SURVIVAL OF CHUCAOS (*Scelorchilus rubecula*) IN RAINFOREST FRAGMENTS ON ISLA CHILOÉ, CHILE

Sobrevivencia de chucaos (*Scelorchilus rubecula*) en fragmentos de bosque lluvioso en la isla de Chiloé, Chile

Mary F. Willson[1,2] & Grey W. Pendleton[3]

[1]Fundación Senda Darwin and Center for Advanced Studies in Ecology and Biodiversity,
Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile
[2]Current address for corresponding author: 5230 Terrace Place, Juneau, Alaska, 99801 U.S.A.
[3]Alaska Dept. of Fish and Game, 802 3rd Street, Douglas, Alaska, 99824 U.S.A.

✉: M. F. Willson, E-mail mwillson@gci.net

ABSTRACT.- Estimated annual probability of survival of color-banded adult chucaos (*Scelorchilus rubecula*) of known age in rainforest fragments on Isla Chiloé was 44% from age one to two years and 72% from age two to seven years. There was marked annual variation in observed adult survival and no difference between survival probability of males and females. **KEY WORDS.-** Chucao tapaculo, *Scelorchilus rubecula,* Isla Chiloé, Chilean rainforest, survival.

RESUMEN.- La probabilidad anual de sobrevivencia estimada para chucaos (*Scelorchilus rubecula*) con anillos de colores de edad conocida en fragmentos de bosque templado en la Isla de Chiloé fue de 44% para la edad de uno a dos años y 72% para la edad de dos a siete años. No hubo diferencias entre las probabilidades de sobrevivencia de machos y hembras. Se observó una marcada variación interanual en la sobrevivencia de adultos. **PALABRAS CLAVE.-** Chucao, *Scelorchilus rubecula,* Isla Chiloé, bosque lluvioso de Chile, sobrevivencia.

INTRODUCTION

Chucaos (*Scelorchilus rubecula* (Kittlitz), Rhinocryptidae) occupy a small geographic range in the temperate rainforests of southern Chile and westernmost Argentina (Fjeldså and Krabbe 1990). Chilean rainforest is rapidly diminishing in extent and increasing in fragmentation (Echeverría *et al.* 2006). As a result, the conservation of chucao populations is a matter of increasing concern. Furthermore, information about these demographic traits are needed for understanding the evolution of life-history patterns, but at present little is known about the demography of passerines in temperate rainforests of South America. Successful management and conservation of endangered, threatened, and at-risk species requires substantial knowledge of the species' natural history, including density, reproduction, dispersal, and survivorship. Annual survival rates have been associated with the observed

risk of extinction for tropical birds on Barro Colorado Island in Panama (Karr 1990), and forest fragments can be viewed as habitat islands. Chucao populations are sensitive to forest-fragment size and lack of connectivity among fragments: smaller fragments support lower densities, nesting success is slightly lower in fragments than in continuous forest, and lack of connectivity impairs natal dispersal and mate-finding (summarized in Willson 2006). The purpose of the present note is to provide information on chucao survival. Chucaos are non-migratory forest birds that typically forage on the forest floor and commonly nest in cavities in logs or hollow trees (Willson 2006); their estimated survival can be compared to that of North American passerines of similar habits and their life-history pattern compared to both North American and other southern hemisphere species.

METHODS

From 1995 to 2001, many chucao nestlings were banded, with individually distinctive combinations of colored plastic leg bands, in ten south-temperate rainforest fragments in northern Chiloé (see Willson 2004 for details). Some of these birds (n = 41, including 6 of unknown gender) were resighted as adults in these fragments and in surrounding fragments in subsequent years, through the breeding season of 2006. Although the sample size is small, our high probabilities of resighting adults mitigate the effects of small sample size, and we use model selection criteria specifically formulated for small samples. These data provide the only existing information on survival of adult chucaos, *i.e.*, those that were one year old when resighted for the first time and followed annually until they disappeared. Male chucaos establish territories in their first winter and reside on them for the rest of their lives despite extensive searching every spring, we never detected a change of location for banded adult males, although the borders of the territories sometimes shifted a little. Marked females occasionally moved between years, particularly after a failed nesting attempt, but they were subsequently sighted on nearby territories.

A series of Cormack-Jolley-Seber mark-resight models (Williams *et al.* 2001) were used to estimate survival (φ) and resight probabilities (p) for these adults. Initially, we fit a series of models for data from 35 known-sex birds allowing adult survival probability to vary by age and sex and resight probability to vary by calendar year and sex. We also fit a second series of models for data from 41 birds, including 6 of unknown sex, that only allowed age variation in survival estimates and time variation in resight probability. For both series we used the following procedures: We used the bootstrap goodness-of –fit procedure in program MARK (version 5.1), with 500 replicates to evaluate the fit of the most complex model in each series and estimate an overdispersion factor ĉ if necessary (Burnham and Anderson 2002). MARK is a software package for analysis of a wide variety of mark-recapture data; depending on the sample format and data, MARK is used to estimate quantities associated with the sampling process (*e.g.*, capture probability) and population structure (*e.g.*, survival probability, population size). (MARK software and documentation are available at http:// welcome.warnercnr.edu/ ~gwhite/mark/ mark.htm and http://www. phidot. org/soft-ware/mark/).

After fitting the initial complex model, we fit simpler models by removing sex or age effects or reducing the complexity of the age effect by constraining survival to be equal for some adjacent ages; models were compared based on the change (Δ) in AIC_c or $QAIC_c$ (Burnham and Anderson 2002). Model weight, based on ΔAIC_c or $\Delta QAIC_c$, is the support for

a model relative to other models considered (summing to 1). Akaike's Information Criteria (AIC) is used to select an optimal statistical model from among a set of models for a data set with the goal of balancing model complexity, to reduce bias, and parsimony, to improve precision (Burnham and Anderson 2002). AIC contains a likelihood-based goodness-of-fit component and a degrees-of-freedom-based 'penalty' to reduce the selection of overly complex models. Alternatively, AIC can be used to rank models to produce weighted estimates based on results across multiple models. A small-sample version of the criteria, AICc (Hurvich and Tsai 1989), gives better results with small samples and is equivalent to AIC with large samples, and hence should always be used (Burnham and Anderson 2002).

RESULTS

The first series of models (known-sex birds only) provided no support for variation between sexes in either survival or resight probabilities (Appendix 1); consequently, we only present results from the second series of models based on all 41 birds. The bootstrap goodness-of-fit procedure for the most complex model (17 parameters) indicated modest overdispersion; we adjusted standard errors and AIC_c (becoming $QAIC_c$) using $\hat{c}$ =1.64. The best model (Appendix 1) was far superior to all others tested, with greater than three times the weight of the second best model. The best model indicated lower survival from age one to two, followed by constant annual survival ($\varphi_{1\text{-}2}$ = 0.442, 95% confidence interval 0.264 to 0.637; $\varphi_{2\text{-}7}$ = 0.718, 95% CI = 0.541 to 0.846). The estimated annual resight probability was very high (P = 0.975, 95% CI 0.865 to 0.996) and did not vary among years; only two birds, one male and one female, were missed in one year but seen the following year. Even without

estimates of juvenile survival, these estimated adult survival probabilities suggest that fewer than 5% of adults would be alive at seven years of age, as was indeed observed – only one banded individual reached seven years of age.

A larger sample from the same sites in the same years but including birds banded as adults documented annual variation in apparent survival over six years, ranging from 36% to 83% of all marked adults (60%, n= 15; 69%, n= 26; 36%, n= 36; 83%, n= 18; 53%, n= 19; 64%, n= 11; a smaller sample of nine birds had 100% survival in another year). These apparent survival percentages likely are close to the true survival because our sighting probability was approximately 1.

DISCUSSION

Our estimates are likely to be unbiased estimates of true annual survival, because of the very low likelihood of adult dispersal. The estimated probabilities of apparent annual survival for chucaos are as high or higher than those of several nonmigratory North American passerine birds that nest, as chucaos usually do, in existing cavities (reviewed in Martin and Li 1992, Martin 1995, Doherty and Grubb 2002). Similarly, estimated chucao survival probability after age 2 (but not from age 1 to 2) is higher than the average survival of several North American ground-foraging forest passerines (including migrants; Martin 1995). Although within-population heterogeneity in demographic traits can affect demographic stochasticity and risk of extinction (Fox *et al.* 2006), present data are too few to analyze such heterogeneity for chucaos in a formal way (except to indicate marked annual variation and no difference between males and females). The observed annual variation in survival estimates covers the range of estimates for both northern temperate and tropical birds (Schaefer *et al.* 2006).

To put the existing information into an evolutionary perspective: High adult

(compared to juvenile) survival is expected to be associated with a relatively low reproductive effort and, conversely, low adult survival is expected to be correlated with a relatively high reproductive effort, although age-specific density-dependence can alter these general expectations (reviewed in Reznick *et al.* 2002). Adult chucao survival is undoubtedly higher than juvenile survival, but clutch size is low (usually 2 eggs; sometimes 3 in forest fragments), although two or sometimes even three broods can be raised per year (Willson 2006). If juvenile mortality were density-dependent (as seems possible, given the year-round territory occupancy of adults), however, there might be some selection for increased reproductive effort (Reznick *et al.* 2002), perhaps seen in the number of broods rather than in clutch size. If breeding seasons are generally longer in south-temperate birds, there is more opportunity for multiple broods (*e.g.*, Russell *et al.* 2004). In continuous forest, assuming an average clutch size of two (De Santo *et al.* 2002) and two broods per year, chucaos would achieve a potential annual fecundity of 4 chicks. In fragmented forest, assuming an average clutch size of 2.4 (De Santo *et al.* 2002) and 2.5 broods per year, chucaos could have a potential annual fecundity of about 6 chicks per year. However, the larger clutches in fragments occurred especially after failure of the first nest (De Santo *et al.* 2002), so the achieved fecundity would be lower than six. These estimates are lower than those of most north-temperate cavity-nesting songbirds with larger clutch size and one or sometimes two broods per year (Martin and Li 1992, Martin 1995).

However, it must be recognized that the clutch sizes, number of nesting attempts, and survival estimates are likely to vary among study sites and years for all the species used in the above calculations; for example, Martin (1995) gives the probability of annual survival for downy woodpeckers (*Picoides pubescens*) at about 60%, but Doherty and Grubb (2002) give a value of 26% in fragmented forest. We lack information on chucao survival and the actual number of nesting attempts in unfragmented forests, so the above estimates of annual fecundity and survival may not apply to chucaos in undisturbed native forest (or to populations in plantations of exotic trees). Ignoring the caveat of spatial and temporal variability, it appears that chucaos have a lower potential output of chicks than the North American species. That is, they tend to have a 'slow' life-history pattern, as do many other southern hemisphere birds (*e.g.*, Russell *et al.* 2004, and others).

At this time, nothing is known about juvenile survival of chucaos (the data in Willson 2004 would provide a large overestimate, because juvenile dispersal from isolated fragments was low, and such patches were represented disproportionately to their occurrence in the present landscape), but it is certainly expected to be much lower than that of adults. Chucaos in fragments appear to have good nesting success, but chucao populations in these fragments are not increasing, indicating that most of the juveniles leave or die before maturity. Juveniles typically disperse from their natal areas, but dispersal is undoubtedly a dangerous enterprise, because the inexperienced birds encounter unfamiliar terrain and may attempt to cross unsuitable habitats. Marked juveniles are known to move up to four km (straight-line distance) among connected fragments (MFW, pers. obs.), and the actual distance traveled would be at least twice that, if the dispersers stayed in dense cover. We suggest that juvenile survival and successful dispersal are critical factors in maintaining viable chucao populations, especially in fragmented forest. Furthermore, female passerines are more dispersive than males (*e.g.*, Clarke *et al.* 1997, Dale 2001),

which would expose them to more risks, and which could contribute to the observed male-biased sex ratios of adult chucaos in isolated fragments (Willson 2004).

Comparative survival estimates for adult chucaos in undisturbed, continuous forest would be useful for understanding the magnitude of the impact of fragmentation on this aspect of chucao life history. Data on juvenile survival in fragmented and unfragmented forest are highly desirable. Similarly, survival and other demographic data for other austral rainforest birds are desirable for understanding the evolution of life-history patterns of south-temperate birds of differing ecology and for devising management and conservation plans. However, a recent meta-analysis of avian demography in fragmented forest discovered no such studies for birds of the Neotropical zoogeographic region (Lampila *et al.* 2005).

LITERATURE CITED

BURNHAM, K. P. & D. R. ANDERSON. 2002. Model selection and inference: an information theoretic approach. Second edition. Springer-Verlag, New York.

CLARKE, A. L., B-E SÆTHER, & E. RØSKAFT. 1997. Sex biases in avian dispersal: a reappraisal. Oikos 79: 429-438.

DALE, S. 2001. Female-biased dispersal, low female recruitment, unpaired males, and the extinction of small and isolated bird populations. Oikos 92: 344-356.

DE SANTO, T. L., M. F.WILLSON, K. E. SIEVING, & J. J. ARMESTO. 2002. Nesting biology of tapaculos (Rhinocryptidae) in fragmented south-temperate rainforests of Chile. Condor 104: 482-495.

