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**FRAGMENTACIÓN DE BOSQUES Y USO DEL HÁBITAT POR  
RINOCRIPTIDOS**

Tesis entregada a la Universidad de Chile  
en cumplimiento parcial de los requisitos  
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Facultad de Ciencias

por

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## INTRODUCCIÓN GENERAL

La fragmentación del hábitat es un proceso que trae como consecuencia una reducción del hábitat original y un aislamiento del hábitat remanente. La fragmentación, en este sentido, puede reducir el uso del espacio de algunos organismos, restringiendo la disponibilidad de hábitats adecuados para persistir y el acceso a estos hábitats. Sin embargo, el efecto de la fragmentación sobre los organismos no siempre es directo, sino que puede estar mediado por otros factores y procesos, como los atributos de historia de vida de cada especie y sus interacciones bióticas. Los atributos de historia de vida de los organismos pueden describir en que medida estos serán afectados por la fragmentación. Por otro lado, un cambio en las interacciones bióticas y en la conducta de dispersión de los organismos, debido a la fragmentación, limitará su persistencia local.

Los bosques templados de la zona costera de Chile central poseen una alta biodiversidad y al mismo tiempo han sido severamente fragmentados y reemplazados por otros tipos de cobertura vegetal en los últimos siglos (Bustamante y Castor 1998). Estos bosques están siendo fuertemente fragmentados por la substitución de ellos por plantaciones de pino (*Pinus radiata*).

Los rinocríptidos son aves asociadas al sotobosque de estos bosques (Johnson 1967, Araya y Millie 1998). Las cuatro especies rinocríptidas que cohabitan en este paisaje, el chucao (*Scelorchilus rubecula*), el churrín (*Scytalopus magellanicus fuscus*), el churrín de la mocha (*Eugralla paradoxa*) y el hues-hues castaño (*Pteroptochos castaneus*), difieren entre sí en sus atributos de historia de vida, y por lo tanto, podrían responder diferencialmente a los efectos de la



fragmentación (Hansen y Urban 1992). Así, las especies más vulnerables a la fragmentación podrían ocupar una menor fracción del espacio que aquellas menos vulnerables (Mac Nally et al. 2000). Este patrón podría resultar por diferencias en los requerimientos de hábitat de las especies, por diferencias en densidad poblacional o en aspectos relacionados directamente con el éxito de nidada.

En estos bosques templados, los nidos de los rinocriptidos podrían ser vulnerables cuando los depredadores aumentan en algunos hábitats y unidades del paisaje que resultan de la fragmentación y las actividades humanas. Así, un incremento en la abundancia y composición de depredadores de nidos en los fragmentos y matriz de pino debería incrementar el riesgo de depredación en esos lugares. Por otra parte, los rinocriptidos ocuparán una mayor proporción del paisaje cuando sus movimientos entre hábitats no sean restringidos por una conducta que limite la recolonización de los hábitats locales donde han ocurrido extinciones.

En esta tesis exploro la relación entre la incidencia, una métrica del uso del hábitat, de los rinocriptidos y su vulnerabilidad a la fragmentación, determinada por sus atributos de historia de vida. Paralelamente, pretendo determinar la vulnerabilidad de estas atribuida a la depredación de sus nidos y sobre su dispersión en el paisaje.

## CAPÍTULO I

### FOREST FRAGMENTATION AND HABITAT-USE BY RHINOCRYPTIDS

#### ABSTRACT

Life-history attributes could be used to predict species responses to habitat fragmentation or sensitivity. We compared the incidence and sensitivity to fragmentation of four understory birds (Rhinocryptidae family). Rhinocryptids inhabit deciduous forests of Central Chile and our study was conducted in a landscape mosaic of pine (*Pinus radiata*) plantations and native forest fragments. Sensitivity was positively and strongly correlated with rhinocryptid incidence. Understory structure was the main factor that predicted rhinocryptid presence and abundance. The least sensitive species, Andean (*Scytalopus magellanicus fuscus*) and the Ochre-flanked Tapaculo (*Eugralla paradoxa*), were positively associated to dead pine branches and negatively to forest fragment size. Rhinocryptids reduced their abundance in mature forest, but they were willing to cross between different habitat types. However, one of the most sensitive species, Chestnut-throated Huet-Huet (*Pteroptochos castaneus*), did not move from forest fragments to pine with poor understory when we displayed playback trials. Overall, rhinocryptid species are affected by fragmentation depending of their life-history attributes. The less sensitive species profited from habitat and landscape transformations. We conclude that rhinocryptids could persist in this landscape, as changes in habitat conditions do not become deleterious, such as understory structure.

*Key words: Life-history attributes, sensitivity index, fragmented forest landscape, rhinocryptids, mature forest, playback trials.*

## INTRODUCTION

Species vulnerability to landscape changes and extinction-proneness are not random processes (McKinney 1997). Extinction depends on properties of both the species and their environment (Tracy and George 1992, Johst and Brandl 1997). Therefore, vulnerability to landscape changes could be different even among closely related species (Lindenmayer and Lacy 1995).

Habitat fragmentation increases the probability of local extinction for forest birds as habitat fragments become smaller and more isolated (Turner 1996). However, bird responses to fragmentation may depend on the species attributes (Karr 1990, Kattan et al. 1994). In this way, a key issue in biological conservation is to identify life-history traits associated with species vulnerability (Maurer et al. 1991) and use these traits to predict species persistence in fragmented habitats (Foufopoulos and Ives 1999).

The fraction of the landscape fragments used, or incidence, by bird species may be predicted from their life-history attributes, as a given suite of them could determine that certain species are more vulnerable than others (Tellería and Santos 1997); exhibiting a lower incidence when habitats are fragmented compared to less sensible species (Hansen and Urban 1992).

Bird abundance could be a good predictor of the ability of bird species to occupy and persist in habitat fragments (MacNally et al. 2000). Habitat specificity, a determinant of rarity (Kattan 1992), also affect vulnerability. Habitat generalist species are less sensible to habitat fragmentation than specialist ones (McKinney 1997). Similarly, nest type could affect reproductive success in fragmented landscapes (Whitcomb et al. 1981). Open nests are more vulnerable to predation than cavity or covered nests (Hanski et al. 1996, Huhta et al. 1998). For those birds

that build nests, nest height may also affect nest success (Yanes and Suarez 1995, Söderström et al. 1998), as ground nests may be more accessible to ground predators (Söderström 1999). Finally, clutch size, a fitness measure of birds, can be directly associated to fledging survival (Arakida, Yoshitaka 1995) and, therefore to species vulnerability (Whitcomb et al. 1981).

Deciduous forests of the coastal range of Central Chile have been severely fragmented in the last century, initially by agricultural practices and presently by commercial silviculture (Donoso 1996). This region was originally covered by *Nothofagus* dominated forests, but at present it comprises extensive pine (*Pinus radiata*) stands that surround small remnants of native vegetation and a few large-sized fragments of *Nothofagus* forest (San Martín and Donoso 1995).

Rhinocryptids are understory birds that inhabit *Nothofagus* forests and *Chusquea* thickets in southern Chile and Argentina (Vuilleumier 1985). Four species inhabit the coastal range forests: Chestnut-throated Huet-Huet (*Pterotochos castaneus*) (endemic species), Chucao Tapaculo (*Scelorchilus rubecula*), Andean Tapaculo (*Scytalopus magellanicus fuscus*) and the Ochre-flanked Tapaculo (*Eugralla paradoxa*) (all of them endemic to Chile and Argentina) (Meyer de Schauensee 1970, Riveros and Villegas 1994, Araya and Millie 1998). While all rhinocryptids are forest-dwellers, their life-history attributes are different (Table 1), and therefore their sensitivity to forest fragmentation may be different. As Chestnut-throated Huet-Huet is the species with the lowest local abundance, could be the more vulnerable species. Comparatively, Chucao Tapaculo and Chestnut-throated Huet-

Table 1. Life history criteria after Hansen and Urban (1992) to estimate Sensitivity Index of rhinocriptid species. Each species was rated from 1 (least sensitive) to 3 (most sensitive) for each of the five traits. A total score per species was derived by summing the scores across traits. Criteria to assess sensitivity to forest fragmentation are listed below.

Species	Life-history attribute				
	Abundance <sup>1</sup>	Habitat specificity <sup>2</sup>	Nest type <sup>3</sup>	Nest height rank <sup>4</sup>	Clutch size <sup>5</sup>
Ochre-flanked Tapaculo	intermediate	low	semi-open	0->10 m	< 5
Andean Tapaculo	intermediate	intermediate	cavity	0-1 m	< 5
Chestnut-throated Huet-Huet	rare	high	cavity	0->10 m	< 5
Chucaco Tapaculo	intermediate	high	cavity	0-1 m	< 5

<sup>1</sup> Abundance in forest habitats: 1: abundant species: >0.5 (ind/ha); 2: intermediate: >0.1-0.5 (ind/ha); 3: rare: <=0.1 (ind/ha)

<sup>2</sup> Habitat specificity: 1: low specificity: mostly thicket cover, with or without any type of canopy; 2: Intermediate: mostly thicket cover (generally *Chusquea* formation) and any type of forest canopy; 3: Large: basically native forest canopy.

<sup>3</sup> Nest type: 1: open; 2: semi-open; 3: cavity.

<sup>4</sup> Nest height rank: 1: 0-10 m; 0-3 m; 3: 0->10.

<sup>5</sup> Mean of number of eggs per brood: 1: >10; 2: 0-3; 3: <5.

Sources: Johnson 1967, Meyer de Schauensee 1970, Cody 1970, Vuilleumier 1985, 1972, Erazo 1984, Ralph 1985, Eraso and Sepulveda 1988, Fjeldsa and 1990, Riveros and Villegas 1994, Araya et al. 1995, Rozzi et al. 1996, Sieving et al. 1996, Estades 1997, Schlatter et al. 1997, Vergara 1997, Araya and Millie 1998, Estades and Temple 1999,



Huet are forest-specialist compared to Andean Tapaculo and Ochre-flanked Tapaculo and, therefore, comparatively more if forest cover is lost. Furthermore, rhinocryptids are associated with rich understory habitats as bushy habitats and *chusquea* thicket (Fjeldsâ and Kabbe 1990, Sieving et al. 2000), therefore open habitats, as pastures are unsuitable habitats and barriers to their movements (Sieving et al. 1996, Estades and Temple 1999). Ochre-flanked Tapaculo is the only semi-open nesting species adding to its vulnerability. Similarly, ground-nesting species, like Chucaco Tapaculo and Andean Tapaculo, should be more vulnerable. Finally, all species have small clutch sizes (two to three eggs per brood). In the present study, our objective was to test whether rhinocryptid incidence is negatively related to an index of vulnerability to forest fragmentation based on their life-history attributes. Concomitantly, we assess habitat and landscape variables that affect the incidence and abundance of each species. We also measured whether birds move between different habitat types, factor that might determine rhinocryptid's persistence in the fragmented *Nothofagus* forest of Central Chile.

## METHODS

### Study site

The study area is located in the Cordillera de la Costa of central Chile (35° 59' S, 72° 41' W), and comprised Los Queules National Reserve (a 145 ha native forest tract embedded in 600 ha of continuous forest), extensive pine (*Pinus radiata*) plantations surrounding native vegetation, acting as a matrix, and native forest fragments. The predominant habitat within the National Reserve is a mature, mixed forest (*Nothofagus glauca*, *N. obliqua* and evergreen tree species) interrupted by *Chusquea quila* under canopy gaps and ravines. Depending on stand age and

rotation period, the pine matrix includes pine plantations with dense understory and with poor understory. Forest fragments were both isolated fragments and strips of native vegetation. Isolated fragments were *Nothofagus* forest and native thicket < 7ha. Native strips included some small creeks covered with native thicket and were less than 140 m wide. Those habitat types differed in structure: total understory cover (foliage of understory plants) was greater in forest fragments and pine with dense understory than pine with poor understory and mature native forest (Table 2). Also, cover of dead ground branches (including <0.3 m of diameter logs) was lower in mature native forest, and native forest canopy was greater in native mature forest and forest fragments (Table 2). The pine plantations comprised a 54% of the total area, forest fragments a 26% and the continuous forest a 20% of the landscape (Acosta 2001).

#### Rhinocryptid sensitivity and incidence

We used Hansen and Urban's (1992) species-sensitivity index to compare it with the incidences of understory bird species. We estimated Hansen and Urban index using five life-history attributes (Table 1), giving to each species a different level of sensitivity to landscape changes (Vásquez and Simonetti 1999). Hansen and Urban index was build using information regarding life history attributes available in the current literature. This information comes from forests other than our study site. Therefore, we assumed that there is no circularity between sensitivity index and incidence (see Vásquez and Simonetti 1999). Thus, we determined the following decreasing sensitivity, and hence vulnerability order: Chucao Tapaculo (12), Chestnut-throated Huet-Huet (11), Andean Tapaculo (10) and Ochre-flanked

Table 2. Some parameters of habitat structure from four different habitat types in Los Queules National Reserve. Values are means  $\pm$  standard error. Significant differences by ANOVA and Tukey test are showed by different letters.

Habitat variable	Habitat types			
	Forest fragments	Pine with poor understory	Pine with dense understory	Mature native forest
Native forest canopy cover (%)	54.5 $\pm$ 10.3 a	7.9 $\pm$ 5.3 b	2.2 $\pm$ 1.1 b	75.8 $\pm$ 7.3 a
Dead ground branch cover (%)	39.3 $\pm$ 4.6 a	45.9 $\pm$ 5.1 a	53.2 $\pm$ 4 a	17 $\pm$ 2.3 b
Total understory cover (%)	60.0 $\pm$ 4.6 a	24.3 $\pm$ 2.7 b	56.2 $\pm$ 5.1 a	37.9 $\pm$ 4.2 c



Tapaculo (10). We calculated the incidence of each species as the proportion of sampling plots (n=50) where individuals of each species were recorded.

We installed census points at random within a landscape area of about 16 km<sup>2</sup>. Sampling points were more than 320 m apart among them. We measured the presence and abundance of each species at the beginning of the reproductive season (October 2000). We used stationary tape-song playback censuses to detect territorial individuals using records of territorial songs broadcast from two 5 watts speakers (Fall 1981, Parker 1991).

Census started at dawn (05:45) until 11:30. At the evening, we repeated censuses between 16:00 to 17:00. In each census, we spent about 20 min per sampling point. For the smaller Andean and Ochre-flanked Tapaculos, we registered only the individuals that were 15 m or less from the observer. For the larger and more mobile Chucao and Chestnut-throated Huet-Huet, we registered the individuals that were 30 m or less. Using only those records we reduced the risk of detecting individuals from neighboring habitats (provoking abundance overestimation). Each visit consisted of three playbacks: the observer stayed 5 min in a central point (2 min to playback and 3 min to detect birds), then he moved as far as 15 m away from the central point, where he displayed again a 2 min playback, repeating the procedure towards the opposite side from the central point. Many times this center point was within a bird territory and birds from next territories did not approach to observer (Rail et al. 1997). For each visit, the maximum number of individuals detected in some of these playbacks was recorded as an abundance index. We performed three to four point visits for each species. For each sampling point, we calculated the mean of abundance index per visit.

## Habitat measures

We measured habitat variables around of each sampling point, in 60 m radius plots. As rhinocryptid are associated with forest understory, we measured 35 habitat variables related to the structure and composition of the understory (Table 3). We included some plant species composing the understory as they are conspicuous elements in the landscape and change the understory structure among plots (*Chusquea quila*, *Aristolelia chilensis*, *Rubus ulmifolius*, *Teline monspessulana*, herbs and vines). Within each plot, understory cover was measured using 30 m line-intercept transects and canopy cover by 0.1 ha circular plots (Higgins et al. 1996). We included some landscape variables that could affect rhinocryptids, like patch size and creek distance from a plot to the nearest creek (i.e., native vegetation; Estades and Temple 1999).

We used Stepwise Discriminant Analysis and Logistic Regression to determine the best habitat-landscape variables that might explain the pattern of rhinocryptid's richness and presence/absence, respectively. We used Wilks's  $\lambda$  transformed into  $F$  statistic to test differences among group (plot richness) positions in Discriminant Analysis. We selected the best Logistic and Discriminant Analysis stepwise models by backward elimination procedure, eliminating previously redundant variables to reduce multicollinearity (Allen 1997, Hosmer and Lemeshow 1998). We also regressed the abundance index of each rhinocryptid species and total rhinocryptid abundance on habitat and landscape variables. We used Ridge Multiple Linear Regression selecting models by backward elimination ( $F$ -to-remove; Bare and Hann 1981).

Table 3. Habitat and landscape variables included in rinocriptid presence/absence and abundance models.

Habitat variables (n=24)	
<i>Chusquea quila</i> cover (%)	Pine height (mean height (m))
<i>Aristolelia chilensis</i> cover (%)	Age of pine stand (years)
<i>Rubus ulmifolius</i> cover (%)	Native forest canopy cover (%)
Total understory cover (%)	Native forest dbh (mean dbh (cm))
Ground dead branch cover (%)	Native forest height (mean height (m))
Herbaceous cover (%)	Native forest density (trees ha <sup>-1</sup> )
<i>Teline montpensulana</i> cover (%)	
Vine cover (%)	Landscape variables (n=11)
<i>Nothofagus glauca</i> cover (%)	Fragment size (ha)
Woody species richness	Pine plantation size (ha)
Snag density (snag ha <sup>-1</sup> )	Fragments of >4 ha (more than 4 ha size (yes=1, no=0))
Log density (logs ha <sup>-1</sup> )	Fragments of < or = 4 ha (yes=1, no=0)
Rock cover (%)	Native corridor (yes=1, no=0)
Dead leaf and litter depth (cm)	Distance to nearest native fragment (m))
Percentage of pine leaves (% in litter)	Distance to nearest native creek (m))
Pine canopy cover (%)	Distance to nearest native fragment >4 ha (m)
Pine density (trees ha <sup>-1</sup> )	Altitude (meters above to a lowest reference point)
Pine dbh (mean dbh (cm))	Slope (%)
	Exposure (N=0, NW and NE=1, SW and SE=2, S=3)



## Bird movements

We also used tape-song playback to test whether birds cross from a given habitat to another when they were motivated by territorial songs (Sieving et al. 1996). Habitat trials were conducted in four habitat types: forest fragments, pine with dense understory stands, pine with poor understory stands and mature native forests. As a large number of birds were initially recorded within forest fragments and dense understory pine stands, we considered those as origin habitats. During each trial, we played territorial songs at the juncture between two habitat types for 3 min until one bird had arrived there (at least to 20 m from the observer; StClair et al. 1998). Then, the observer moved about 20 m into the destination habitat and played a territorial song for another 5 min (Sieving et al. 2000). If the bird entered into the destination habitat, speakers were moved 40 m far from the source habitat, and a new 5 min playback was displayed. We scored trials as positive when an individual moved into the destination habitat. It was regarded as negative, if animal was reluctant to cross habitat edges.

Similarly, we tested animal movements within the same habitat of origin as controls, moving speakers about 60 m within of this habitat (using the same protocol). Trials were 250 m or more apart among them, in order to avoid recording the same individual more than once. We compared trials done in the same habitats and those done in different through the Fisher exact test (one-tailed; Siegel 1956).

## RESULTS

### Sensitivity analysis

Species differed in their incidence. The species with largest incidence was Ochre-flanked Tapaculo (42 plots with individual presence) followed by Andean Tapaculo

(35 plots with individual presence), Chestnut-throated Huet-Huet (28 plots), with Chucao Tapaculo had the lowest incidence (just three plots). On the other hand, Chucao Tapaculo was also the most sensitive species (Index value:12) because of its low abundance, coupled to its comparatively habitat specificity and low nest height. Chestnut-throated Huet-huet was the second more sensitivity species (Index value:11) due to its low abundance and habitat specificity. Andean Tapaculo (Index value:10) and Ochre-flanked Tapaculo (Index value:10) were comparatively, the least sensitive species. Andean Tapaculo is less sensitive than Ochre-flanked Tapaculo, since it has comparatively larger types of habitat used, and additionally, nesting in cavities should also reduce its nest predation risk (cf. Hansen and Urban 1992). Ochre-flanked Tapaculo is less sensitive than Andean Tapaculo due to its larger nest height rank.

Incidence was negatively correlated to sensitivity (Figure 1). Due to low sample size (four species), correlation however was not statistically significant, despite being high ( $r = -0.94$ ,  $P = 0.12$ ). Therefore, we used a randomization procedure to test whether this pattern was expected by chance alone (Manly 1998). Values from presence/absence matrix were resampled at random with replacement (within sampling points) to obtain incidence values. Then, we recomputed the correlation coefficient, keeping constant the values of the sensitivity index (Legendre and Legendre 1998). Repeating the permutation 5,000 times we obtained a distribution of the random-generated correlation coefficients. In this way, we compared the empirically obtained  $r$  to this null  $r$ . The probability of randomly obtaining a  $r = -0.94$  is lower than 2 % (Figure 2). Consequently, we rejected the null hypothesis that the negative association observed between sensitivity and incidence of rhinocryptids

was generated by chance. Therefore, more sensitive species have a lower incidence (Figure 1).

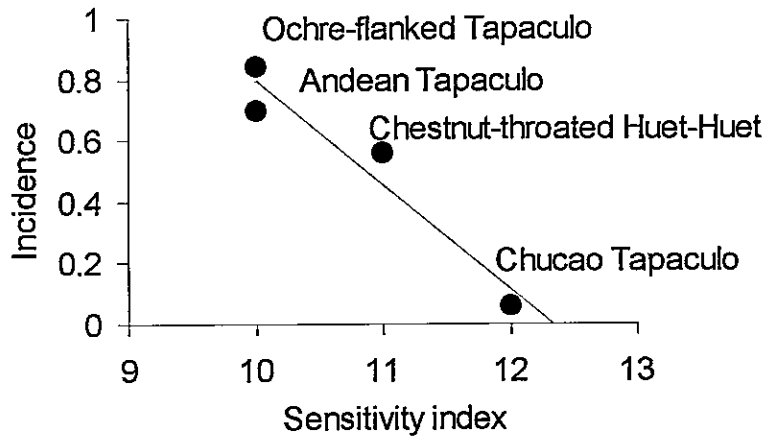


Figure 1. Relation between incidence and sensitivity of four rhinocryptid species.

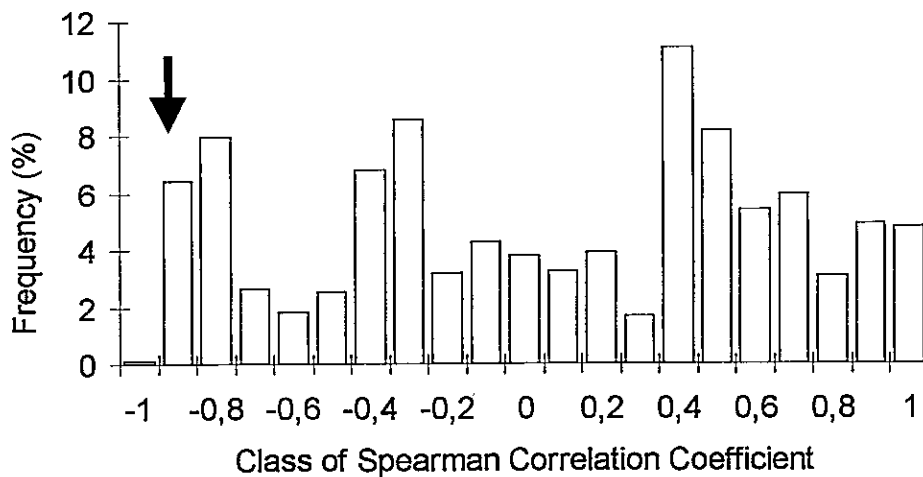


Figure 2. Frequency distribution of random generated correlation coefficients between rhinocryptid incidence and sensitivity index. Arrow shows the estimated  $r = -0.94$ .

## Habitat effect

Rhinocryptid presence and abundance was associated to habitat and landscape variables. The number of rhinocryptid species per sampling point was accounted for by two structural variables: *Chusquea* and dead branch cover (Discriminant analysis,  $F_{8,88}=14.9$ ,  $P<0.001$ ). Sampling plots without presence had less dead branch cover than plots with one or more species. Sampling points with four species had the greatest *Chusquea* cover (Figure 3). A bi-dimensional ordination of sampling plots, considering the number of rhinocryptid species, indicated that *Chusquea* cover is the main variable correlated with canonical axis I ( $r=-0.95$ ) and dead branch cover with canonical axis II ( $r=-0.98$ ).

At the species level, understory cover was the primary predictor of the presence of Chestnut-throated Huet-Huet, Andean and Ochre-flanked Tapaculos. Further, the presence of these species was predicted by different habitat-landscape variables (Table 4). Presence of Ochre-flanked and Andean Tapaculos was negatively associated to the size of forest and positively associated to pine and ground dead cover. Presence of Chestnut-throated Huet-Huet was also predicted by woody species richness. Habitat variables correctly classified over 65 % of overall cases in logistic models. Plots without rhinocryptids were proportionally better fixed to predictive models than plots with rhinocryptid presence (Table 4).

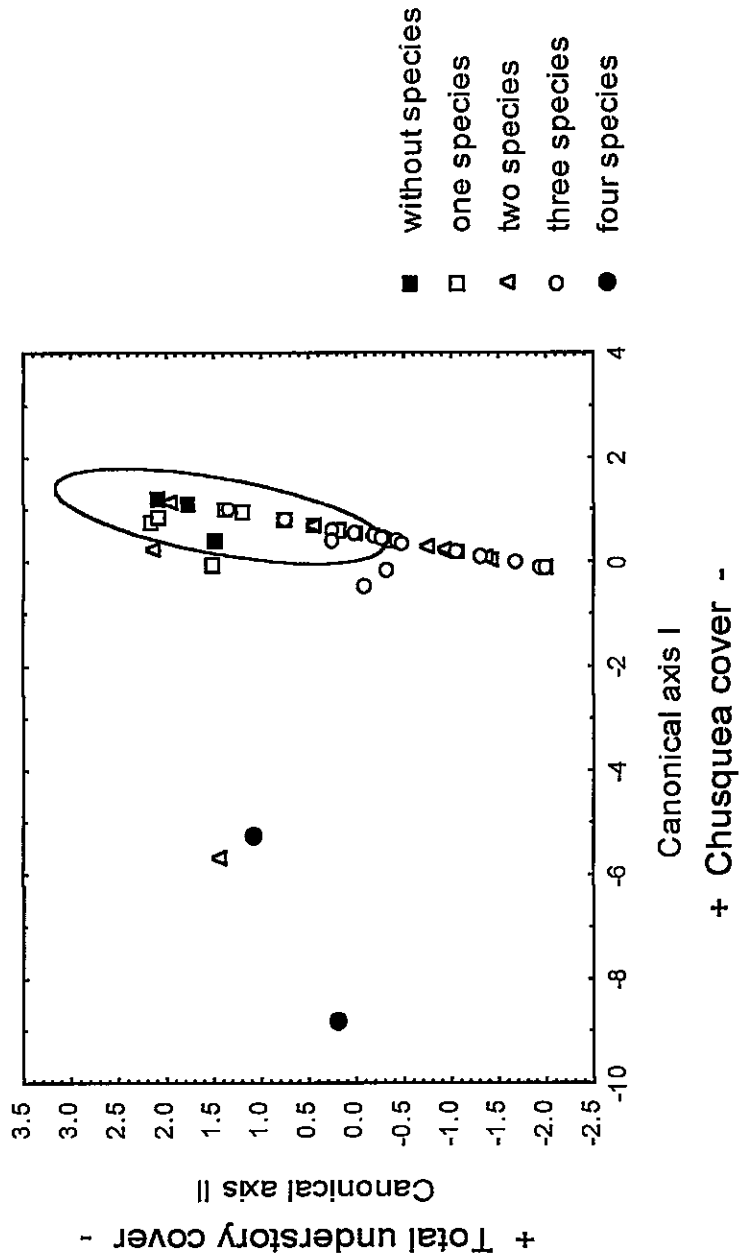


Figure 2. A two-dimensional ordination diagram of number of rhinocryptid species within sampling points in the canonical discriminant space. 95% ellipse is showed only for plots without species.



Table 4. Predictive Logistic Regression models for rhinocryptid incidence using habitat-landscape variables.

Species	Variables in the model	d.f.	X <sup>2</sup>	P	% Correctly classified (n)		
					presence	absence	overall
Ochre-flanked Tapaculo	Total understorey + pine canopy - fragments of >4 ha	3	19.5	0.0011	81 (42)	100 (8)	84
Andean Tapaculo	Ground dead branches + pine canopy - fragment size	3	25.3	0.0007	65,7 (35)	86,7 (15)	72
Chestnut-throated Huet-Huet	Total understorey + woody species richness	2	8.6	0.0064	50 (28)	72,7 (22)	62

Table 5. Multiple regression models that included the best habitat-landscape variables in the rhinocryptid abundance explanation.

Species	Variables in the model	r <sup>2</sup>	d.f.	F	P
Ochre-flanked Tapaculo	Total understorey + <i>A. chilensis</i> + ground dead branches	0.57	3,46	20.5	<0.0001
Andean Tapaculo	Total understorey + ground dead branches - native canopy	0.66	3,46	22.1	<0.0001
Chestnut-throated Huet-Huet	Total understorey + woody richness - creeck distance	0.38	3,46	9.5	<0.0001
Pooled	Total understorey + ground dead branches	0.63	2,47	41.1	<0.0001

The abundance of three most frequent rhinocryptid species individually and of rhinocryptids as a whole was also explained by understory cover (Table 5).

Abundance of Ochre-flanked and Andean Tapaculos was explained by dead branch cover. Aristotelia cover also accounted for abundance of Ochre-flanked Tapaculo, but the abundance of Andean Tapaculo was negatively related to native canopy cover. The Chestnut-throated Huet-Huet abundance decreased with the distance to creeks (Table 5).

#### Bird movements

In general, individuals of all species crossed from a source to a sink habitat when were motivated by playback songs. The proportion of Ochre-flanked and Andean Tapaculos that crossed from forest fragments to pine with poor understory was not different from the proportion that moved within forest fragments (Table 6). The proportion of Chestnut-throated Huet-Huet individuals that moved from pine with dense understory to pine with poor understory and from forest fragments to mature native forest was not different from the proportion that moved within pine with dense understory and forest fragments, respectively (Table 6). However, Chestnut-throated Huet-Huet individuals crossed less often from forest fragments to pine with poor understory than individuals that moved within forest fragments (Table 6).

Table 6. Habitat trial results indicating both the number of times that individuals of a particular species crossed from a origin to a destination habitat and the total number of taped song playback experiments. Difference in proportions between individuals moving between habitat and controls (see text) are tested by Fisher exact test.

Species	From	To*			
		Forest fragments	Pine with poor understory	Pine with dense understory	Mature native forest
Chestnut-throated Huet-Huet	Forest fragments	9/10	0/9 ( $P=0.01$ )	-	3/7 ( $P=0.31$ )
Chestnut-throated Huet-Huet	Pine with dense understory	-	3/4 ( $P=0.59$ )	4/4	-
Ochre-flanked Tapaculo	Pine with dense understory	7/8	6/8 ( $P=0.56$ )	-	-
Andean Tapaculo	Forest fragments	6/6	6/7 ( $P=0.58$ )	-	-

\*Blank cells mean that no trials were done.

## DISCUSSION

Life-history attributes are good predictors of bird species vulnerability to fragmentation changes (Lynch and Whighan 1984, Kattan et al. 1994). In fact, the incidence of rhinocryptids is negatively related to their sensitivity to landscape changes, such as fragmentation. Regarding life-history attributes of rhinocryptids, broader amplitude of habitats determines less sensitivity in Chestnut-throated Huet-Huet and Chucao Tapaculo, triggering a reduced incidence in fragmented landscapes. Chestnut-throated Huet-Huet and Chucao Tapaculo are largely associated with understory of native forests, and Ochre-flanked and Andean Tapaculos also inhabited the understory of pine plantations (Table 1). Thus, forest specialists, like Chestnut-throated Huet-Huet and Chucao Tapaculo, are more sensitive to fragmentation, because of a reduction in forest interior habitat and increase in forest edges (Whitcomb et al. 1981). In the other hand, the least sensitive species, Ochre-flanked and Andean Tapaculos, had comparatively a lower habitat specificity and intermediate abundance local. Abundance, in this way, may be an important variable determining local persistence (Hanski 1982). Further, species with lower habitat specificity may use resources opportunistically (Wiens 1992), allowing these two rhinocryptid species to use more habitats of the current landscape.

Rhinocryptids are understory cover-dependent, and like this pine with dense understory would be therefore, a suitable habitat. Forest fragmentation by pine plantations could be, in this way, a deleterious habitat-transformation process only to Chestnut-throated Huet-Huet and Chucao Tapaculo, but not to Ochre-flanked and Andean Tapaculos.

Mobile species may have a larger incidence than relatively sedentary species in fragmented landscapes (Wiens 1990). Like in other fragmented forests (Sieving 1996), Andean Tapaculo was the most mobile of all species, and thus its larger incidence together with Ochre-flanked Tapaculo, may reflect their large mobility among habitats. Although, in general Chestnut-throated Huet-Huet individuals were able to move between two structural different habitats, some individuals did not cross from forest fragment to pine with poor understory. This behavior could reduce individual flows among no-connected habitat (such as isolated fragments), affecting species incidence, as landscape become more fragmented by pine with poor understory stands (Gardner et al. 1987, Wiens 1990).

Deciduous forest of Central Chile, a fragmented landscape dominated by pine plantations, comprises a mosaic of different habitats for forest birds (Estades and Temple 1999). Further, many bird species would profit from forest fragmentation, increasing their abundance in pine matrix and in the smaller forest fragments (Estades and Temple 1999, Vergara Capítulo IV). In fact, habitat use by rhinocryptids is related mainly to availability of understory structures in both pine matrix and forest fragments.

On the other hand, forest fragmentation by pasture, such as human-dominated landscapes in Chiloé Island (Willson et al. 1993, Sieving et al. 1996, 2000), where an open matrix encloses native fragments and corridors, could impose more severe problems for rhinocryptid persistence, because of the pasture matrix.

There, bird territories would be more isolated and packed than in forest fragmented by pine, and therefore individual movements could be more limited among fragments (Willson et al. 1994). Therefore, native fragments enclosed by pine

plantations could be a less restrictive landscape to rhinocryptids than forest landscape fragmented by pasture.

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## CAPÍTULO II

### FOREST FRAGMENTATION AND NESTS PREDATION

Abstract: Fragmentation of forest landscapes can increase the effect of nest predator by increasing generalist or introduced predators' abundance and richness. Understory foraging birds could be highly vulnerable to the nest predation in fragmented landscapes because they place their nests usually on the ground. Temperate deciduous forests in South America have been intensely fragmented in the last centuries causing changes in nest predator's densities. We tested if nest predation in artificial nests placed in ground and shrub increased in the remnant fragments due to an increase in predator' abundance and determined the associations of nest predation and understory bird abundance. There was larger nest predation in the remnant fragments versus a reserve of native forest (continuous forest), but only ground nest predation was larger. The main nest predators, identified using plasticine eggs, were small mammals. However, understory birds increased also in remnant fragments, suggesting that fragments might constitute trap habitats.

*Key word: Forest fragmentation, understory birds, nest predation, artificial nests, trap habitats.*

## 1. Introduction

Nest predation is one of the main causes of avian reproductive failure in different types of habitats, and may affect the dynamics of bird populations to such a point that it could provoke local extinctions (Ricklefs 1969, Zarette 2000). Forest fragmentation changes habitat conditions of both breeding birds (Andr n 1994) and their nest predators (Keyser et al. 1998, S derstr m 1999). Populations of habitat-generalist predators increase when landscape becomes more diverse (Oehler and Litvaitis 1996, Nour et al. 1993, Tewksbury et al. 1998, Dijak and Thompson 2000), increasing the risk of nest predation in both the matrix and the remnant fragments (Hoover et al. 1995, Keyser et al. 1998, Small and Hunter 1988, Kurosawa et al. 1999, Zarette and Jenkins 2000), menacing avian persistence (Heske et al. 1999, Zarette 2000). This effect could be particularly significant for ground nesting birds (Martin 1993). As predators easily detect ground nests of forest understory birds (Arango-Velez and Kattan 1997), forest fragmentation could increase vulnerability of understory birds (Andrianarimisa et al. 2000, Dale et al. 2000).

The native forest in the Coastal range of Central Chile supports a high biodiversity associated with the occurrence of several endemic taxa and the convergence of the faunas from the northern sclerophyllous and the southern rain forests (Bustamante and Castor 1998). Among this unique flora and fauna, there are four understory bird species of the Rhinocryptidae family (Johnson 1967, Fjelds  and Kabbe 1990). One species is endemic to the Central Chile region (Chestnut-throated Huet-Huet, *Pteroptochos castaneus*). The other three species are endemic to Chile and Argentina: Chucao Tapaculo (*Scelorchilus rubecula*), Andean Tapaculo (*Scytalopus magellanicus*) and Ochre-flanked Tapaculo (*Eugralla paradoxa*) (Meyer de Schauensee de 1970, Riveros and Villegas 1994, Araya and

Millie 1998). Regarding nesting, Ochre-flanked Tapaculo and Chestnut-throated Huet-Huet nests preferentially off-ground, while, Chucao and Andean Tapaculos are mostly ground nesters, placing their nests in soil cavities.

Native forests in the Coastal range of Central Chile have been severely fragmented by silvicultural practices (Donoso 1996). Deciduous forests originally covered this region. At present, the landscape comprises extensive pine (*Pinus radiata*) plantations that enclose small remnants of native forests (San Martín and Donoso 1995). Land use changes have triggered changes in the abundance and distribution of both rhinocryptids and generalist predators. There are more omnivorous small mammals (rodents and marsupials), and generalist foxes as well as raptors in both small forest fragments and the pine matrix than in large forest fragments (Saavedra and Simonetti unpublished, Acosta 2001, Vergara Capítulo IV). On the other hand, Andean and Ochre-flanked Tapaculos are common in pine habitat (Estades and Temple 1999, Vergara Capítulo I) and all species are more abundant in pine with dense understory and small forest fragments than in large fragments of mature forest (Vergara Capítulo I). Therefore, predation risk for rhinocryptids should be larger in forest fragments and pine matrix than in continuous forest due to a larger abundance of generalist predators there. Here, we studied the effect of forest fragmentation on nest predation in an experimental way, using artificial nests mimicking rhinocryptid nests. We also determined the effect of fragmentation on predation of both ground and off-ground nests, identifying also the nest predators.



## 2. Method

### Study site

Our study site (35° 59' S, 72° 41' W) included Los Queules National Reserve (a 145 ha reserve embedded in a tract of 600 ha of continuous forest), several adjacent small forest fragments and pine plantations that surrounded them, acting as a matrix. The National Reserve is conformed by a mature mixed forest (basically of *Nothofagus glauca* and *Nothofagus obliqua* and sclerophyllous trees) that in parts is interrupted by *Chusquea quila* thickets in gaps and ravines. The pine matrix is heterogeneous. There are plantations with a dense understory composed by *Teline montpessulana* and *Rubus ulmifolius* (both introduced) and *Aristotelia chilensis*, and others with poor understory. Native forest included both isolated fragments and creeks with native vegetation. Isolated fragments are smaller than 7 ha, and riparian corridors are less than 140 m wide. The pine matrix comprises a 54% of the total area, the fragments 24% and the continuous forest a 22% (Acosta 2001).

### Nest predation

We simulated the nests of the four rhinocryptid species living in the area: Andean Tapaculo (*Scytalopus magellanicus*), Ochre-flanked Tapaculo (*Eugralla paradoxa*), Chestnut-throated Huet-Huet (*Pterotochos castaneus*) and Chucao Tapaculo (*Scelorchilus rubecula*) (Araya and Millie 1998; Vergara Capítulo I). Of these, only Ochre-flanked Tapaculo builds semi open nests and the remainder species build their nests within soil cavities, decaying roots or tree holes (Johnson 1967).

Although Chestnut-throated Huet-Huet and Ochre-flanked Tapaculo can nest

above the ground, such as in a tree cavity, we only found off-ground nests of Ochre-flanked Tapaculo. Eggs measure from 2.2 cm in the Andean Tapaculo to 3.5 cm in Chestnut-throated Huet-Huet ; rhinocryptid usually lay three eggs per brood (Johnson 1967).

Rhinocryptid nests were simulated using the same nesting materials (Sieving 1992), and placed them in agreement to their real nest position (soil or off-ground). We allocated a total of 400 nests in 50 plots. Each plot had a 60 m radius. Plots were allocated in a stratified way (proportional to the area): 28 (56%) plots in the pine matrix, 11(22%) in forest fragments and 11(22%) in the reserve (a continuous forest). The distance between plots was over 300 m. Within each plot, we put eight nests, six were placed in the ground (soil cavities) and two were placed between 0.4 and 2.5 m over a tree. We constructed soil cavities of 50 cm deep per 7 cm in diameter. At its end, we placed a grass-twigs nest. The off-ground nests were placed in tree branches or tree holes; these nests were also made of grasses, sticks and twigs, but were more compact and bigger than ground nests. Within each plot, nests were at least 25 m apart. At each nest, we set two Japanese Quail (*Coturnix japonica*) eggs and also baited it with one plasticine egg. This egg allowed us to detect predators through the identification of its dentition (Bayne et al. 1997). We could identify signs of small mammals and carnivores' teeth and claw by comparing them with signs left by animals in captivity and skulls.

Nests were checked after one week. The experiment started at the beginning of the rhinocryptid reproductive season (October 2000), when we detected the first nesting activities. For each plot, we calculated the proportion of preyed nests. We considered the plot as the sampling units because of spatial dependence at nests

within plots (Söderström et al. 1998). We compared proportions of preyed nests using one way ANOVA, and normalized them by arcsine transformation (Zar 1998). Differences in nest predation of off-ground nests were tested using  $X^2$  test (Siegel 1956).

### 3. Results

A total of 162 (41%) nests were preyed. Of preyed nests, 26 (16%) were in the reserve, 51 (31%) in forest fragments, and 85 (52%) in the pine matrix. These values correspond to 29% of the nests of the reserve, 57% of the forest fragment nests and 38% of the pine matrix nests (Figure 1). On the other hand, 300 (38%) eggs were preyed. Of these, 47 (16%) were in the reserve, 96 (32%) in forest fragments, and 157 (52%) in the pine matrix. Preyed eggs correspond to 27% of the eggs of the reserve, 54% of the forest fragment eggs and 35% of the pine matrix eggs. Overall, nest predation was nearly two times greater in forest fragments than the reserve and nest predation in forest fragments was 1.5 times greater than in pine matrix. In fact, there was a significant difference in nest predation among the reserve, pine matrix, and forest fragments (ANOVA,  $n=50$ ,  $F_{2,47}= 3.6$ ,  $P=0.03$ ; Figure 1). The proportion of nests preyed was larger in the forest fragments than the reserve (Tukey  $P=0.03$ ) but it was not different between forest fragments and pine matrix (Tukey  $P=0.18$ ).

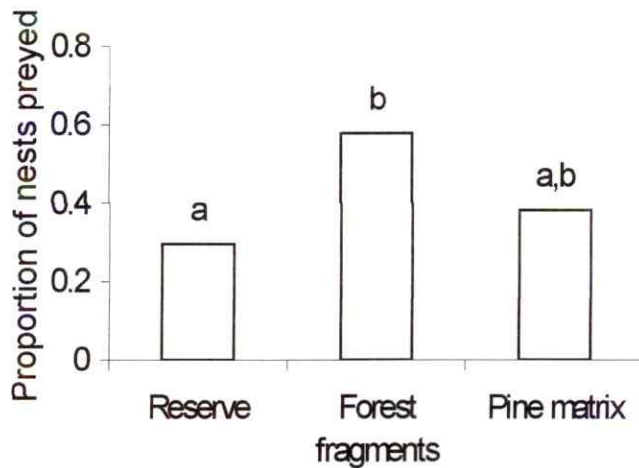


Figure 1. Proportion of nests preyed in forest continuous, forest fragments and pine matrix. Different letters represent significant differences.

Regarding nest position, ground nests were more preyed than off-ground nests. From 152 ground nests preyed, 23 (15%) were in the reserve, 50 (33%) in forest fragments and 79 (52%) in the pine matrix. These correspond to 36% of the nests of the reserve, 71% of the forest fragment nests and 45% of the pine matrix nests (Figure 2). Predation upon ground nests differed among the reserve, forest fragments and pine matrix (ANOVA,  $n=50$ ,  $F_{2,47}= 3.46$ ,  $P=0.039$ ). The proportion of ground nests preyed was larger in the forest fragments than the reserve (Tukey  $P=0.04$ ) and it was not different between forest fragments and pine matrix (Tukey  $P=0.23$ ). Of the 10 off-ground nests preyed, 2 (20%) were in the reserve, 4 (40%) in forest fragment and 4 (40%) in the pine matrix. These nests correspond to 9% of the nests of the reserve, 18% of the forest fragment nests and 7% of the pine matrix nests (Figure 2). The proportion of off-ground nest preyed did not change significantly with fragmentation ( $X^2=0.76$ ,  $P=0.68$ ) (Figure 2).

A total of 95 plasticine eggs (24 % of the total plasticine eggs) had clear predator's marks. Of these, 19 (20%) were bitten by foxes (*Pseudalopex culpeus*) and 76 (80%) by small mammals. Rodents marked 68 eggs (71%) and 8 eggs were bitten by the marsupial *Thylamys elegans* (8%). The proportion of plasticine egg marked was larger in the forest fragments than the reserve (ANOVA,  $n=50$ ,  $F_{2,47}= 3.92$ ,  $p=0.03$ , Tukey  $P= 0.03$ ) and there was not difference between forest fragments and the pine matrix (Tukey  $P=0.31$ ; Figure 3).

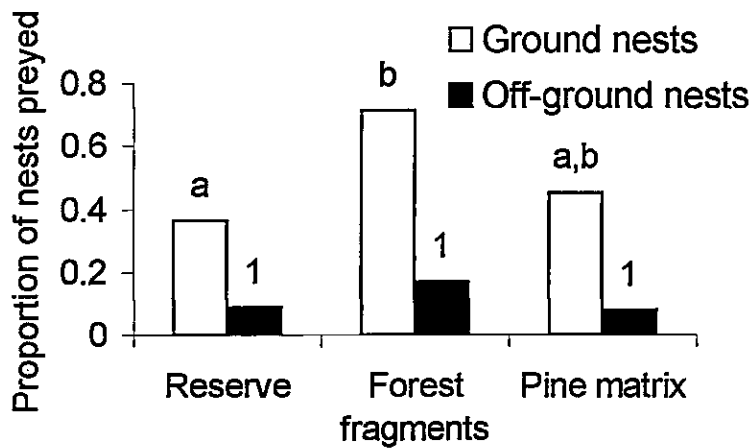


Figure 2. Proportions of the ground and off-ground nests preyed in the reserve, forest fragments and pine matrix. Different letters and number represent significant differences.

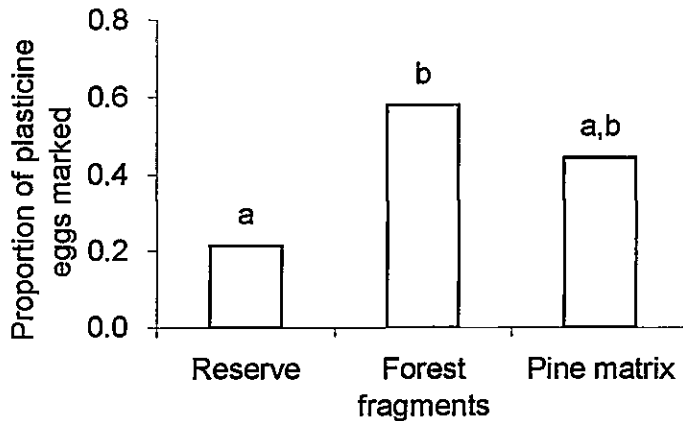


Figure 3. Proportion of marked plasticine eggs in the reserve, forest fragments and pine matrix. Different letters represent significant differences.

#### 4. Discussion

Fragmentation generally increases predation of artificial nests (Huhta 1995). An increase of predation risk in forest fragments is associated with an increase in predator density (Hoover 1995). Furthermore, nest predation in fragmented landscapes is affected by an increased abundance of predators adapted to human settlements (Saunders 1990) and a greater diversity of predators along habitat edges (Donovan et al. 1997). In this way, rhinocryptid nests are more preyed in small forest fragments due to an increase of generalist predators. However, in contrast with our results, fragmentation by forestry or pine plantations in holartic woodlands has not affected nest predation (Bayne and Hobson 1997), because of the low edge contrast associated with pine-enclosed stands appears to attract fewer nest predators (Sargent et al. 1998). On the other hand, habitat conditions imposed by pine fragmentation in our deciduous forests can sustain a larger predator fauna, favoring a larger nest predation. In this way, a habitat mosaic



composes by forest fragments enclosed by a heterogeneous pine matrix, may benefit those habitat generalist nest predators.

Predators in forest fragments could prey opportunistically, increasing nest predation risk only by their increased abundance. Foxes and small mammals (largely rodents) were the main predators of ground nests in forest fragments. Further, rodents are also the most important nest predators in other fragmented landscapes, such as tropical and temperate forests (Santos and Tellería 1992, Hogstad 1995, Arango-Velez et al. 1997, Leite and Marini 1999).

Nest position could affect nest failure (Yanes and Suarez 1995, Söderström et al. 1998, Söderström 1999). However, arboreal nest predation was not greater in forest fragments. Possibly, small mammals have a reduced arboreal behavior (Meserve 1981), foraging basically on the ground (Amarasekare 1993, Hernández et al. 1999). Thus, nest position may be important to avoid nest predation (Wilson and Cooper 1998, Degraaf et al. 1999).

Rhinocryptid abundance is larger in forest fragments than the reserve as forest fragment supply rhinocrypts with a dense understory cover, habitat selected to nest and possibly to forage (Vergara Capítulo I). On the other hand, a larger small mammal density in the fragments could be also associated to the denser understory cover there (Saavedra and Simonetti unpublished). In this way, forest fragments are the riskiest habitats and therefore fragments can be ecological traps for breeding rhinocryptids (Ratti and Reese 1988, Marini et al. 1995, Donovan and Thompson 2001). The use of forest fragments by rhinocryptids should serve to avoid another predator types, but not against small mammals associated to human fragmentation.

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### CAPÍTULO III

#### DOES NEST-SITE COVER REDUCE NEST PREDATION FOR RHINOCRYPTIDS?

*Abstract.* Cover at nesting sites selected by breeding birds could reduce the risk of nest predation. Using artificial nests we tested whether dense cover reduces nest predation on understory birds (rhinocryptids) in temperate forest of Chile. We compared nest predation for artificial nests placed under a dense thicket, nest places with no cover and nests located randomly regarding available cover. Contrary to predictions, we found no differences in nest predation probabilities for the three covered nest-site treatments. Cover at nesting sites is not an effective anti-predator mechanism as its main predators, generalist small mammals also prefer to thrive in the same sites.

*Key word:* nest-site cover, rhinocryptids, nest predation, artificial nests, small mammals.

*Resumen.* Las aves pueden seleccionar sitios con alta cobertura para anidar con objeto de reducir el riesgo de depredación. Mediante nidos artificiales analizamos si una alta cobertura vegetal sobre el nido reduce la depredación de nidos en rinocriptidos, aves del sotobosque en los bosques templados de Chile. Para ello comparamos la tasa de depredación de nidos colocados bajo una densa cobertura con aquellos ubicados sin cobertura o al azar respecto la cobertura disponible. Contrario a las expectativas, no hubo diferencias entre las probabilidades de depredación de nidos por parcela entre los tres tratamientos. A los rinocriptidos, una alta cobertura en sus nidos no le confiere a una propiedad antidepredatoria, al menos contra los pequeños mamíferos, sus principales depredadores, que prefieren usar los mismos hábitats.

## INTRODUCTION

Nesting birds display several behavioral traits to reduce nest predation risk, such as hetero-specific associations, nest-spacing patterns, specific nest-forms (cavities vs open nests) and the selection of safe breeding habitats and nesting sites (Cody 1985, Martin 1988, Wiens 1993, Hogstad 1995, Hanski et al. 1996). Vegetation cover directly over the nest, assumed to be a measure of nest concealment (Howlett 1996), could reduce the risk of nest predation if it reduces detection by or access to predators (Rangen et al. 1999). Thus, a dense cover over nests could improve egg and nestling survival rates (Huhta 1995, Knutson et al. 2000). However, whether these nest site characteristics improve nest success is open to question (e.g., Wilson and Cooper 1998, Schmidt and Whelan 1999).

In deciduous forest of Central Chile, rhinocryptids preferentially nest in soil and root cavities, hidden under a dense understory thicket (Johnson 1967). In fact, rhinocryptids nest at sites with significantly more vegetation cover than that available at a given habitat (Table 1). Here, we experimentally test whether rhinocryptids are selecting these high cover sites in order to reduce nest predation. If cover does convey lower predation risks, the predation rate in nests placed at random regarding understory cover should be higher than in nests located under dense cover. Similarly, nests placed at sites with no cover at all should sustain the highest predation rate. Using artificial nests, we tested these predictions aiming to unravel whether rhinocryptids are selecting safe nesting sites.



Table 1. Nest site and available cover of rhinocryptid nests in deciduous forests. Available cover was measured using 20 1-m radius plots located around of each nest (see text). The mean of nest site cover was greater than the mean of available nest site cover ( $t_{\text{paired},7} = 5.5, P < 0.001$ )

Species	Nest-site cover Mean $\pm$ S.E. (n*)	Available cover Mean $\pm$ S.E. (n**)
Andean Tapaculo	74.15 $\pm$ 3.61 (4)	49.21 $\pm$ 11.13 (20)
Ochre-flanked Tapaculo	80.55 $\pm$ 4.45 (2)	62.07 $\pm$ 12.34 (20)
Chestnut-throated Huet-Huet	45.30 $\pm$ 10.4 (2)	39.41 $\pm$ 10.91 (20)
* number of rhinocryptid nests.		
** number of nest-site plots used to measure available cover.		

## METHODS

The study area is located in the coastal range of central Chile (35° 59' S, 72° 41' W), and comprises Los Queules National Reserve, and surrounding pine plantations, native forest fragments (< 7 ha) and creeks. The predominant habitat within the National Reserve is a mature *Nothofagus* forest mixed with evergreen species. Creeks are habitats dominated by thickets. Understory is less dense in the Reserve and denser at creeks and some pine plantation stands. Small mammals, largely rodents, are the main nest predators (Vergara 2001).

We simulated the nests of rhinocryptid species living in the area: Andean Tapaculo (*Scytalopus magellanicus*), Ochre-flanked Tapaculo (*Eugralla paradoxa*), Chestnut-throated Huet-Huet (*Pteroptochos castaneus*) and Chucao Tapaculo (*Scelorchilus rubecula*) (Araya and Millie 1998; Vergara 2001).

We allocated a total of 300 nests to three different cover treatments: actual cover, available cover and without cover (100 nests were set per treatment). Cover was estimated as the proportion of a pole-shaped cover board visually obstructed by vegetation (Higgins et al. 1996). Cover was assessed up to 1-m height and a standard radial distance of 1-m. Nests with actual cover were allocated to sites with cover greater than 2 S.E. of the plot cover mean. In this treatment, understory cover was always  $\geq 60\%$  in order to mimic nesting sites actually used by rhinocryptids (Table 1). Nests without cover were allocated to sites with 0 to 10% of cover. Finally, nests with available cover were allocated at random within the plots. We set six artificial nests in each of 50 plots of 60-m of radius, nests being at least 25-m apart. At each nest, we placed two Japanese Quail (*Coturnix japonica*) eggs. Nests were placed in soil cavities 50-cm depth and 7-cm in diameter, with a grass-twigs nest at the bottom, mimicking actual rhinocryptid nests. The experiment started at the beginning of the rhinocryptid reproductive season (October 2000). Nests were checked after one week.

For each cover treatment, we calculated the depredation probability per plot as the proportion of depredated nests per plot and compared them using non-parametric Friedman ANOVA-*test* (Siegel 1956).

## RESULTS

A total of 154 (51%) nests were depredated. Of these, 46 (30%) were nests with actual cover, 52 (34%) were located under available cover and 56 (36%) were nests without cover (Figure 1). Nests with actual cover had a depredation probability of 0.46. For nests placed under available cover it was 0.52 and in nest

without cover, it was 0.56. These probabilities did not differ significantly (Friedman ANOVA,  $X_2^2 = 4.6$ ,  $n = 50$ ,  $P = 0.1$ ).

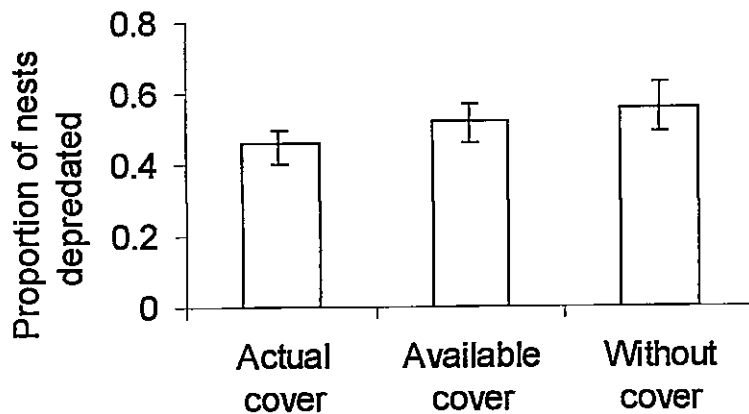


Figure 1. Proportions of nest depredated in three-cover nest-site treatment. 95% C.I. obtained by 10,000 random permutations of nest preyed values (Manly 1998).

## DISCUSSION

Rhinocryptids locate their nests in dense cover understory vegetation (Johnson 1967, Table 1). However, unlike other birds, such as some passerines, a high understory cover did not reduce the risk of nest predation (e.g., Howlett and Stutchbury 1996). When nest cover does not reduce nest predation, it could be influenced by predator abundance rather nest-site structure (Valkama et al. 1999, Cotterill and Hannon 1999). Thus, the relative importance of concealment varies according to the types of predators and their behavior (Rangen et al. 1999). Small mammals are the main nest predators of rhinocryptids (Vergara 2001). These predators are more abundant in habitats with dense understory cover, just like

rhinocryptids (Saavedra & Simonetti, unpublished). Therefore, such nest sites may render them vulnerable to nest failure.

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## CAPÍTULO IV

### AVIAN RESPONSES TO FOREST FRAGMENTATION

**Abstract:** Forest fragmentation can reduce the abundance and diversity of forest birds depending on the matrix habitat conditions. Temperate deciduous forests in South America are being intensely replaced by pine plantations, causing changes in the habitat conditions of breeding birds. We determined differences in the avian richness, and the abundance of species and habitat use categories among a reserve of native forest (continuous forest), forest fragments and the pine matrix. Four species were negatively affected by fragmentation reducing their abundance from forest continuous to pine matrix. Fourteen species were not affected by fragmentation and eight species increased significantly their abundance from pine matrix to the reserve. Pooled abundance and abundance of ground-understory birds was larger in both forest fragments and pine matrix than the reserve. The abundance of granivorous was greater in pine matrix than the reserve. Further, the abundance of trunk-branches insectivorous was greater in the reserve and forest fragments than pine matrix. Thus, fragmentation by pine affects few species, but can reduce the abundance especially of forest specialist birds.

*Key word: pine (Pinus radiata) fragmentation, breeding birds, ground-understory, granivorous, trunk-branches insectivorous.*

## INTRODUCTION

Forest fragmentation triggers a reduction in the number of forest bird species (Boulinier 1998). Particularly, landscapes fragmented and dominated by pine plantations may be considered as unsuitable habitats (Armstrong et al. 1996), because it could affect the reproductive success of breeding birds (Rosenfield et al. 2000). Forest specialist, frugivorous, woodpeckers and hole-nesters are vulnerable to pine fragmentation due to inhospitable of pine plantations (Clout and Gaze 1984, Mitra and Sheldon 1993, Hayes and Samad 1998). However, in some cases pine plantations and small forest fragments may act as foraging or breeding habitats (Estades and Temple 1999, Renjifo 2001). Pine plantations, with a mosaic of heterogeneous vegetation, can support large bird diversity and individuals (Hanowski et al. 1997), depending of the initial site conditions, rotation ages and management intensity (Dickson et al. 1993, Summers et al. 1993). Furthermore, some species can benefit from pine plantations because it may supply seeds to granivorous species (Marquiss and Rae 1994) and as well as insects (Kleintjes and Dahlsten 1994).

Deciduous forests of the coastal range of central Chile have been severely fragmented in the latest centuries by agricultural practices, being confined only to some places of the Cordillera de la Costa (Donoso 1996). However, current of a afforestation with pine (*Pinus radiata*) is changing the landscape, turning croplands and remnant native forests into pine plantations (Donoso and Lara 1996).

Fragmentation of continuous deciduous forest in small fragments enclosed by an extensive pine matrix has triggered important changes in the original habitat mosaic of the breeding birds. However, such habitat transformations do not affect



all forest birds because of the pine matrix and small forest fragments constitute a habitat mosaic of different-quality (Estades and Temple 1999). Such habitat mosaic implies that changes in the availability of resources for birds along the landscape are relatively independent of the forest composition. In fact, understory cover, a variable associated with understory bird abundance (Sieving et al. 2000, Vergara Capítulo I), has increased both in some pine stands and second-growth forest fragments (Acosta 2001). There has been a reduction in native forest canopy from continuous forest to forest fragments and pine stands, variable important in the abundance of canopy foliage birds (Estades 1997a). There is a larger abundance of ground insects, resources for some understory birds, in both the pine matrix and forest fragments than continuous forest (Moreno 2001). Further, some birds would take advantage of the larger amount of seeds (for example pine seeds) in pine plantations (Donoso 2001), such as some finches and the introduced California Quails (*Callipepla californica*). Therefore, fragmentation of continuous forest could affect differentially the forest bird species. We studied changes in the abundances and habitat use categories of forest birds in a deciduous forest within a pine matrix.

## METHODS

### Study site

We studied an area located in the Cordillera de la Costa of central Chile (35° 59' S, 72° 41' W). This area comprises part of the Los Queules National Reserve (a 145 ha reserve inserted in 600 ha of continuous native forest), plus pine (*Pinus radiata*) plantations and small fragments of native forest. The predominant habitat within

the National Reserve is a mature-mixed forest composed principally by *Nothofagus glauca*, *Nothofagus obliqua* and evergreen-sclerophyllous tree species. The pine matrix included both pine with dense understory and with poor understory. Forest fragments were both isolated fragments and corridors of native vegetation. Isolated fragments were *Nothofagus* forest and native thicket, being smaller than 7 ha. Native vegetation corridors included some small creeks covered with dense native vegetation and were less than 140 m wide. The pine matrix comprised a 54% of the total area, the fragments and corridors 24% and the continuous forest a 22% (Acosta 2001).

#### Avian sampling

During breeding season (october-november 2000) we established 50 circular plots of 50 m radius, in a stratified way (proportional to the area): 28 plots in the pine matrix, 11 in forest fragments and 11 in the reserve. The distance between plots was at least 300 m. We measured abundance of each species detected within the plot using point counts (Reynolds et al. 1980). An observer stayed for 10 min in each plot, performing a total of 3 to 5 visits per plot during the breeding season. Censuses were always done in the morning (5:20-11:30 hrs).

We estimated abundance as individuals per hectare. We considered as rare those species that were recorded less than three individuals in all plots. Richness was estimated as the number of bird species per plot and also we pooled abundance of all species. We used an a-priori classification of habitat use and trophic categories (Wiens 1992), grouping species into these categories that could be more affected by fragmentation. Categories were not mutually exclusive in species composition. We pooled bird abundance into the following categories (Johnson 1967, Araya et

al. 1995, Rozzi et al. 1996, Schlatter et al. 1997, unpublished): resident and migratory; cavity and open nesters; granivorous; primary frugivorous; nectarivorous; insectivorous; ground and understory insectivorous; foliage insectivorous; trunk and branch insectivorous.

Additionally, we measured habitat and landscape variables in each sampling plot. We included structural and floristic measures of the vegetation canopy and understory such as cover (%), diameter (dbh), density (trees ha<sup>-1</sup>), tree height (m) and age (years of pine plantations). Landscape variables included size native fragment (ha) and distance from a plot to the nearest creek or native fragment (including its size). Those variables were used to determine the best predictors of the avian richness and pooled abundance, using stepwise regression analysis.

## RESULTS

We recorded a total of 32 bird species during our censuses (Table 1) and from those six were rare species. Of the total, 24 (75%) were recorded the reserve, 28 (88%) in forest fragments and 29 (91%) in the pine matrix. Species richness was not significantly different among the reserve ( $8.5 \pm 0.84$ ) (mean  $\pm$  standard error), forest fragments ( $11.0 \pm 0.88$ ) and the pine matrix ( $10.2 \pm 0.51$ ) (ANOVA,  $n=50$ ,  $F_{2,47}= 2.28$ ,  $P=0.11$ ). In terms of abundance, pooled abundance was larger in pine matrix and forest fragments than the reserve (Table 2). Four species were negatively affected by fragmentation. Of these, three reduced their abundance from the reserve and forest fragments to pine matrix, and only one species reduced its abundance from the reserve to pine matrix (Table 1). Abundances of Thorn-tailed Rayadito, Chilean Pigeon and Austral Pygmy-Owl were greater in the

reserve and forest fragments than pine matrix. White-throated Treerunner abundance was greater in the reserve than pine matrix (Table 1).

Thirteen species were not affected by fragmentation. The abundance of Tufted Tit-Tyrant, Black-chinned Siskin, Chilean Flicker, White-crested Elaenia, Plain-mantled Tit-Spinetail, Chimango Caracara, Patagonian Sierra-Finch, Striped Woodpecker, Chestnut-throated Huet-Huet, , Rufous-legged Owl, Chilean Swallow, Austral Thrush and Fire-eyed Diucon did not significantly differ among the reserve, forest fragments and pine matrix (Table 1). Eight species increased significantly in abundance in the pine matrix. The abundance of California Quail, Common Diuca-Finch, Ochre-flanked Tapaculo, Andean Tapaculo, Des Murs's Wiretail, House Wren and Rufous-collared Sparrow was greater in forest fragments and pine matrix than the reserve. Austral Blackbird had a greater abundance in pine matrix than the reserve (Table 1). The abundance of only three categories, from 13 compared, had significantly different abundance among the reserve, forest fragment and the pine matrix (Table 2). The abundance of granivorous was greater in pine matrix than the reserve, but it was not different between pine matrix and forest fragments. The abundance of ground-understory insectivorous was greater in forest fragment and pine matrix than the reserve. Further, the abundance of trunk-branches insectivorous was greater in continuous forest and forest fragments than pine matrix (Table 2).

Regression models accounted for a little fraction of the variation in avian richness and pooled abundance ( $r^2 < 0.25$ ). Understory cover was the single variable that explained avian richness (Table 3). Understory cover also accounted for pooled abundance in addition to native fragment size (Table 3).

Table 1. Abundance of breeding birds in Los Queules National Reserve, pine plantations and forest fragments. Bird abundance was calculated as number of birds ha<sup>-1</sup>. Rare species (recorded less than three times) that are showed as presence of individuals (p) were not compared. Significant differences were tested using ANOVA and Kruskal-Wallis test\*. Different letters indicate post-tests significant differences.

Species	Landscape component (number of plots)						test*	
	Reserve (28)	Forest fragments (11)		Pine matrix (11)		F <sub>2,47</sub>	H <sub>2</sub>	P
	Abundance ± SE	Abundance ± SE	Abundance ± SE	Abundance ± SE				
Great Shrike-Tyrant ( <i>Agriornis livida</i> )	-	p	-	-	-	3.3	0.191	<0.001
Tufted Tit-Tyrant ( <i>Anairetes parulus</i> )	0.12 ± 0.00	0.18 ± 0.02	0.14 ± 0.01	0.14 ± 0.01	8.2			
Thorn-tailed Rayadito ( <i>Aphrastura spinicauda</i> )	1.62 ± 0.16 a	1.37 ± 0.17 a	0.62 ± 0.11 b	0.62 ± 0.11 b				
Red-backed Hawk ( <i>Buteo polysoma</i> )	-	-	p	p				
California Quail ( <i>Callipepla californica</i> )	0 a	0.22 ± 0.11 b	0.20 ± 0.03 b	0.20 ± 0.03 b		5.7	0.038	
Black-chinned Siskin ( <i>Carduelis barbata</i> )	0.22 ± 0.08	0.33 ± 0.10	0.36 ± 0.12	0.36 ± 0.12	0.3		0.746	
Chilean Flicker ( <i>Colaptes pitius</i> )	0.06 ± 0.00	0.06 ± 0.00	0.07 ± 0.00	0.07 ± 0.00		0.60	0.76	
Chilean Pigeon ( <i>Columba araucana</i> )	0.26 ± 0.11 a	0.07 ± 0.00 a	0 b	0 b		20.5	<0.001	
Austral Blackbird ( <i>Corvus curaeus</i> )	0.12 ± 0.01 a	0.52 ± 0.19 a,b	0.80 ± 0.10 b	0.80 ± 0.10 b	5.4		0.008	
Common Diuca-Finch ( <i>Diuca diuca</i> )	0 a	0.04 ± 0.00 b	0.29 ± 0.09 b	0.29 ± 0.09 b		7.1	0.029	
White-crested Elaenia ( <i>Elaenia albiceps</i> )	1.57 ± 0.11	1.43 ± 0.17	1.40 ± 0.12	1.40 ± 0.12	0.3		0.776	
Ochre-flanked Tapaculo ( <i>Eugralla paradoxa</i> )	0.19 ± 0.08 a	0.84 ± 0.05 b	0.75 ± 0.08 b	0.75 ± 0.08 b	5.2		0.009	
American Kestrel ( <i>Falco sparverius</i> )	-	-	p	p		8.7	0.013	
Austral Pygmy-Owl ( <i>Glacidium nanum</i> )	0.09 ± 0.00 a	0.19 ± 0.18 a	0 b	0 b		0.1	0.963	
Plain-mantled Tit-Spinetail ( <i>Leptasthenura aegitaloides</i> )	0.03 ± 0.00	0.03 ± 0.00	0.05 ± 0.02	0.05 ± 0.02		0.2	0.926	
Chimango Caracara ( <i>Milvago chimango</i> )	0.117 ± 0.051	0.16 ± 0.11	0.13 ± 0.05	0.13 ± 0.05				
Chilean Tinamou ( <i>Nothoprocta perdicaria</i> )	-	p	p	p				
Giant Hummingbird ( <i>Patagona gigas</i> )	-	-	p	p				
Patagonian Sierra-Finch ( <i>Phrygilus patagonicus</i> )	0.25 ± 0.07	0.19 ± 0.04	0.24 ± 0.02	0.24 ± 0.02	1.1		0.349	
Striped Woodpecker ( <i>Picooides lignarius</i> )	0.09 ± 0.00	0.12 ± 0.00	0.07 ± 0.00	0.07 ± 0.00		2.0	0.376	
Chestnut-throated Huet-Huet ( <i>Pterotochus castaneus</i> )	0.29 ± 0.16	0.42 ± 0.19	0.23 ± 0.04	0.23 ± 0.04	2.0		0.149	
White-throated Treerunner ( <i>Pygarrhichas albogularis</i> )	0.64 ± 0.15 a	0.39 ± 0.08 a,b	0.17 ± 0.05 b	0.17 ± 0.05 b	5.9		0.005	
Chuco Tapaculo ( <i>Scelorchilus rubecula</i> )	-	p	p	p				
Andean Tapaculo ( <i>Scytalopus magellanicus</i> )	0.06 ± 0.00 a	0.47 ± 0.16 b	0.75 ± 0.05 b	0.75 ± 0.05 b	11.4		<0.001	
Green-backed Firecrown ( <i>Sephanoides galeritus</i> )	p	-	p	p				
Rufous-legged Owl ( <i>Strix rufipes</i> )	0.09 ± 0.03	0.03 ± 0.00	0.07 ± 0.02 b	0.07 ± 0.02 b		1.7	0.421	
Des Murs's Wiretail ( <i>Sylviorthorhynchus desmursii</i> )	0.14 ± 0.09 a	0.78 ± 0.16 b	0.69 ± 0.06 b	0.69 ± 0.06 b	3.9		0.027	
Chilean Swallow ( <i>Tachycineta meyeri</i> )	0.55 ± 0.09	0.05 ± 0.00	0.22 ± 0.10	0.22 ± 0.10	2.9		0.066	
House Wren ( <i>Troglodytes aedon</i> )	0.17 ± 0.02 a	1.02 ± 0.11 b	1.18 ± 0.12 b	1.18 ± 0.12 b	4.5		0.016	
Austral Thrush ( <i>Turdus falklandii</i> )	0.71 ± 0.14	0.50 ± 0.05	0.63 ± 0.06	0.63 ± 0.06	0.5		0.642	
Fire-eyed Diucon ( <i>Xolmis pyrope</i> )	0.13 ± 0.00	0.24 ± 0.00	0.21 ± 0.11	0.21 ± 0.11		1.6	0.444	
Rufous-collared Sparrow ( <i>Zonotrichia capensis</i> )	0.06 a	0.18 ± 0.00 b	0.22 ± 0.04 b	0.22 ± 0.04 b		6.4	0.039	

Table 2. Pooled abundance and abundance of habitat use categories in continuous forest, forest fragments and pine matrix. Results of ANOVA (two tails) are showed, and different letters correspond to significant Tukey post-test.

Category (species number)	Reserve		Forest fragments		Pine matrix		F <sub>2,47</sub>	P
	Abundance ± SE	Abundance ± SE	Abundance ± SE	Abundance ± SE	Abundance ± SE	Abundance ± SE		
Pooled (32)	7.66 ± 0.64a	9.82 ± 0.52 b	9.53 ± 0.38 b	4.68	0.01			
Resident (18)	5.35 ± 0.37	7.33 ± 0.52	6.47 ± 0.27	3.16	0.05			
Migratory (14)	2.20 ± 0.26	2.45 ± 0.17	3.06 ± 0.25	0.55	0.58			
Cavity nesting (13)	3.85 ± 0.47	4.65 ± 0.23	4.15 ± 0.25	0.56	0.47			
Open nesting (19)	3.67 ± 0.37	4.86 ± 0.41	5.38 ± 0.29	2.41	0.10			
Granivorous (6)	0.36 ± 0.15 a	0.81 ± 0.12 a,b	1.31 ± 0.12 b	3.85	0.03			
Primary frugivorous (2)	0.97 ± 0.48	0.57 ± 0.18	0.63 ± 0.11	2.69	0.08			
Nectarivorous (7)	2.71 ± 0.19	2.76 ± 0.15	3.04 ± 0.21	1.22	0.30			
Insectivorous (24)	5.46 ± 0.58	5.54 ± 0.53	4.88 ± 0.39	1.15	0.33			
Ground-understory insectivorous (6)	0.92 ± 0.31 a	3.53 ± 0.35 b	3.62 ± 0.21 b	16.17	<0.001			
Foliage insectivorous (10)	4.49 ± 0.32	4.52 ± 0.29	3.68 ± 0.24	1.79	0.18			
Trunk-branches insectivorous (5)	2.44 ± 0.24 a	1.97 ± 0.29 a	0.96 ± 0.13 b	9.95	<0.001			

Table 3. Multiple regression models that included the best habitat-landscape variables in the explanation of avian richness and pooled abundance.

Variables in the model		r <sup>2</sup>	d.f.	F	P
Avian richness	Total understory	0.14	1,48	7.7	0.008
Pooled abundance	Total understory - native fragment size	0.24	2,47	11.9	0.003



## DISCUSSION

Habitat fragmentation often increase the probability of local extinction to forest bird species because it may reduce and isolate available habitats (Turner 1996).

However, bird responses to fragmentation may depend of their attributes (Karr 1990, