis palmarum*	R			0.30
Spot-crowned Euphonia	*Euphonia imitans*	R	0.08	0.39	
Bay-headed Tanager	*Tangara gyrola*	R	0.15	0.19	0.30
Golden-hooded Tanager	*Tangara larvata*	R	0.06		1.66
Blue Dacnis	*Dacnis cayana*	R	0.02		1.51
Green Honeycreeper	*Chlorophanes spiza*	R	0.48		0.75
Shining Honeycreeper	*Cyanerpes lucidus*	R	0.04	0.97	0.60
Red-legged Honeycreeper	*Cyanerpes cyaneus*	R	0.17	0.78	3.02
Blue-black Grassquit	*Volatinia jacarina*	R	0.10		1.06
Variable Seedeater	*Sporophila corvina*	R	1.61		2.11
Yellow-bellied Seedeater	*Sporophila nigricollis*	R	0.13		
Thick-billed Seed Finch	*Oryzoborus funereus*	R	0.75	0.19	0.60
Orange-billed Sparrow	*Arramon aurantiirostris*	R	2.19	3.11	0.90
Black-striped Sparrow	*Arremonops conirostris*	R	0.27		1.21
Buff-throated Saltator	*Saltator maximus*	R	0.61		0.30
Blue-black Grosbeak	*Cyanocompsa cyanoides*	R	0.69	0.58	0.15
Great-tailed Grackle	*Quiscalus mexicanus*	R			0.60
Yellow-billed Cacique	*Amblycercus holosericeus*	R	0.02		
Scarlet-rumped Cacique	*Cacicus uropygialis*	R	0.06	0.58	