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Apparent Survival Estimates for Five Species of Tropical Birds in an Endangered Forest Habitat in Western Ecuador¹

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ABSTRACT

Estimates of annual survival are essential for addressing topics in evolutionary and conservation ecology. However, most demographic studies of land birds are based on north temperate species, and few robust estimates of survival based on mark–recapture statistics are available for continental South American birds. We used time–since–marking models to estimate apparent survival of adult birds from 7 yr of mist netting data in the Colonche Hills. This site is one of few remaining large tracts of premontane forest in southwestern Ecuador, and an area of high priority for avian conservation. Species with sufficient data for analysis included three hummingbirds (*Adelomyia melanogenys*, *Heliodoxa jacula*, *Phaethornis baroni*), a cotinga (*Schiffornis turdinus*), and a wren (*Henicorbina leucophrys*). Our parameter estimates had reduced precision because the number of recaptures was small. Probability of recapture was low in three species ($\hat{p} < 0.23$), and moderate in two others ($\hat{p} = 0.49–0.62$). *Adelomyia* and *Phaethornis* had moderate apparent survival ($\hat{\phi}^{2+} = 0.36–0.48$; probability that a bird neither died nor emigrated from our survey area in a given year). Adults of *Adelomyia* moved seasonally, and it is possible that permanent emigration from our survey area contributed to low estimates of apparent survival. The other three species had relatively high estimates of adult apparent survival ranging from $\hat{\phi}^{2+} = 0.62–0.70$ in *Heliodoxa* and *Schiffornis* to a high of $\hat{\phi}^{2+} = 0.92$ in *Henicorbina*.

RESUMEN

Estimaciones de la sobrevivencia anual son esenciales en investigaciones enfocadas en temas de evolución y conservación ecológica. Sin embargo, la mayoría de los estudios demográficos de aves terrestres están basados en especies de la parte norte de las zonas templadas y son pocos los datos disponibles para hacer buenas estimaciones de sobrevivencia basados en captura–recaptura para las aves del continente Sudamericano. Usamos estadísticos de captura–recaptura para analizar patrones de trapeo de aves mediante redes de neblina obtenidos durante 7 años en la Cordillera de los Colonche, esta área es una de las pocas largas extensiones del bosque premontano en el occidente de Ecuador con alta prioridad para la conservación de la avifauna. Las especies con suficiente datos para analizar incluyeron tres especies de colibrí (*Adelomyia melanogenys*, *Heliodoxa jacula*, y *Phaethornis baroni*), una cotinga (*Schiffornis turdinus*), y un troglodito (*Henicorbina leucophrys*). Los datos históricos de captura fueron analizados para las cinco especies, tres presentaron baja re–captura ($\hat{p} < 0.23$), lo cual sugiere que la mayoría de individuos no fueron capturados durante algún año específico. Dos especies presentaron bajos ($\hat{\phi} < 0.50$) índices de sobrevivencia aparente (probabilidad de que un ave no haya muerto ni emigrado en un año determinado). Adultos de una de las especies emigraron estacionalmente, y es posible que la emigración de adultos de nuestro sitio de estudio contribuya en los bajos índices de sobrevivencia aparente. Las otras tres especies presentaron altos índices de sobrevivencia aparente ($\hat{\phi} = 0.62–0.92$).

Key words: Colonche Hills; mark–recapture; program mark; South America; time–since–marking.

MOST ESTIMATES OF SURVIVAL FOR TROPICAL BIRDS have been derived using methods subject to bias, such as maximum longevity records, age ratios, or return rates (Sandercock *et al.* 2000). A growing number of robust estimates of annual survival based on mark–recapture statistics for live encounter data are now available

for island (Faaborg & Arendt 1995, Johnston *et al.* 1997) and continental populations of tropical birds (Karr *et al.* 1990, Francis *et al.* 1999, Jullien & Clobert 2000, Sandercock *et al.* 2000, Peach *et al.* 2001, Martin 2002). However, the vast majority of tropical species remain unknown in terms of their life history parameters, especially juvenile and adult survival (Martin 1996).

Mark–recapture methods for live encounter data estimate survival from captures or sightings of individuals in a fixed sampling area and have difficulty distinguishing mortality from permanent emigration (departure from the fixed sampling area; Nichols 1992).

