NESTING BIOLOGY OF TAPACULOS (RHINOCRYPTIDAE) IN FRAGMENTED SOUTH-TEMPERATE RAINFORESTS OF CHILE

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Abstract. We studied the effect of forest fragmentation on the nesting biology and reproductive success of three species of tapaculos (Rhinocryptidae) in relation to forest size, edge effects, and disturbance from livestock or logging over a 6-year period (1993–1999) in Chilean temperate rainforest. Overall, Mayfield nest success ($n = 360$) among the three species ranged from 64% to 85%, and predation accounted for 64% of nest losses. Considering all types of losses, nest mortality was similar in fragmented and unfragmented forest, but predation was higher in fragmented forest. Successful nest sites of the Chucao Tapaculo (*Sclerochilus rubecula*; the species with the largest sample size) were nearer forest edges, better concealed, closer to the ground, and had longer entrance tunnels, on average, than depredated nests. Reuse of nest sites by chucaos was more common in forest fragments with livestock or logging than in undisturbed forests, but reuse was independent of forest size. Success of second broods was lower in reused nest sites than in new nest sites. Nestling growth in fragmented forest and forest with livestock or logging activity was similar to that in unfragmented and undisturbed forest. Clutch size was typically two, but birds nesting at low densities in forest fragments often laid three-egg clutches following a nest failure. In addition to negative effects of forest fragmentation during nesting (greater use of less-successful nest sites, higher nest predation), there was an indication that early juvenile survival was lower in forest fragments.

Key words: clutch size, forest fragmentation, juvenile survival, nest-site availability, nest-site reuse, nest success, Rhinocryptidae.

Biología de Nidificación de Tapaculos (Rhinocryptidae) en la Selva Lluviosa Templada Fragmentada de Chile

Resumen. Durante seis años (1993–1999) estudiamos los efectos de la fragmentación de bosques templados del sur de Chile sobre la biología y éxito reproductivo de tres especies de tapaculos (Rhynocriptidae) en relación al tamaño del fragmento boscoso, efectos de borde, y perturbación por ganado doméstico y tala de árboles. En general, el éxito de nidificación ($n = 360$) estimado por el método Mayfield para las tres especies varió entre 64% y 85%. La depredación explicó un 64% de las pérdidas de nidos. Tomando en cuenta todas las causas de mortalidad, la pérdida de nidos fue equivalente en bosques fragmentados y continuos, pero la depredación fue mayor en bosques fragmentados. Los sitios de nidificación exitosa de *Sclerochilus rubecula* (chucao; la especie con el mayor número de muestras) se encontraron, en promedio, más cerca de los bordes, mejor ocultos, más cerca del suelo y con túneles de entrada más largos que los nidos depredados. La reutilización de nidos por parte de los chucaos fue más común en los fragmentos perturbados por tala de árboles o pisoteo de ganado que en bosques no perturbados, pero fue independiente del tamaño del fragmento. El éxito de la segunda nidada fue menor en nidos re-utilizados que en nidos nuevos. El crecimiento de los juveniles en los nidos ubicados en bosques fragmentados y perturbados fue similar al del observado en los bosques continuos no perturbados. El número de crías de los chucaos fue típicamente dos, pero las aves que anidaron en fragmentos boscosos, donde la densidad local era baja, frecuentemente pusieron tres huevos por nido luego de un intento de nidificación fallido. Además de los efectos negativos de la fragmentación del bosque durante el período de nidificación (i.e., mayor uso de sitios

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de nidificación inseguros, mayor depredación de nidos), la sobrevivencia temprana de los juveniles sería menor en fragmentos boscosos.

INTRODUCTION

The effects of fragmentation on forest communities have been widely studied in north-temperate forests of North America, where many forest-dwelling songbirds have experienced population declines and reduced reproductive success (Robbins et al. 1989, Askins 1995, Faaborg et al. 1995, Hobson and Bayne 2000), primarily as a result of increased nest predation and brood parasitism concentrated at forest edges (Robinson 1992, Hoover et al. 1995, King et al. 1996). The rainforests of the south-temperate zone of South America have been little studied, even though many endemic forest species there are particularly vulnerable to habitat modification because of small geographic ranges (Fjeldså and Krabbe 1990, Ridgely and Tudor 1994, Willson and Armesto 1996). Furthermore, fragmentation is particularly detrimental to nonmigratory terrestrial insectivorous birds of tropical forests in Central and South America (Terborgh 1974, Karr 1982, Lovejoy et al. 1984, Canaday 1996, Renjifo 1999). The avifauna of the temperate rainforest of Chile includes several species of nonmigratory understory insectivores that are phylogenetically related (Ridgely and Tudor 1994) to tropical species identified as vulnerable to forest fragmentation, and therefore, these Chilean species may be similarly at risk.

Previous work in south-central Chile demonstrated that many species of forest birds in the region are sensitive to habitat modification (Willson et al. 1994, Sieving et al. 1996, 2000). Members of the family Rhinocryptidae, commonly referred to as tapaculos, are particularly sensitive to forest fragmentation, showing distinctly lower abundances in smaller fragments (Willson et al. 1994) and an aversion to leaving forest cover and entering open fields (Sieving et al. 1996, 2000). Four species of tapaculos are endemic to south-temperate rainforest in Chile and western Argentina (Ridgely and Tudor 1994) and are considered globally threatened as a result of deforestation in this area (Glade 1988, Collar et al. 1992). We documented the nesting biology and reproductive success of endemic tapaculos in fragmented and unfragmented forest. Specifically, we examined nest-site selection, nesting density, nest success, nest reuse, clutch size, and nestling growth with respect to several habitat features and nest-site characteristics.

METHODS

STUDY AREA

Our study was conducted on Isla Grande de Chiloé, Region X, south-central Chile (41°55′S, 73°35′W), in the austral spring and summer (late October–early February) of six consecutive years (1993–1994 through 1998–1999). Chiloé Island is a large continental island that lies within 10 km of the mainland and supports similar communities of birds (Johnson 1967, Fjeldså and Krabbe 1990, Ridgley and Tudor 1994).

When Charles Darwin visited Chiloé in 1834–1835, the land was covered by dense forest (Darwin 1959). Much of the natural vegetation of this zone now has been removed and the land converted to agriculture. Today, the landscape in south-central Chile consists of numerous patches of forest embedded in agricultural land (Willson and Armesto 1996). Remnant forest fragments are maintained by landowners as shelter for livestock in winter and as a source of firewood for cooking and heating. Most fragments are connected to larger forest tracts or other forest fragments by wooded corridors, often along streams and deep ravines, or strips of shrubby vegetation.

Study sites (Fig. 1) included (1) a 25-ha (2 km × 100–200 m) area within a 43 000-ha continuous forest in the Parque Nacional de Chiloé on the west coast of the island, near the settlement of Colé-colé; and (2) 16 forest fragments within 15 km of each other on northeastern Chiloé Island, where agriculture was the predominant land use. Fragments were defined as discrete patches of mature forest bordered by pastureland on most sides. Large fragments ranged in size from 101–136 ha (mean ± SE = 116 ± 8 ha, $n = 4$) and small fragments were 4–33 ha (12 ± 3 ha, $n = 12$) in size. Many of the fragments had been selectively logged and were used as winter shelter for livestock. Six fragments (two large, four small) had no current livestock or logging activity. Five fragments (one large, four small) had minimal anthropogenic disturbance as indicated by few domestic cattle trails, used only in winter, and current log-
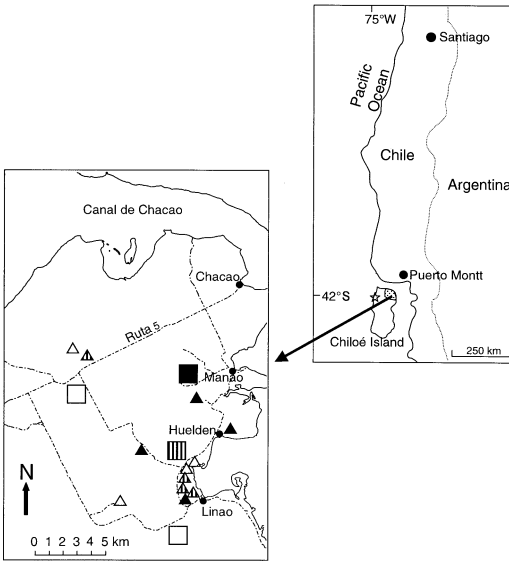
FIGURE 1. Map of study area on Chiloé Island, Chile. The national park site is indicated by a star; small fragments are denoted by triangles and large fragments by squares (size of symbol does not reflect actual fragment size). Condition of fragments relative to livestock or logging activity is indicated by pattern: no pattern = no activity; striped = minimal activity; solid = considerable activity.

ging limited to the periphery of the fragment. Five fragments (one large, four small) had considerable anthropogenic disturbance, as indicated by numerous cattle trails used year round and selective timber harvest occurring within the fragments during the study. Unlike many of the forest fragments, disturbance within the national park site was very low, with human activity limited to one hiking trail and a campground along the coastal periphery.

We measured fragment area from aerial photographs (1:20 000 scale), using a 10 × 10 mm gridded transparency placed over the photo. Trails within each study area were flagged and maps of sites were drawn using measurements from compasses and meter tapes. Landmarks (i.e., trails, nests, creeks, fences, etc.) were designated on maps. These maps were used to mark bird movements and territory boundaries.

The native old-growth rainforest in the fragments was characterized by emergent *Nothofagus nitida* and a canopy of *Drimys winteri*, *Weinmannia trichosperma*, several myrtaceous species, and *Podocarpus nubigena* (Armesto and Figueroa 1987, Veblen et al. 1996). The under-

story included dense *Chusquea* spp. (bamboo) thickets and sapling trees. The tree composition of the forest of the national park was characterized by more *Aextoxicon punctatum* and *Luma apiculata*, and less *P. nubigena*. Epiphytic bromeliads were common.

STUDY SPECIES

The family Rhinocryptidae is represented by at least 30 species, over half of which occur in southern South America (Ridgely and Tudor 1994). Within southern Chilean forests, the family is represented by four species, the Black-throated Huet-huet (*Pteroptochus tarnii*; hereafter referred to as huet-huet), the Chucao Tapaculo (*Sclerochilus rubecula*; chucao), the Magellanic Tapaculo (*Scytalopus magellanicus*), and the Ochre-flanked Tapaculo (*Eugralla paradoxa*). All four species are endemic to the south-temperate rainforest of Chile and westernmost Argentina, occurring primarily in mature *Nothofagus* forest (Vuilleumier 1985, Ridgely and Tudor 1994). The huet-huet is the largest member of the family (122–145 g), and the Magellanic Tapaculo is the smallest (11–12 g; De Santo et al., unpubl. data). The chucao (35–43 g) and Ochre-flanked Tapaculo (24–30 g) are intermediate in size (De Santo et al., unpubl. data). The first three species are known to be multi-brooded and defend territories at least through the breeding season (September through February) and probably for much longer. All species are understory insectivores, permanent residents, and give strong vocal territorial responses. These features make them relatively easy to follow and study, but their nests are cryptic and difficult to find. Chucaos are perhaps the most tractable of the four species as they are abundant and often unwary of humans. In order to locate a sufficient number of nests for calculation of Mayfield daily survival rates, we chose the chucao as our focal species. We encountered nests of the other three species of tapaculos while searching for chucao nests and have included them in our overall analysis of tapaculos, and as individual species when possible and appropriate.

BANDING AND TERRITORY MAPPING

Twenty-five adult chucaos at 19 nests were banded with an aluminum alphanumeric band (National Band and Tag Co., Newport, Kentucky) and a unique combination of colored

plastic leg bands (Avinet, Dryden, New York). Ten adults were lured with song playback (Falls 1981, McGregor 1992) to mist nets placed along known travel lanes; once the bird was close to the net, observers herded the bird into the net. Fifteen adults were captured with hoop nets placed over nest entrances during nestling feeding trips; this method was more successful than the former. All nests with banded adults survived for at least a week after banding, and most fledged young (75% of 19 nests); thus we do not believe that banding impaired nesting effort.

We concentrated on finding chucao nests on adjacent territories, which enabled us to keep track of most nesting adults (including unbanded individuals) within a known area and mark their activities on maps. We indexed local breeding density of chucaos by counting (and mapping) the number of territories contiguous to each focal territory. The position of territories within fragments influenced the number of possible neighbors: birds occupying territories on forest edges or within narrow strips of habitat had fewer neighbors because their territories were bounded on one or more sides by unsuitable habitat (pastures and open fields; Sieving et al. 1996, 2000). The density of birds per whole patch was unknown for large fragments, because we did not measure the actual area searched in large fragments; in any case that value is less relevant than the number of interacting territorial pairs.

NEST MONITORING

Our nest-searching effort varied among years, and most nests were found in four field seasons (austral spring and summer of 1994–1999). Between 4 and 10 observers searched for nests during daylight hours (06:30 to 12:30 and 14:00 to 20:00 local time). We found nests by following birds that were carrying nesting material or food or that were giving vocalizations characteristic of nesting.

Nests were monitored every 1–3 days until the young fledged or the nest failed. We manually checked shallow nests and used a fiberoptic scope (Olympus America Inc., Long Beach, California) to see into nests within cavities up to 1 m deep. Status of inaccessible nests was determined by watching nesting behavior of adults. We considered a nest to be (1) active, if there was evidence that eggs or young were being tended; (2) depredated, if the nest showed obvious signs of depredation (eggshell fragments or torn nesting material) or if nest contents were missing before possible fledging age (based on nestling measurements, plumage development, and comparison to known-age birds); (3) failed due to weather, if the nest showed obvious signs of disturbance from wind, rain, or flooding; (4) abandoned, if the nest was not tended but cause of failure was unknown; or (5) successful, if adults were observed feeding ≥ 1 nestling near fledging age, ≥ 1 young was observed in the territory after fledging, or adults were seen within their territory carrying food and making characteristic vocalizations to fledglings. Nests abandoned during nest building or not used for reproduction were excluded from analyses.

Chucaos and possibly other species of tapaculos retain their territories for at least the current breeding season, renesting within the territory, and often within the same nest. Therefore, after a nest completed, we closely monitored adult birds for signs of renesting and monitored old nest sites for signs of reuse. Tapaculos only reused nests that had fledged young that season, so we used only these nests to calculate the frequency of reuse.

NEST-SITE CHARACTERISTICS AND NEST-SITE AVAILABILITY

Once a nest was no longer active (following failure or fledging of all nesting attempts for the season within that nest site), we measured its physical characteristics, including (1) distance of nests to nearest edge (pastureland, logged areas, or agricultural fields); (2) height of nest (noncavity nests) or entrance hole (cavity nests) above ground; (3) support structure of nest (tree, snag, stump, log, root disk of uprooted tree, stream bank, ground, tree branch, bromeliad, root-and-limb tangles); (4) length of cavity entrance from opening to proximal lip of nest (designated as zero for noncavity nests); and (5) percentage of concealment of nest in the four cardinal directions and from above and below, estimated (to nearest 10%) at 1 m from nest or entrance. We also noted evidence of recent livestock or logging activity (domestic animal tracks, harvested trees) in the area of the nest. Not all measurements could be obtained for all nests because some nests were inaccessible.

Thirty-seven chucao nest sites with known outcomes were used more than once by breeding chucaos, either within or among breeding sea-

sons. We examined the characteristics of nest sites of differing levels of predation risk; we categorized nest sites as ''successful,'' if all nesting attempts at the nest site were successful, or ''depredated,'' if one or more of the nesting attempts at the nest site were depredated. Nests reused within the same breeding season were measured once, at the end of the season, and thus the data appear only once in the dataset. Nine nests were reused in subsequent seasons and were remeasured each season. While some nest-site measurements (support structure, height above ground, and cavity length) did not change from one season to the next, others (distance to edge, percent cover) sometimes did. In most cases, measurements differed by 10% or less, and when they did, we used an average of the measurements. In two instances, percent cover changed by more than 15% between nesting attempts, once due to removal of vegetation by livestock and once due to collection of debris on the roof of a nest. For the univariate analysis of percent cover, both estimates of percent cover for these two nests were included in the dataset, and the full suite of nest-site measurements for each of these nests was included in the logistic regression analysis. For analysis of substrates used, we counted nests only once (i.e., reused nests were not included).

We estimated the relative abundance of potential chucao nest sites within a subset of forest fragments (two large and five small fragments) and the national park in 1996. We judged potential nest sites based on the kinds of sites used for nests in the past. The number of potential nest sites (logs, stumps, snags, cavities in live trees, root disks of uprooted trees, and bromeliads) was counted in 20 plots (5-m radius) placed at 20-m intervals along a 400-m transect. Plots were placed 5–10 m off the transect line alternating from the right to the left side of the transect at each station. One transect was placed in each forest fragment; three transects, located 0.5 km apart, were placed within the national park. Our judgments of potential chucao nest sites were consistently applied, and thus serve as a comparative index of potential nest sites present at different levels of fragmentation. We did not attempt to measure the amount of stream bank available as nesting substrate.

NEST SUCCESS, NESTLING GROWTH, AND EARLY JUVENILE SURVIVAL

Nest success was calculated using the Mayfield method (Mayfield 1961, 1975) as detailed by Hensler and Nichols (1981), including nests with uncertain fate (Manolis et al. 2000). We used average values for clutch sizes (two eggs for chucao and huet-huet, three for Magellanic Tapaculo), incubation periods (23 days for chucao, 22 for huet-huet, 19 for Magellanic Tapaculo), and nestling periods (21 days for chucao, 21 for huet-huet, 11 for Magellanic Tapaculo), to determine observation days in each period of the nesting cycle (De Santo et al., unpubl. data). For calculations of percent nest success, we included the period of egg laying as part of the incubation period.

Chucao nestlings in accessible nests were color banded just before fledging (when nestlings were at least approximately 15 days old, an age at which adult mass was achieved; De Santo et al., unpubl. data). Mass of nestlings was determined to the nearest 1 g using a 100-g Pesola spring scale. Fluctuating asymmetry (nondirectional deviations from bilateral symmetry; Palmer and Strobeck 1986) of morphological characters occurs in many organisms (Leary and Allendorf 1989, Parsons 1990), including nestlings (Møller 1995), raised under stressful conditions. Because asymmetric individuals have been shown to be at a selective disadvantage (Møller 1994), we tested for fluctuating asymmetry of nestlings raised in forests of different sizes and in forests with and without livestock or logging activity. Using Vernier calipers, we measured the lengths of both tarsometatarsal bones (tarsi) to the nearest 0.1 mm; we measured the ninth primary of each wing and the length of each relaxed wing to the nearest mm, using a straight ruler.

In the final year of our study, we estimated early juvenile survival by searching systematically for banded fledgling chucaos within their natal territories at 14 days postfledging and calculating the proportion of nests for which at least one juvenile was resighted. A standard amount of time (3 person-hr) was spent in each territory (unless the juveniles were resighted in less than the minimum) in an effort to obtain results that were comparable among study sites. Fledgling chucaos commonly remain with their parents in or near their natal territories for at least 45 days postfledging and are dependent on their parents for food until at least 21 days postfledging (De Santo et al., unpubl. data). Adults and young make vocalizations that are unique to this period of the nesting cycle (TLD, pers.

obs.), and adults typically are not wary of observers while delivering food to young. Both behaviors facilitated our efforts to relocate young, even those concealed in vegetation.

STATISTICAL ANALYSES

The number of chucao nests in our dataset far exceeded that of any other species. When data were sufficient to analyze all four tapaculo species pooled, we randomly selected a subset of chucao nests to use such that chucao nests outnumbered no other species. Daily nest survival rates were analyzed with the computer program CONTRAST, which uses a chi-square analysis with multiple comparisons (Hines and Sauer 1989, Sauer and Williams 1989).

Differences in nest-site characteristics among species (Kruskal-Wallis test) and differences in nest-site characteristics of successful and depredated chucao nest sites (Wilcoxon two-sample test and stepwise logistic regression) were examined in SAS (SAS Institute Inc. 2000). The logistic regression model used nest-site characteristics to predict nest success and had an entry criterion of $P < 0.25$. Logistic regression was performed on a dataset that included only nest failures from predation, because predation was the principal cause of failure and because we were particularly interested in the relationship between predation and nest characteristics. Goodness-of-fit of the logistic model was determined with the Hosmer-Lemeshow statistic (Hosmer and Lemeshow 1989).

Some breeding pairs were monitored during several breeding seasons; others were monitored in only one season. For pairs that were monitored in several seasons, we randomly selected one year of data to use for the analysis of nest reuse within a breeding season. Mutual independence among clutch size of renests, breeding density, and fate of previous nest was tested in a three-dimensional contingency table (Zar 1999). Subsequent tests of partial independence and tests of independence of two variables were conducted when appropriate (Zar 1999).

To examine nestling mass and symmetry of body parts in forests of differing degrees of fragmentation and disturbance, we used data from only one nestling per nest, chosen randomly, to avoid pseudoreplication. Differences in nestling body mass among forests of different sizes were analyzed with ANOVA and between disturbed and undisturbed forest by independent t-test

(SAS Institute Inc. 2000). Size of body part (ninth primary, wing, tarsus) was plotted against the absolute value of the difference between right and left sides to detect any scaling relationship. Fluctuating asymmetry was independent of character size (all $r^2 < 0.13$), so we did not transform the data (Palmer and Strobeck 1986). Differences in fluctuating asymmetry among nestlings from forests of different sizes were analyzed by Kruskal-Wallis test; Wilcoxon two-sample tests (SAS Institute Inc. 2000) were used to compare disturbed with undisturbed forests and forest edge with forest interior.

All percent data were angular transformed, and nest-site availability data were log-transformed prior to analysis. For *post hoc* multiple pairwise comparisons, we used an adjusted alpha value to control for experimentwise error (Zar 1999). For all analyses, we accepted $P \leq 0.05$ as the level of significance, and we report values as mean $\pm$ SE.

RESULTS

TAPACULO NESTING SUCCESS

We monitored 360 tapaculo nests, including 265 chucao, 47 Magellanic Tapaculo, 42 huet-huet, and six Ochre-flanked Tapaculo nests (Table 1). There was no difference in daily nest survival among the main years of our study (1994–1995 to 1998–1999) for tapaculo nests considered as a group ($\chi^2_3 = 2.1$, $P > 0.5$) or for chucaos considered separately ($\chi^2_3 = 0.7$, $P > 0.8$). Therefore, subsequent analyses were pooled over years. Nest survival during the incubation and nestling periods did not differ for tapaculos considered as a group ($\chi^2_1 = 0.8$, $P > 0.4$) or chucaos considered separately ($\chi^2_1 = 0.5$, $P > 0.4$; Table 1).

Twenty-one percent of 278 tapaculo nests with known outcome failed, most often as a result of known nest predation (64% of 59 nest failures). Other types of nest failure included flooding of nests near streams or rivers ($n = 2$), collapse of nest-support structures as a result of storms ($n = 2$), and abandonment of nonviable eggs ($n = 3$); 14 nests failed from unknown causes.

Nest success of three tapaculo species ranged from 64% to 85% (Table 1). Daily survival differed among species ($\chi^2_2 = 9.9$, $P < 0.01$); pairwise comparisons showed that daily survival was significantly higher for huet-huets than for

TABLE 1.   Mayfield daily nest survival rate ± SE (DSR) and nest success of tapaculos, Chiloé Island, Chile, 1993–1999.

Species	n (nests)	Incubation		Nestling		Nesting period		
		DSR (SE)	Exposure days	DSR (SE)	Exposure days	DSR (SE)	Exposure days	Nest success (%)
Black-throated Huet-huet	42	0.995 (0.005)	209	0.998 (0.002)	402	0.997 (0.002)	611	85
Chucao Tapaculo	265	0.989 (0.002)	1966	0.990 (0.002)	3116	0.990 (0.001)	5082	64
Magellanic Tapaculo	47	0.986 (0.008)	221	0.997 (0.003)	323	0.993 (0.004)	544	74
All species[a]	360	0.989 (0.002)	2421	0.991 (0.001)	3879	0.991 (0.001)	6300	—[b]

[a] Insufficient data for separate Mayfield analysis of Ochre-flanked Tapaculo, but the six nests monitored (2 failed, 4 successful; 25 exposure days during incubation, 38 exposure days during nestling period) are included in the species total.
[b] Not calculated for all species pooled because of variation in incubation and nestling periods among species.

chucaos (χ^2_1 = 9.8, P < 0.01). Recently fledged juveniles were observed for 77% of 172 successful chucao nests, 61% of 21 successful Magellanic Tapaculo nests, 64% of 22 successful huet-huet nests, and 100% of four successful Ochre-flanked Tapaculo nests.

CHUCAO NEST SUCCESS AND FOREST FRAGMENTATION

Daily mortality of chucao nests from all causes did not differ between the forest fragments (0.011 ± 0.002) and the national park (0.007 ± 0.002; χ^2_1 = 2.0, P = 0.15), but daily mortality from predation was higher on nests in fragments (0.009 ± 0.001) than in the national park (0.003 ± 0.002; χ^2_1 = 7.2, P < 0.01). Overall percent nest success for chucaos was 63% in the forest fragments and 72% in the national park.

Chucaos in fragments commonly nested within 25 m of an edge (54% of 147 chucao nest sites). Over all study sites, there was no relationship between the safety of chucao nests from predation and distance from forest edge (Table 2). Within forest fragments, however, successful

TABLE 2.   Characteristics (mean ± SE) of successful and depredated Chucao Tapaculo nest sites, Chiloé Island, Chile, 1993–1999.

|	Successful nest sites (n)	Depredated nest sites (n)	Z[a]	P
Distance to forest edge (m)				
All sites	283.5 ± 30.7 (141)	121.6 ± 27.6 (35)	−0.7	0.46
Fragments	69.9 ± 12.4 (93)	87.7 ± 15.9 (32)	2.3	<0.05
Average nest concealment (%)				
All sites	95 ± 1 (138)	87 ± 3 (35)	−2.8	<0.01
Fragments	95 ± 1 (90)	85 ± 3 (32)	−3.1	<0.01
Lowest nest concealment score (%)				
All sites	82 ± 3 (139)	61 ± 7 (35)	−2.8	<0.01
Fragments	82 ± 3 (91)	57 ± 8 (32)	−3.0	<0.01
Nest cavity entrance length (cm)				
All sites	28.3 ± 3.3 (133)	14.1 ± 2.9 (36)	−2.5	0.01
Fragments	30.5 ± 4.1 (90)	13.4 ± 3.0 (33)	−3.2	0.001
Nest or entrance height above ground (cm)				
All sites	154.5 ± 15.4 (140)	154.8 ± 16.4 (36)	1.4	0.17
Fragments	128.1 ± 18.4 (92)	159.1 ± 16.8 (33)	2.8	<0.01

[a] Wilcoxon two-sample test.
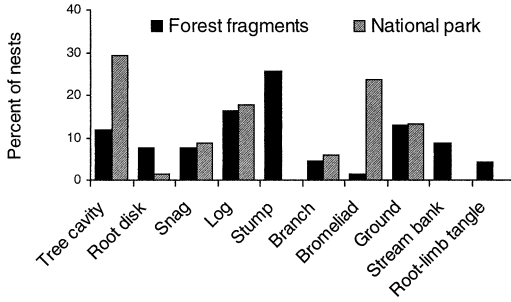
FIGURE 2.   Use of nest substrates by Chucao Tapaculos in forest fragments ($n = 150$ nests) and in the national park (unfragmented; $n = 59$ nests), Chiloé Island, Chile, 1993–1999.

nests were closer to edges than depredated nests. Daily nest mortality was identical between areas with and without livestock or logging activity (mean = 0.010 ± 0.002).

CHUCAO NEST-SITE CHARACTERISTICS AND NEST-SITE AVAILABILITY

Chucaos placed nests in different types of substrates in the unfragmented forest of the national park than in forest fragments ($G_9 = 72.9$, $P = 0.001$). Most nests in the national park were placed in cavities of live trees or logs, or within the leaves of bromeliads; stumps were not used (Fig. 2). By comparison, most nests in forest fragments were placed in or on stumps or in logs, but live-tree cavities and bromeliads were used far less often. The abundance of potential nest sites was greater in the national park than in forest fragments (two sample t-test, equal variances, $t_8 = -2.4$, $P < 0.05$); this result was due primarily to the greater abundance of live-tree cavities ($t_8 = -3.1$, $P < 0.05$) and bromeliads ($t_8 = -4.2$, $P < 0.01$) in the national park (Fig. 3).

Although chucaos are usually nonexcavating cavity nesters, occasionally they build nests outside of cavities (13% of 208 nest sites). Noncavity nests typically are woven of bamboo leaves and other vegetation fibers and may have a partial roof. The noncavity nests were placed on branches ($n = 10$), on tops of stumps or snags ($n = 8$), in tree forks ($n = 5$), or on the ground ($n = 3$). Noncavity nests occurred equally often in the park (6 of 59 nest sites) and in the forest fragments (20 of 149 nest sites; $G_1 = 0.4$, $P > 0.5$), and in forests with (16 of 135 nest sites) and without livestock or logging activity (10 of 73 nest sites; $G_1 = 0.2$, $P > 0.7$).
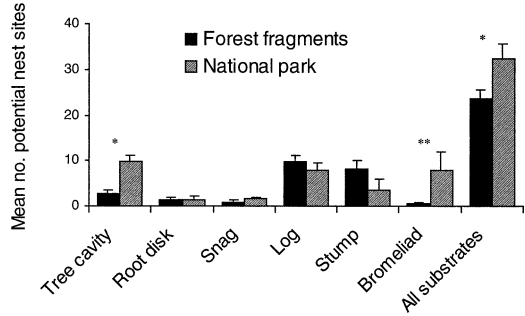

FIGURE 3.   Relative abundance of potential nest substrates (mean $\pm$ SE) for Chucao Tapaculos in forest fragments and in the national park (unfragmented), Chiloé, Chile, 1996. Numbers are potential nest sites counted in 20 plots (5-m radius; 1570 m^2 total area) at each site. Asterisks indicate significance between groups (*$P < 0.05$; **$P < 0.01$; see text).

Among all forest sites and within fragments only, successful chucao nest sites were better concealed and had longer entrance tunnels than depredated nest sites (Table 2). Within fragments, successful nest sites were also closer to the ground than depredated nest sites (Table 2). Daily mortality from predation was greater for noncavity nests (0.019 ± 0.006, $n = 33$ nests) than cavity nests (0.006 ± 0.001, $n = 232$ nests; $\chi^2_1 = 4.6$, $P < 0.05$), resulting in lower nest success for noncavity nests (49% compared to 68% for cavity nests). Reuse of nests within chucao territories was common but occurred only in nest sites that were initially successful. Sixty-five percent of territories ($n = 49$) contained at least one nest site that was reused during the study period, and 56% of 68 nest sites within these territories were used at least twice in the same breeding season. Even noncavity chucao nest sites were occasionally reused (7 of 26 noncavity nest sites were reused at least once). Frequency of nest reuse within a breeding season by chucao pairs was similar in fragments (68% of 34 chucao breeding pairs) and the national park (47% of 15; $G_1 = 1.9$, $P > 0.15$) but was more common in forests disturbed by livestock or logging (79% of 19 chucao breeding pairs) than undisturbed forests (52% of 31; $G_1 = 3.9$, $P < 0.05$). Within a breeding season, Mayfield daily survival of second or third broods that occurred in new nest sites (0.995 ± 0.002, $n = 38$) exceeded that of second or third broods that occurred in the same nest site (0.986 ± 0.004, $n = 40$; $\chi^2_1 = 4.1$, $P < 0.05$).

TABLE 3.   Results of stepwise logistic regression analyses comparing characteristics of successful and depredated Chucao Tapaculo nest sites, Chiloé Island, Chile, 1993–1999.

Variable	Coefficient	SE	Wald χ^2	P
All-sites model (178 nest sites)				
Intercept	0.748	0.535		
Lowest nest concealment score	0.013	0.007	3.5	0.06
Forest size (park, fragment)	0.860	0.320	7.1	<0.01
Nest cavity entrance length	0.019	0.012	2.7	0.10
Fragments model (127 nest sites)				
Intercept	−0.021	0.536		
Lowest nest concealment score	0.017	0.007	5.5	0.02
Nest cavity entrance length	0.018	0.012	2.2	0.14
Nest or entrance height above ground	−0.003	0.002	3.1	0.08

The best model for predicting safety of chucao nest sites from predators, as determined by stepwise logistic regression, included lowest nest cover in one direction, forest size, and entrance length. There was a good fit between the model and the data (Table 3; Hosmer-Lemeshow goodness of fit test, $\chi^2_8 = 8.5$, $P > 0.3$). Successful chucao nest sites were positively associated with nest concealment, entrance length, and forest size. Using only nest sites in forest fragments in the model yielded similar results, including the positive effect of nest concealment and entrance length, and an additional feature, nest height above ground, which was negatively associated with nest success. The fit of the fragment model was better than the all-sites model ($\chi^2_8 = 4.4$, $P > 0.8$). Nest type (cavity vs. noncavity), average nest concealment, and distance to forest edge were significant in the single-factor comparisons of successful and depredated nest sites but did not meet the significance level for entry into the logistic regression model. Livestock or logging activity near the nest was not significant in single-factor comparisons, nor did it meet the significance level for entry into the model.

CLUTCH SIZE, NESTLING GROWTH, AND EARLY JUVENILE SURVIVAL

Clutch size of chucaos ranged from one to three, but most nests contained two eggs (average clutch size: 2.32 ± 0.05, $n = 106$). Mean clutch size was significantly different among forests of different sizes (small fragments: 2.42 ± 0.06, $n = 65$; large fragments: 2.28 ± 0.09, $n = 25$; national park: 2.0 ± 0, $n = 16$; Kruskal-Wallis test, $H_2 = 10.3$, $P < 0.01$), largely due to the common occurrence of three-egg clutches in small forest fragments (42% of 65 nests had three eggs) and their absence in the national park ($G_3 = 15.8$, $P = 0.001$). Mean brood size at fledging did not differ among forests of different sizes (small fragments: 2.16 ± 0.06, $n = 70$; large fragments: 1.92 ± 0.10, $n = 25$; national park: 1.96 ± 0.04, $n = 23$; $H_2 = 4.7$, $P = 0.09$).

Three-egg clutches in fragments were more common later in the season; 9% of clutches produced before mid-November ($n = 77$) contained three eggs or young vs. 39% of later clutches ($n = 101$; $\chi^2_1 = 21.8$, $P < 0.001$). This pattern occurred because clutches of three were more common after partial or total loss of first broods than after successful nesting, particularly in territories with few neighbors (Fig. 4). Clutch size of renests, breeding density, and fate of previous nest were not mutually independent (Three-way
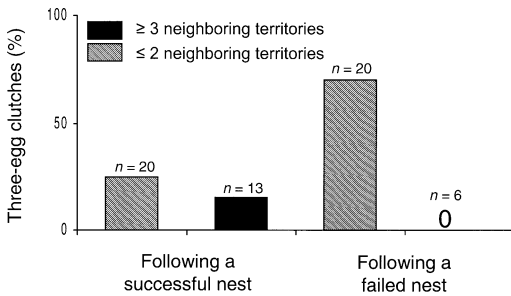

FIGURE 4.   Percentage of three-egg clutches for Chucao Tapaculo nests initiated after mid-November, in relation to success of the pair's previous breeding attempt and local breeding density. Failure of nesting attempt refers to either partial or complete loss of a clutch or brood or the premature disappearance (prior to 14 days postfledging) of fledglings before laying of following clutch.

test of mutual independence: $\chi^2_4 = 19.6$, $P < 0.001$). Testing for partial independence revealed that clutch size was not independent of breeding density or fate of previous nest ($\chi^2_3 = 16.6$, $P < 0.001$). Two-way contingency tests revealed that both nest fate ($\chi^2_1 = 5.4$, $P < 0.03$) and density ($\chi^2_1 = 6.2$, $P < 0.03$) were related to clutch size. The absence of three-egg clutches in the national park was related to the low nest-failure rate and the high frequency of territories that shared borders with ≥ 3 neighbors.

No difference in the mass of nestling chucaos was found among forests of different sizes ($F_{2, 86} = 0.4$, $P > 0.6$), between forests with and without livestock or logging activity (t_{87}, equal variances $= -0.8$, $P > 0.4$), or between forest edge and interior forest (Satterthwaite t_{75} unequal variances $= 0.5$, $P > 0.6$). No asymmetry was found for any body part (ninth primary, wing, or tarsus) among forests of different sizes (all $\chi^2_2 < 1.1$, all $P > 0.5$), between forests with and without livestock or logging activity (all $Z < 0.9$, all $P > 0.5$), or between forest edge and interior forest (all $Z < 0$, all $P > 0.7$).

Juveniles were resighted from a greater proportion of successful nests in the national park (100% of 12 nests) than in forest fragments (76% of 46 nests; $G_2 = 5.7$, $P < 0.02$), and within undisturbed forests (90% of 39 nests) than in forests with livestock or logging disturbance (63% of 19 nests; $G_2 = 5.5$, $P < 0.02$). The proportion of nests with resighted juveniles was not related to proximity to forest edges (78% of 23 nests within 25 m of edges vs. 82% of 35 nests in forest interior; $G_1 = 0.2$, $P > 0.6$).

NESTING BIOLOGY AMONG TAPACULO SPECIES

Like chucaos, other tapaculos often nested near edges of forest fragments (29% of 17 huet-huet nest sites and 76% of 25 Magellanic Tapaculo nest sites were within 25 m of forest edges; the sample size for Ochre-flanked Tapaculo was only 6, but 5 of these were within 25 m of a forest edge). Daily nest mortality from all causes did not differ between the national park (0.009 $\pm$ 0.004) and the forest fragments (0.008 $\pm$ 0.002) for all tapaculos collectively ($\chi^2 = 0.1$, $P > 0.8$). In contrast to the variable nest sites of chucaos, nests of huet-huets and Magellanic Tapaculos were always in cavities, and Ochre-flanked Tapaculos characteristically built shaggy, woven, domed nests on branches of shrubs

or bamboo, or on the ground. Five huet-huet nest sites were known to be reused (one in a large fragment, four in small fragments) at least twice in the same season and up to five times over the period of our study. One Magellanic Tapaculo nest site, in a large fragment, was reused twice in one season and at least three times over the course of the study.

Few Magellanic Tapaculo and no huet-huet nests were depredated. Because all Magellanic Tapaculo and huet-huet nests were located within cavities, they were better concealed (average nest concealment: 100 $\pm$ 0%, $n = 42$ for huet-huet; 99.6 $\pm$ 0.4, $n = 38$ for Magellanic Tapaculo; lowest concealment in one direction: 100 $\pm$ 0%, $n = 42$ for huet-huet; 97.6 $\pm$ 2.4, $n = 38$ for Magellanic Tapaculo) than chucao nests (average nest concealment: 93.2 $\pm$ 1.0%, $n = 173$; $\chi^2_2 = 35.4$, $P < 0.001$; lowest nest concealment 77.6 $\pm$ 2.7%, $n = 174$; $\chi^2_2 = 37.4$, $P < 0.001$). Compared to chucao nests, huet-huet nests were located higher above ground (545.0 $\pm$ 69.7 cm, $n = 42$, vs. 154.6 $\pm$ 12.7, $n = 176$; $\chi^2_2 = 51.4$, $P < 0.001$) and deeper in cavities (37.2 $\pm$ 6.7 cm, $n = 19$, vs. 25.3 $\pm$ 2.7, $n = 169$; $\chi^2_2 = 10.6$, $P < 0.01$), whereas Magellanic Tapaculo nests were closer to the ground (74.3 $\pm$ 13.8 cm, $n = 42$) and had shorter entrances (20.9 $\pm$ 2.5 cm, $n = 27$).

Few nests of other species of tapaculos were investigated, primarily because they were inaccessible. However, of those inspected, clutch sizes appeared to vary less for these species than chucaos (nine huet-huet nests with two eggs or young; nine Magellanic Tapaculo nests with three eggs or young and one nest with two young; four Ochre-flanked Tapaculo nests with two eggs or young).

DISCUSSION

NEST SUCCESS

Mayfield nest success estimates of three species of tapaculos in Chilean temperate rainforest ranged from 64% to 85%. These estimates of nest success are within the ranges reported for other nonexcavating cavity nesters (Li and Martin 1991, Martin and Li 1992, Martin 1995, Robinson et al. 2000). Chucaos had lower nest success than huet-huets and Magellanic Tapaculos; chucaos sometimes nested in less safe locations outside of cavities, in contrast to the other two species, and the cavity nests of chucaos were not

as deep as those of huet-huets. Nest concealment has been suggested to be less important for cavity nesters than for many open-cup nesters (Li and Martin 1991), contrary to our findings for chucaos.

The best regression model for predicting chucao nest survival from predators included positive effects of nest concealment, entrance length, and forest size, and the negative effect of nest height above ground. Despite significant univariate effects of nest type (cavity vs. noncavity nests), average nest concealment, and distance to edge in single-factor comparisons, and the probable biological significance of these factors, they were not included in the final logistic regression model. The exclusion of these factors from the model may simply have resulted from the relatively small number of depredated nests available for use in the dataset.

The effects of forest fragmentation on reproductive success of chucaos were varied. Several lines of evidence suggest that forest fragmentation may not limit the reproductive success of chucaos. Overall nest success, chick size, and growth symmetry were similar in fragmented and continuous forest and in forests with and without livestock or logging activity. Furthermore, there were no negative effects of forest edge on nest success, nestling growth, or early juvenile survival. Clutch size was larger in fragments, on average. On the other hand, mortality rates from nest predation were higher in fragments, and juveniles were resighted less frequently than in continuous and undisturbed forest, possibly because of higher mortality.

Most other studies of nest success of birds using covered nests have reported no negative effect of fragmentation (Kuitunen and Helle 1988, Matthysen and Adriaensen 1998, Ortega and Capen 1999, Walters et al. 1999), with one exception (Porneluzi et al. 1993). Contrary to the open-cup nesters in the study area (De Santo et al., unpubl. data), predation on chucao nests was not higher near forest edges.

Nest predators in our study area include terrestrial and arboreal mammals and at least two species of birds (a blackbird and a caracara; Willson et al. 2001). Both species of birds tend to forage along forest edges, rather than in forest interior (MFW, pers. obs.). Mammals may be responsible for most of the predation of chucao nests, especially within the forest interior. The small forest cat *Oncifelis guigna* may avoid for-est edges when hunting, although it is known to travel among forest patches (Sanderson et al. 2002). We have watched this cat prey on nestlings in interior-forest nests and have found evidence of this predator (fur and claw marks) at several depredated nests in forest interior. Rodents are capable of entering nest tunnels, and rodent predation was more common on eggs in experimental nests in forest interior than on forest edges (Willson et al. 2001).

NEST-SITE LIMITATION

Nest-site availability often limits population density of cavity nesters (Newton 1994; but see Waters et al. 1990), and nest reuse, common among cavity nesters (Brawn and Balda 1988), has been shown to increase with fragmentation elsewhere (Matthysen and Adriaensen 1998). Nest sites may have been limited for chucaos in forest fragments. Patterns of nest-site use and relative availability of nest sites suggested that nest sites were limiting in fragments and forests disturbed by livestock or logging. We found fewer potential nest sites in fragments, nest substrate use differed between fragments and continuous forest, and nest sites were reused more often in disturbed forests. However, noncavity nests, a less safe but more available nest site compared to cavities, were used with similar frequency in fragments, continuous forest, and forests with and without livestock or logging activity.

CLUTCH SIZE VARIATION

Chucaos nesting at lower local density, with fewer neighboring territories, often laid three-egg clutches especially if an earlier nesting attempt failed. At least two nonexclusive proximate factors might contribute to the apparent effects of lower local density: (1) pairs with fewer neighbors spend less time interacting with their neighbors and their dispersing juveniles and have more time and energy to allocate to raising young, and (2) pairs with fewer neighbors generally have less-compressed territories and have access to "extra" undefended foraging area and more food resources. It is unclear why three-egg clutches should be more common following failure of earlier nests; perhaps curtailment of effort for earlier broods releases energy to be reallocated to the next brood. In any case, food supply in fragments is clearly adequate to raise larger broods, although the cost to the parents is un-

known. The forests of Chiloé Island have been severely fragmented for 100 years or more, constituting at least 100 generations of chucaos. That is sufficient time for evolutionary change, but we have no way to assess whether the observed pattern of three-egg clutches represents an evolutionary change.

OTHER EFFECTS OF FRAGMENTATION

In addition to fragmentation effects during the period of nest occupation, fragmentation may also decrease early juvenile survival of chucaos. Because tapaculos spend the majority of their time on or near the ground, understory vegetation is critical as cover, especially for fledglings. Recently fledged chicks are typically hidden in thick vegetation, usually bamboo thickets, where they are fed by parents. Bamboo is generally sparser in forest fragments than in the unfragmented forest of the national park (Sieving et al., unpubl. data). Decreased understory cover in fragments might account for our observation of fewer fledglings in forest fragments, either through decreased survival or increased movement of fledglings away from the natal territory. In addition, dispersal of juveniles is probably impaired in landscapes with fragmented habitat and poor connectivity (Sieving et al. 1996, 2000). Poorly connected patches are sometimes occupied at low densities, often late in the breeding season, and with low pairing success (KES, pers. obs.).

Although huet-huets had higher nest success than chucaos, they may be more vulnerable to forest fragmentation because of their large body size and correspondingly large home ranges; very small fragments (<3 ha) cannot support a breeding pair of huet-huets (TLD, pers. obs.). On the other hand, Magellanic Tapaculos may be less vulnerable to fragmentation, because their home ranges are small, they sometimes nest in unforested areas (De Santo et al., unpubl. data), and they are the most likely of all the tapaculos in these forests to cross nonforested land (Sieving et al. 1996, Cornelius et al. 2000). Ochre-flanked Tapaculos nest only in dense thickets (McPherson 1999, De Santo et al., unpubl. data), which limits their breeding distribution, and they are reluctant to cross open habitats (Sieving et al. 1996).

The factors affecting reproductive success of tapaculos in these forests are undoubtedly complex. The differences we detected between frag-ments and the national park suggest that patch size and internal condition of the fragment both affect reproductive success of tapaculos. While continuous, undisturbed forest is perhaps better breeding habitat, it should be pointed out that fragments also appear to be important for regional demographics of chucaos, not only as travel corridors, but also as breeding habitat. Aside from fragmentation, several other potential threats to tapaculo reproductive success exist in this landscape. In addition to direct loss of habitat from deforestation, conversion of the native forest to exotic tree plantations, such as pine and eucalyptus, may reduce nest-site availability (Estades and Temple 1999). Although exotic eucalyptus provides suitable nesting habitat for some bird species that build nests on branches of trees (Navarro et al. 1992, Safford 1997), other studies have found native cavity nesters to be absent from eucalyptus plantations (Garcia et al. 1998). Brood parasites, although rare in the study area, will undoubtedly increase as agricultural land becomes more abundant. The Shiny Cowbird (*Molothrus bonariensis*) parasitizes several species of open-cup nesters in our area (De Santo et al., unpubl. data) and is capable of parasitizing covered nests (Wiley 1988). Its hosts include at least one species of tapaculo (Wetmore 1926), but it is not known to parasitize Chilean tapaculos. Noncavity nests of chucaos might be particularly vulnerable to parasitism. Furthermore, the relative safety of nests may also decrease as a result of nest predation, especially along streams, as the introduced mink (*Mustela vison*) increases its range in southern Chile (Medina 1997).

Maintenance of healthy tapaculo populations in Chile depends on the existence of native forest patches large enough to contain territories, sufficiently undisturbed to contain suitable nest sites, and with sufficient connectivity to permit successful movement among patches. The present landscape configuration on northeastern Chiloé Island appears to permit population maintenance, but increasing habitat loss, disturbance, isolation, and potential increases in predation signal risk for these populations in the near future.

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