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SURVIVAL RATES OF FOREST PASSERINES IN SOUTH-CENTRAL CHILE

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Resumen. – Tasas de supervivencia de paserinos forestales en el centro sur de Chile. – Presentamos las primeras estimaciones de tasas de supervivencia para cinco especies de paserinos que habitan los bosques templados de la zona Centro Sur de Chile. Los cálculos fueron realizados sobre datos de captura obtenidos entre 1998 y 2002 en la zona costera de la región del Maule, donde el paisaje está compuesto por un mosaico de bosques nativos del género *Nothofagus* y plantaciones exóticas de pino. Encontramos que la condición corporal es el principal factor que explica la supervivencia de *Aphrastura spinicauda* y *Troglodytes aedon*. Para esta primera especie, los datos también respaldan un efecto anual sobre la supervivencia, lo cual sugerimos está relacionado a un año de condiciones climáticas atípicas, además encontramos un efecto temporal en la supervivencia de otras tres especies, relacionado a estaciones y época reproductiva. Para dos especies de matorrales, los modelos que mejor explicaron sus supervivencias incluyeron un factor de tamaño corporal, pero intrigantemente los análisis mostraron una mayor supervivencia para las aves de menor tamaño. Al comparar con datos publicados, nuestros resultados sugieren que la tasa de supervivencia aparente de paserinos que habitan las zonas templadas del Neotrópico están más cercanos a paserinos que habitan otras zonas templadas que a especies emparentadas que se encuentran en menores latitudes. Finalmente, la falta de información demográfica básica para aves de bosques templados de Sudamérica dan a nuestros hallazgos un carácter de invaluable para manejadores e investigadores, y también deja planteadas preguntas acerca del impacto de los cambios en el hábitat sobre estas aves forestales.

Abstract. – We present the first estimates of survival for five passerines inhabiting the temperate forests of south-central Chile. Calculations were performed based on capture data obtained between 1998 and 2002 in the coastal range of the Maule region, where the landscape is comprised of a mosaic of native *Nothofagus* forests and pine plantations. We found that body condition is the main factor explaining survival for both *Aphrastura spinicauda* and *Troglodytes aedon*. For this first species, a *year effect* on survival is also supported by the data, which we suggest is related to a year of atypical weather conditions. We also found a *time effect* on the survival of three other species, related to seasons and breeding time. For two scrubland bird species, the models that better explained their survival contained a body size factor, but intriguingly the analysis showed higher survival for smaller birds. Comparison of published data with our results suggests that the apparent survival for temperate Neotropical passerines is closer to that of passerines inhabiting other temperate regions than for birds belonging to the same family occurring at

lower latitudes in the Neotropics. Finally, the lack of basic demographic information for South American temperate forest birds makes our findings invaluable for managers and researchers, but leaves unresolved questions about the impact of habitat changes on these forest birds. *Accepted 1 December 2011*.

INTRODUCTION

Survival is a key component of individuals' fitness. On average, variation in survival rates has a higher effect on bird population dynamics than other life history traits such as fecundity, particularly in long-lived species (Sæther & Bakke 2000, Stahl & Olib 2006).

Estimating the survival rates of birds usually involves monitoring the fate of individually marked animals either periodically or in a continuous manner (Murray & Patterson 2006). Although the latter poses an important restriction to the study of avian survival, the continual development of capture-recapture theory (Lebreton *et al.* 1992, Nichols 1992, Nott & DeSante 2002, Caswell & Fujiwara 2004) and the associated software (Cooch *et al.* 1997, White *et al.* 2006, Choquet *et al.* 2009) have improved the models to estimate survival rates and to explore the ecological factors that affect them.

For example, different studies have documented the relationship between survival and individuals' traits, such as body weight (Tinbergen & Boerlijst 1990), body condition indices (Schmutz & Ely 1999, Dinsmore & Collazo 2003, Benson & Bednarz 2010), or fat reserves (Pfister *et al.* 1998, Miller *et al.* 2003), among others, providing important mechanistic links to understand the relationship between species' foraging ecology and demographics.

Most of our current knowledge on the factors affecting avian survival rates comes from experience in the northern hemisphere. The fact that there is evidence pointing to a general pattern in which southern birds tend to have higher survival than their northern counterparts (Ghalambor & Martin 2001) poses a restriction to the extrapolation of such knowledge to birds in the Neotropics.

Among the few survival studies conducted in the region, most have been done in tropical sites (e.g., Blake & Loiselle 2008, Cohen & Lindell 2004, Parker *et al.* 2006, Ruiz-Gutierrez *et al.* 2008, Sandercock *et al.* 2000). To our knowledge, the only published assessment of the survival rate of a bird species of the temperate forests of South America is that of Willson & Pendleton (2008) for the Chucao Tapaculo (*Scelorchilus rubecula*) at Chiloé, southern Chile.

Poor knowledge of survival of forest birds is a clear limitation to population management and conservation planning. Chilean temperate forests provide habitat to many endemic species (Vuilleumier 1985). Unfortunately, most of these forests have been extensively cleared and fragmented, and landscapes in south-central Chile are mostly dominated by exotic pine plantations (Estades & Escobar 2005).

In this work, we report the results of an analysis of capture-recapture data for some forest passerines in south-central Chile, as a contribution to our knowledge on the biology of these little-known species. Our main goal was to provide a robust estimation of apparent survival rates that can be used to construct population models useful for management and conservation.

METHODS

Study area. This study was conducted at the Dr. Justo Pastor Leon Field Station (35º26'S, 72º17' W) of the University of Chile, and in

neighbouring areas near the town of Constitution, south- central Chile. The area is dominated by exotic Monterey pine (*Pinus radiata*) plantations, and scattered *Nothofagus* forests fragments cover no more than 10% of the landscape (Estades & Temple 1999, Echeverría *et al.* 2006). Most pine plantations in the area are thinned heavily during rotation thus allowing the development of a significant native understory and, consequently, of an important bird community (Estades & Escobar 2005).

Bird capture and banding. Between the spring of 1998 and the spring of 2002, we conducted a total of 12 seasonal (spring, summer, and winter) field campaigns that lasted for 20 (winter and summer) and 40 days (spring). During each campaign we established 38 mist-netting stations throughout the study area. We used 32 mm-mesh mist-nets of 10 and 12 m length. We opened between 6 and 12 nets per day for an average of 4.5 h to complete the same capture effort (meter/h) in every defined station. To avoid a seasonal time effect we rotated all the nets through the stations during every season.

Although there were two clearly defined forest types in the study area (plantations and native forest), they were highly intermixed, preventing us from associating individual netting stations to specific habitat types. Therefore, we treated the entire study area as a mosaic of pine plantations and *Nothofagus* forests.

All captured individuals were subject to standard biometric measurements and immediately released at the site of capture. Body mass was measured to the nearest 0.1 g with a spring scale. We only considered data for species with more than 10 recaptures (Parker *et al.* 2006).

Data analysis. We focused our analysis only on resident species, in order to avoid the effect of transient individuals on the estimation of the apparent survival (Pradel *et al.* 1997).

In order to determine the effect of body condition on the survival of individuals we calculated a Body Condition Index (BCI), represented by the residual of the regression between the individual's body mass and tarsus length (Hochachka & Smith 1991, González *et al.* 2004). To estimate the effect of BCI, we divided the individual birds into three groups, using the average of the residuals (i) (BCI1: $i < -1$; BCI2: $-1 \leq i < 0$; BCI3: $i \geq 0$).

To include the effect of body size, we used the individuals' body length (total length minus tail length), and subsequently grouped the individuals into two groups (Size 1: below average; Size 2: above average).

Using the capture-recapture data we built a presence-absence matrix (rows: individuals, columns: capture campaigns). This matrix was then analyzed with a "recaptures only" model using the package MARK (White & Burnham 1999).

Under the Cormack-Jolly-Seber (CJS) scheme, marked individuals are released into the population two or more times. With the latter information, survival (Φ) and capture probability (p) are estimated for each interval between captures.

We used the U-CARE package (Choquet *et al.* 2005, version 2.3.1) to perform a goodness-of-fit test on the most complex model in order to verify that the assumptions of the CJS model (Lebreton *et al.* 1992) were met. Among the latter, ruling out of the effect of transient individuals is important, because it can result in an underestimation of both survival rate and recapture probability (DeSante *et al.* 1995).

Finally, we fitted the data to different models including the effect of BCI, body size groups, and time (t, subdivided in years, breeding season, and all seasons), and all potential interactions.

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TABLE 1. Total individuals captured, subsequently re-captured, and their Goodness of Fit statistics from sum of tests over groups (U-Care). Upper row, results for the data including two body size groups. Lower row, results for the data including three BCI groups.

Species	Captures	Recaptures	χ^2	df	P
Plain-mantled Tit-Spinetail	35	17	1.6441	10	0.998
(*Leptasthenura aegithaloides*)			0.9352	12	0.999
Dusky-tailed Canastero	42	12	0.935	10	0.999
(*Asthenes humicola*)			0.935	5	0.967
Desmurs' Wiretail	44	17	0.935	7	0.995
(*Sylviorthorhynchus desmursii*)			0.935	13	0.999
Thorn-tailed Rayadito	336	90	16.644	37	0.998
(*Aphrastura spinicauda*)			22.422	43	0.995
House Wren	298	123	38.024	70	0.999
(*Troglodytes aedon*)			33.843	69	0.999

For model comparison, we used the Akaike Information Criterion (AIC) calculated by MARK (White & Burnham 1999). For each species, an overdispersion correction factor c-hat (Variance inflation factor) was calculated through the Bootstrap GOF procedure included in MARK (DeSante *et al.* 1995). Values of c-hat > 1 are considered an indication of data overdispersion. In this case, the program uses c-hat to calculate the Quasi-Akaike Information Criterion ($QAIC_C$) adjusted for small samples (Lebreton *et al.* 1992).

RESULTS

We captured and banded a total of 3270 individual birds. There were five resident species for which we had at least 10 recaptures. Table 1 shows the numbers of birds captured of each species along with the main results of the Goodness-of-Fit test. The data for all species adequately fit ($P >> 0.05$) the most general model (Φtpt), considered as the starting point for our analyses, indicating that the assumptions of the CJS model were satisfied.

Effect of body condition on survival. The only species in which the best models included an effect of the BCI on the apparent survival rate were Thorn-tailed Rayadito (*Aphrastura spinicauda*) and House Wren (*Troglodytes aedon*) (Table 2). Both species showed a positive association between an individual's BCI and apparent survival (Fig. 1).

Effect of body size on survival. In the case of the Dusky-tailed Canastero (*Asthenes humicola*), the best model supported by the data included the effect of body size on survival, although the model was not significantly different from that containing a constant term ($\Delta AIC_C = 0.17$, Table 2). The other species for which there was an effect of body size was the Desmurs' Wiretail (*Sylviorthorhynchus desmursii*), although in this case the best model was the one including the constant term ($\Delta AIC_C = 1.99$, Table 2). Interestingly, in both cases apparent survival was lower for larger birds.

Effect of time on survival. In the case of the Thorn-tailed Rayadito, there was a clear year effect on the apparent survival, with survival declining from 1999 to 2002 (Table 2). The support of the data for this model was only slightly lower than that of the best model ($\Delta AIC_C = 0.18$, Table 2).

TABLE 2. Estimated monthly survival (Φ) and SE for five passerine species in south-central Chile. Only models with ΔAIC_C value < 2 are shown for each analysis. w_i: Akaike weights; $\mathcal{L}$: Model Likelihood; K: Number of parameters. [1]Calculation omitted due to insufficient data. [2]For the general model of the Plain-mantled Tit-Spinetail, the lack of fit was adjusted with c-hat: 1.3409. Only for this species the values AIC_C ΔAIC_C AIC_C Weights, and Deviance refer to $QAIC_C$ $\Delta QAIC_C$ $QAIC_C$ Weights, and Q deviance.

| Species	Model	AIC_C	ΔAIC_C	w_i	$\mathcal{L}$	K	Deviance	Φ	SE	Factor
Thorn-tailed Rayadito	Φ(BCI) p(t)	636.14	0.00	0.46	1.00	14	173.54	0.859	0.033	BCI 1
								0.910	0.020	BCI 2
								0.934	0.014	BCI 3
	Φ(year) p(t)	636.32	0.18	0.42	0.91	14	173.72	–	–	19981
								1.000	0.000	1999
								0.909	0.025	2000
								0.901	0.037	2001
								0.669	0.041	2002
Plain-mantled Tit-Spinetail[2]	Φ(.) p(.)	85.54	0.00	0.38	1.00	2	67.32	0.890	0.036	All
	Φ(repro) p(.)	87.25	1.71	0.16	0.42	3	66.78	0.856	0.058	Breeding
								0.957	0.095	Non-breeding
Desmurs' Wiretail	Φ(.) p(size)	123.18	0.00	0.46	1.00	3	74.07	0.953	0.027	All
	Φ(size) p(size)	125.16	1.99	0.17	0.37	4	73.73	0.981	0.055	Size 1
								0.944	0.034	Size 2
Dusky-tailed Canastero	Φ(size) p(.)	86.34	0.00	0.28	1.00	3	57.08	0.902	0.041	Size 1
								0.608	0.157	Size 2
	Φ(.) p(size)	86.52	0.17	0.25	0.92	3	57.25	0.891	0.041	All
	Φ(size) p(size)	88.27	1.92	0.11	0.38	4	56.63	0.898	0.041	Size 1
								0.733	0.236	Size 2
House Wren	Φ(BCI) p(t)	808.02	0.00	0.37	1.00	17	293.24	0.841	0.045	BCI 1
								0.926	0.014	BCI 2
								0.935	0.013	BCI 3
	Φ(season) p(t)	808.70	0.68	0.27	0.71	17	293.92	0.990	0.040	Spring
								0.824	0.042	Winter
								0.968	0.046	Summer
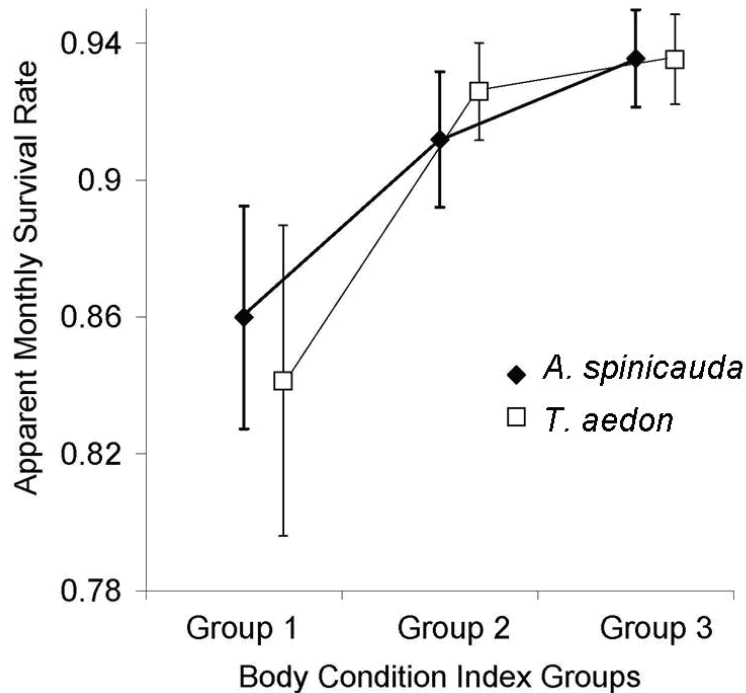
FIG. 1. Monthly survival rate ($\Phi \pm 1$ SE), for three Body Condition Index groups of the Thorn-tailed Rayadito (*Aphrastura spinicauda*) and the House Wren (*Troglodytes aedon*).

The second best model for the survival of the Plain-mantled Tit-Spinetail (*Leptasthenura aegithaloides*) showed a higher individual apparent survival during the nonbreeding season ($\Delta AIC_C = 1.71$, Table 2), whereas for the House Wren, there appeared to be a clear reduction in apparent survival during the winter seasons (Table 2).

DISCUSSION

Although individual variation in fitness-related features is a critical factor of population dynamics (Blums *et al.* 2005), survival is among the least studied aspects of the natural history of Neotropical forest birds. We produced the first survival estimates for five temperate forest passerines (Table 2), and, although our data were not obtained in a completely natural setting, our study area is representative of a large portion of the Chilean territory.

Our survival estimates for the studied Furnariidae (all species except the House Wren) are at least 10% lower than those obtained for some tropical members of the family (Blake & Loiselle 2008), but fall within the range of survival rates obtained for temperate forest passerines (Karr *et al.* 1990), supporting the hypothesis of a temperate-tropical survival gradient (Murray 1985, Johnston *et al.* 1997).

The apparent survival of the Chucao (*Scelorchilus rubecola*, Rhinocryptidae) (Willson & Pendleton 2008), is significantly greater than the values obtained for the five species of passerines in this study. However, we believe that characteristics of size, habits, and life-

span, do not allow comparisons between this rainforest-inhabiting tapaculo and the small forest passerines.

Survival is clearly affected by habitat quality (Van Horne 1983). Two species had a significantly lower apparent monthly survival than the others: the Dusky-tailed Canastero and Plain-mantled Tit-Spinetail (Table 2). This result may reflect the fact that forest environments represent a marginal habitat for these typically scrubland species (Lazo & Anabalón 1992).

Food availability, expressed as the individual's body condition, strongly influences bird reproduction and survival rates (Newton 1998). Accordingly, survival of Thorn-tailed Rayaditos and House Wrens was clearly affected by the body condition of individuals.

In the case of the Thorn-tailed Rayadito, apparent monthly survival of those individuals with the least favorable BCI was, on average, 92% of that of the group with the highest BCI (only 37% when expanded to annual survival). Thus, birds with a higher BCI were more likely to survive or less likely to emigrate.

Survival rates of Thorn-tailed Rayaditos clearly declined over the study years (Table 2). That trend might be explained by a weather effect on the species' BCI (González *et al.* 2004). Year 2002 spring precipitation was 5 times higher than that of the three previous years and included relatively low temperatures (González *et al.* 2004). The latter was also associated with a continuous decrease in the Thorn-tailed Rayadito's BCI between 1999 and 2002 (González *et al.* 2004).

The fact that there was a negative effect of body size on survival of two species (Dusky-tailed Canastero and Desmurs' Wiretail) seems intriguing. Although Van Buskirk *et al.* (2010) found a general decline in body sizes of North American birds, presumably as a response to warmer climates, we do not have sufficient evidence to associate our results with such phenomenon.

The temperate forests of South America are under significant pressure from humans (Dinerstein *et al.* 1995). However, our current knowledge of the basic demographics of most forest bird populations is scant, preventing managers from making specific predictions regarding population trends under different conservation scenarios. Thus, improving survival estimates is crucial for conservation (Anders & Marshall 2005), particularly of those species living in the most threatened ecosystems.

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