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A population with high apparent survival has high true survival and high site fidelity, but a population with low apparent survival may have low true survival, low site fidelity, or both. For some groups, such as frugivorous and nectarivorous birds, estimating true survival may be difficult because wide-ranging movements in search of food may lead to low site fidelity (Martin & Karr 1986, Loiselle & Blake 1992, Powell & Bjork 1995). In more sedentary species, site fidelity is likely to be higher, and apparent survival should better approximate true survival (Sandercock *et al.* 2000).

Apparent survival and probability of recapture frequently vary with time and between sex and age classes (Lebreton *et al.* 1992, Nichols 1992). One model that is often a parsimonious fit to mark–recapture data from systematic mist net studies is the time–since–marking (TSM) model for apparent survival (Johnston *et al.* 1997, Pradel *et al.* 1997, Sandercock *et al.* 2000, Cooch & White 2005). A TSM model structure accounts for the possibility that many first–captures are of young or transient individuals with different probabilities of apparent survival than birds that have already been captured at least once already, and are presumably resident adults (Johnston *et al.* 1997, Pradel *et al.* 1997, Sandercock *et al.* 2000).

Estimates of apparent survival for tropical land birds have been generated by systematic mist net studies that mark and recapture birds (Karr *et al.* 1990, Faaborg & Arendt 1995, Johnston *et al.* 1997, Francis *et al.* 1999, Jullien & Clobert 2000, Peach *et al.* 2001), and by focal population studies in which marked individuals are encountered by resighting (Sandercock *et al.* 2000, Martin 2002). Systematic mist netting can generate data on a large number of bird species simultaneously, although sample sizes for each species are often relatively small (*e.g.*, Karr *et al.* 1990, Johnston *et al.* 1997). Focal population studies are usually limited to one species, but may offer more detailed data on a larger sample of individuals (Sandercock *et al.* 2000).

We applied TSM models to systematic mist netting data to generate mark–recapture estimates of apparent annual survival (ϕ) for tropical land birds at a site in southwestern Ecuador. We examine the hypothesis of high adult survival in tropical birds and generate important life history information for several poorly known species of South American birds from a site of global conservation importance.

METHODS

STUDY SITE.—We surveyed forest birds in the 3000 ha Reserva Ecológica de la Comuna de Loma Alta (RECLA), located in the Colonche Hills 17 km east of the coastal town of Manglaralto in western Ecuador. This site is in the 50,000 km² Tumbesian Endemic Bird Area (EBA), a region of high priority for conservation of avian biodiversity (Parker & Carr 1992, Best & Kessler 1995). The Loma Alta community initially created RECLA because fog captured in the premontane tropical moist forest of the watershed was critical to water supply in the lowlands (Becker 1996, 1999). Later, RECLA was designated as an Important Bird Area by Birdlife International. Cerro la Torre (01°49'S, 80°36'W), the highest and most pristine

peak in RECLA, has been the focus of biodiversity monitoring since the creation of the ecological reserve (Becker & Elao 1995, Becker & López-Lanús 1997, this study).

MIST NETTING AND SURVEYS.—We used mist nets to capture birds in mature forest at Cerro la Torre during seven consecutive dry seasons (1998–2004). Two netting areas, Casita (500–550 m) and a ridge (600–650 m), separated by about 1 km and each >1 km from forest edge, were sampled annually in the dry season between late December and early February. At each area, we placed 20 mist nets (12 × 2.8 m, 36 mm mesh) along footpaths at *ca* 50-m intervals depending on suitable topography. Thus at each area, the transect of 20 nets was spread across approximately 1200 m. Nets were open from 0600 to 1100 h for three consecutive days for a total of 300 net hours per area. Captured birds were identified to species and uniquely marked with numbered aluminum leg bands. We attempted to sex birds, but for four of the five species analyzed here the sex of a large proportion of individuals was not determined.

DATA ANALYSIS.—We used Cormack–Jolly–Seber (CJS) models to estimate the annual probabilities of apparent survival (ϕ) and recapture (p) for each species. Apparent survival is the product of true survival and the probability that the individual has not permanently emigrated from the sampling area (site fidelity). The probability of recapture is the product of the probability that the marked individual is present in the area of survey and available for recapture and the probability of recapture if an individual is present. Analyses were conducted in Program Mark (version 4.1) using Parameter Index Models (PIMs) and the sine link function.

When selecting parameters for inclusion in our global model, we were constrained by small sample sizes and a low recapture rate (see Results). Thus, we did not attempt to fit models with time dependence. For each species analyzed, we fit two models to the encounter histories. We tested a TSM model (ϕ_{TSM}, p_c) in which apparent survival during the interval after first capture (ϕ^1) was estimated separately from apparent survival during all subsequent intervals (ϕ^{2+}) and recapture probability was constant (c). We also considered a model with constant apparent survival and constant recapture probabilities (ϕ_c, p_c).