DOHERTY, P. F. JR. & T. C. GRUBB JR. 2002. Survivorship of permanent-resident birds in a fragmented forested landscape. Ecology 83: 844-857.

ECHEVERRÍA, C., D. COOMES, J. SALAS, J. M. REY-BENAYAS, A. LARA & A. NEWTON.2006. Rapid deforestation and fragmentation of Chilean temperate forests. Biological Conservation 130: 481-494.

FJELDSÅ, J. & N. KRABBE. 1990. Birds of the high Andes. Zoological Museum, University of Copenhagen and Apollo Books, Svendborg, Denmark.

FOX, G. A., B. E. KENDALL, J. W. FITZPATRICK & G. E. WOOLFENDEN. 2006. Consequences of heterogeneity in survival probability in a population of Florida scrub-jays. Journal of Animal Ecology 75: 921-927.

HURVICH, C. M. & C-L TSAI. 1989. Regression and time series model selection in small samples. Biometrika 76: 297-307.

KARR, J. R. 1990. Avian survival rates and the extinction process on Barro Colorado Island, Panama. Conservation Biology 4: 391-397.

LAMPILA, P., M. MÖNKKÖNEN & A. DESROCHERS. 2005. Demographic responses by birds to forest fragmentation. Conservation Biology 19: 1537-1546.

MARTIN, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. Ecological Monographs 65: 101-127.

MARTIN, T. E. & P. LI. 1992. Life history traits of open vs. cavity-nesting birds. Ecology 73: 579-592.

REZNICK, D., M. J. BRYANT & F. BASHEY. 2002. *r*- and *K*-selection revisited: the role of population regulation in life-history evolution. Ecology 83: 1509-1520.

Russell, E. M., Y. Yom-tov & E. Geffen. 2004. Extended parental care and delayed dispersal: northern, tropical, and southern passerines compared. Behavioral Ecology 15: 831-838.

Schaefer, H-C. G. W. Eshiamwata, F. B. Munyekenye, E.M. Griebeler & K. Böhning-Gaese. 2006. Monthly survival of African *Sylvia* warblers in a seasonally arid tropical environment. Ibis 148: 411-424.

Williams, B. K., J. D. Nichols & M. J. Conroy. 2001. Analysis and management of animal populations: modeling, estimation, and decision making. Academic Press, San Diego, CA.

Willson, M. F. 2004. Loss of habitat connectivity hinders pair formation and juvenile dispersal of chucao tapaculos in Chilean rainforest. Condor 106:166-171.

Willson, M. F. 2006. Chucaos in Chiloé. Boletín Chileno de Ornitología 12: 40-44.

Appendix 1. Models and accompanying fit statistics for estimating chucao adult survival and resight probabilities.

Series 1 ($\hat{c}$ = 1.41)

Model*	QAIC$_c$	QAIC$_c$ weight	Parameters
$\varphi_{(1-2, 2-7)}$; $p_{(.)}$	98.4	0.446	3
$\varphi_{(1-7)}$; $p_{(.)}$	98.8	0.368	2
$\varphi_{(a)}$; $p_{(.)}$	100.8	0.135	7
$\varphi_{(s)}$; $p_{(.)}$	102.8	0.050	3
$\varphi_{(a*s)}$; $p_{(.)}$	110.6	0.001	13
$\varphi_{(a*s)}$; $p_{(s)}$	113.2	0.000	14
$\varphi_{(a*s)}$; $p_{(t)}$	134.3	0.000	23
$\varphi_{(a*s)}$; $p_{(t*s)}$	170.7	0.000	34

Series 2 ($\hat{c}$ =1.64)

Model	QAIC$_c$	QAIC$_c$ weight	Parameters
$\varphi_{(1-2, 2-7)}$; $p_{(.)}$	90.2	0.771	3
$\varphi_{(1-7)}$; $p_{(.)}$	92.5	0.229	2
$\varphi_{(a)}$; $p_{(.)}$	95.1	0.060	7
$\varphi_{(a)}$; $p_{(t)}$	116.0	0.000	17

* φ represents survival probability and p represents resight probability. Subscripts are a (separate parameters for each age), s (separate parameters for both sexes), t (separate parameters for each year), and their interactions. Numeric subscripts on φ indicate separate survival probability for age 1-2 and a composite annual survival probability for all older age classes (i.e., 2-7) or a single annual survival probability for all ages (i.e., 1-7)