For each species, we calculated an overdispersion correction factor (\hat{c}) with the median \hat{c} method based on the global model (ϕ_{TSM}, p_c). We corrected for overdispersion by adjusting for the appropriate \hat{c} value in all analyses in Program Mark.

We assessed the effectiveness of the TSM model relative to the constant model using quasi-Akaike's Information Criterion (QAICc) adjusted for \hat{c} and corrected for small sample sizes. We concluded that the more complex (TSM) model was best if the ΔQAICc (QAICc of the model of interest – lowest QAICc) value of the constant model were >2. If this were not the case, we concluded that the constant model was at least as effective at explaining the data. We could not ask whether the constant model was superior because we were assessing two models differing by only one parameter and the TSM model could not have a ΔQAICc value greater than approximately 2 (Guthery *et al.* 2005). We report Akaike weights (w_i), which can be used to assess the relative strength of support

between models (w_i/w_j), and estimates of ϕ and p from both models. We assessed the precision of $\hat{\phi}$ and \hat{p} by examining standard errors (SE) and 95 percent confidence intervals (CI).

RESULTS

We recorded 2385 captures of 1956 individuals of 88 species of birds during dry season sampling in our 7-yr study at Cerro Torre, Ecuador. In our sample, the median number of individuals captured per species was four (range: 1–220), and the median number of between-year recaptures was 0 (range: 0–32). Five species had at least 10 between-year recaptures, and we assessed recapture and apparent survival probabilities for this subset of the avian community (Tables 1 and 2). The three nectarivorous hummingbirds and two insectivorous songbirds were all small-bodied species (<30 g).

For all species, \hat{c} was <1.7, indicating minor overdispersion. For four of five bird species, the constant model did not have a ΔQAICc value >2, and so the TSM model was not more effective at explaining encounter histories than the constant model (Table 1). However, for the green-crowned brilliant, the TSM model for apparent survival was the minimum QAICc model and had nearly five times the support of the constant model (Table 1).

Estimates of $\hat{\phi}$ and \hat{p} varied among the five species ($\hat{\phi}$ range: 0.34–0.86; \hat{p} range: 0.10–0.58; Table 2). As predicted for systematic mist net data, the estimate of apparent survival in the year after first capture ($\hat{\phi}^1$) was consistently lower than the estimate of apparent survival in subsequent years ($\hat{\phi}^{2+}$), though estimates differed significantly between these classes only for the green-crowned brilliant. Two of the three nectarivorous hummingbirds had estimates of $\hat{\phi}^{2+}$ below 0.50, but the third species had a higher estimate of

$\hat{\phi}^{2+}$ at 0.70. The two insectivorous songbird species had estimates of $\hat{\phi}^{2+}$ of 0.62 and 0.92. The gray-breasted wood-wren, the species with the largest sample size, had the highest estimates of $\hat{\phi}$ (0.86), $\hat{\phi}^{2+}$ (0.92), and even $\hat{\phi}^1$ (0.54). Estimates of \hat{p} for gray-breasted wood-wren were low (<0.15). Estimates of \hat{p} were also low for speckled hummingbird and Baron's hermit; however, the two other species had estimates ≥ 0.49 . For all parameter estimates, standard errors were moderately large, and our estimates of $\hat{\phi}$ and \hat{p} had relatively low precision.

DISCUSSION

This study had three major results. First, despite marking a large sample of birds, we recaptured few individuals per species, and for the few species with sufficient recaptures for analysis, our estimates of the probability of recapture (\hat{p}) were generally low (0.10–0.62). Second, TSM estimates of adult annual survival ($\hat{\phi}^{2+}$) were consistently higher than estimates of survival in the first year after capture ($\hat{\phi}^1$), though this difference was significant for only one species. Third, estimates of apparent survival were high (≥ 0.70) for a subset of our study species.

Few robust estimates of apparent annual survival are available for tropical forest birds (Sandercock *et al.* 2000). To our knowledge, our results are the first estimates of annual survival for four of our five study species and the first estimates for any land birds from mainland Ecuador. In the past, one method of estimating survival was to assess return rate, the proportion of previously banded birds recaptured in subsequent years (Sandercock *et al.* 2000). Because return rate is the product of both apparent survival and recapture probability, it is an underestimate of both apparent and true survival.

TABLE 1. Numbers of captures and recaptures for five bird species in the Colonche Hills of Ecuador and the mark–recapture models of the probability of apparent annual survival (ϕ) and the probability of recapture (p) ranked according to quasi-Akaike's Information Criterion (ΔQAICc) and Akaike weight (w_i).

Species	Individuals captured during the first 6 yr ^a	Number of recaptures	Number of individuals recaptured	Model ^b	ΔQAICc	w_i
Apodiformes: Trochilidae						
Green-crowned brilliant (<i>Heliodoxa jacula</i>)	113	14	10	ϕ_c, p_c	3.1	0.171
				ϕ_{tsm}, p_c	0.0	0.828
Speckled hummingbird (<i>Adelomyia melanogenys</i>)	169	15	13	ϕ_c, p_c	0.0	0.653
				ϕ_{tsm}, p_c	1.3	0.347
Baron's hermit (<i>Phaethornis baroni</i>)	174	12	11	ϕ_c, p_c	0.0	0.730
				ϕ_{tsm}, p_c	2.0	0.270
Passeriformes: Pipridae						
Thrush-like Schiffornis (<i>Schiffornis turdinus</i>)	24	14	9	ϕ_c, p_c	0.0	0.741
				ϕ_{tsm}, p_c	2.1	0.258
Passeriformes: Troglodytidae						
Gray-breasted wood-wren (<i>Henicorhina leucophrys</i>)	104	32	26	ϕ_c, p_c	0.0	0.591
				ϕ_{tsm}, p_c	0.7	0.409

^aIndividuals captured for the first time in the final (7th) year of the study could not be recaptured, and so provide no information to the calculation of p and ϕ .

^btsm = time-since-marking, c = constant.

TABLE 2. Estimates of the probabilities of apparent annual survival ($\hat{\phi}$) and recapture (\hat{p}) from two models for five species of tropical birds in the Colónche Hills of Ecuador.

Species	ϕ_{ω}, p_c					ϕ_{ω}, p_c									
	$\hat{\phi}$		\hat{p}		$\hat{\phi}^1$		$\hat{\phi}^{2+}$		\hat{p}						
	Estimated	SE	95% CI	Estimated	SE	95% CI	Estimated	SE	95% CI	Estimated	SE	95% CI			
Green-crowned brilliant	0.44	0.16	0.18–0.74	0.17	0.10	0.04–0.46	0.12	0.05	0.04–0.27	0.70	0.18	0.31–0.93	0.49	0.20	0.16–0.82
Speckled hummingbird	0.42	0.12	0.22–0.66	0.13	0.06	0.05–0.31	0.23	0.14	0.06–0.60	0.48	0.14	0.24–0.74	0.22	0.14	0.05–0.59
Baron's hermit	0.34	0.13	0.15–0.62	0.14	0.08	0.04–0.37	0.27	0.24	0.03–0.81	0.36	0.14	0.15–0.65	0.17	0.16	0.02–0.66
Thrush-like Schiffornis	0.56	0.11	0.35–0.75	0.58	0.16	0.27–0.84	0.49	0.15	0.22–0.76	0.62	0.15	0.31–0.85	0.62	0.17	0.29–0.87
Gray-breasted wood-wren	0.86	0.10	0.56–0.97	0.10	0.03	0.05–0.18	0.54	0.20	0.19–0.85	0.92	0.10	0.40–0.99	0.14	0.06	0.06–0.29

This is especially true when recapture probabilities are low, in which case it is particularly important to use appropriate mark–recapture methods.

For four of the five species, the simplest possible model (ϕ_c, p_c) was a parsimonious fit to the capture history data, a result we anticipated because sample sizes were small (Lebreton *et al.* 1992). However, the TSM model (ϕ_{TSM}, p_c) for estimates of apparent annual survival was unambiguously superior for one species. Further, for all species, the TSM models produced lower estimates of survival for the interval after the first capture than for subsequent intervals, though this difference was only significant for the green-crowned brilliant. There are at least two reasons to favor estimates of apparent survival from TSM models. At the time of first capture, some individuals may have been transients that emigrated from the study site or may have been moving beyond their typical territorial boundary. Second, young birds may have survived less well than adults. TSM models that separate apparent survival after capture from the later intervals will generally better explain the data than standard CJS models that fit one survival probability to all time intervals (Johnston *et al.* 1997, Sandercock *et al.* 2000), and we recommend that TSM models be included as candidate models for any analysis of tropical birds.

Some of our estimates of annual survival were high, but confidence intervals around these estimates were large. Species with the highest estimates of apparent survival ($\hat{\phi}^{2+}$) included the green-crowned brilliant (0.70) and the gray-breasted wood-wren (0.92). For species with particularly high apparent survival, we can conclude that they have high annual probabilities of both true survival and site fidelity.

Low estimates of apparent survival for some nectarivores may have resulted from low site fidelity. The speckled hummingbird had moderate estimates of apparent annual survival (0.42–0.48). This species appears on the study site in December and January to feed on flowers of *Psychotria* spp. and *Razisea ericae*, but blooms did not occur every year (C. D. Becker, pers. obs.), and may have led to dispersal. Baron's hermit, endemic to this area of western Ecuador, is a trap-line forager and appears to reside on our site year-round. It was the most commonly seen and captured hummingbird at the site. However, this species had estimates of apparent annual survival (0.34–0.36) that approach the low end of estimates found in the literature for tropical birds (Karr *et al.* 1990, Sandercock *et al.* 2000). Despite the year-round presence of Baron's hermits, individuals of this nectarivorous species may also have low site fidelity, at least at the scale of our sampling area. High mobility in response to variable food resources may be a challenge for obtaining reliable apparent survival estimates for many tropical hummingbirds (Martin & Karr 1986, Loiselle & Blake 1992, Powell & Bjork 1995).

Our estimates of apparent survival were comparable to the range of mark–recapture apparent survival estimates for other small tropical birds captured in systematic mist net studies ($\hat{\phi} = 0.33 - 0.87$, $N = 6$ studies, Sandercock *et al.* 2000; see also, Francis *et al.* 1999, Jullien & Clobert 2000). We could make direct comparisons for only one of our study species. Our Ecuadorian population of the thrush-like Schiffornis had moderate annual survival ($\hat{\phi}^{2+} = 0.62 \pm 0.17$ (SE), $N = 24$). At a study site in Panama, Karr *et al.*

(1990) estimated apparent annual survival for this species as $\hat{\phi} = 0.72 \pm 0.07$ (SE), $N = 23$, an estimate not significantly different from ours.

Our estimates of recapture probabilities (\hat{p}) varied substantially among species (Table 2). Some estimates were at the low end of those reported for other tropical systematic mist netting studies ($P = 0.08\text{--}0.49$, $N = 4$ studies, reviewed in Sandercock *et al.* 2000). As with estimates of apparent survival, recapture probabilities might be lowered by movements associated with a nectarivorous diet (Martin & Karr 1986, Loiselle & Blake 1992, Powell & Bjork 1995). Such movements need not have taken birds off the reserve, just temporarily away from our net transect. Two of our low estimates of recapture probability were from hummingbirds, though our lowest estimate was from a sedentary insectivore, the gray-breasted wood-wren. For the other two species in our study, estimates of probability of recapture were higher than those reported from other tropical systematic mist netting studies (>0.5) suggesting that individuals present were likely to be caught (Table 2).

Our ability to obtain precise estimates of apparent survival and recapture probabilities was hampered by a small number of recaptures. Even though we captured a large number of individuals over the course of the 7-yr study, only 5 of 88 species had adequate numbers of between-year recaptures for mark-recapture analyses. Because our estimates rely on the behavior of a relatively small number of birds, they must be evaluated with caution, and this is reflected in the large confidence intervals surrounding individual estimates.

A low number of recaptures may be related to three factors. For some species, the true probability of recapture for an individual present on the study site was probably low, possibly because of low sampling intensity. Our mist net sampling protocol was designed to monitor community patterns rather than to maximize individual recaptures, and our nets were spaced far apart and opened for only 3 d per sampling period. Second is the potential for net avoidance by experienced individuals, though a low netting intensity may have minimized this problem in our case (Sandercock *et al.* 2000). Finally, bird communities of tropical forests often contain a high overall density of birds but rarely a high density of individuals of any one species (Karr *et al.* 1990).

Two possible solutions are evident. A mark and resight effort could address all these problems, but would generally be limited to one or a few species, and so is unlikely to be effective for determining community-wide patterns. For systematic mist netting to be successful, more intensive efforts than ours will be required. We suggest placing nets at closer intervals, and netting for more days. Combining resighting and recapture methods might also be an option, depending on the goals of the individual project. Encountering enough individuals from any given species will remain a major challenge for investigators attempting to estimate apparent survival for tropical forest birds, especially through systematic mist netting (Karr *et al.* 1990, Sandercock *et al.* 2000). Despite these logistical challenges, estimation of apparent survival for tropical forest bird species will remain an important facet of developing conservation priorities.

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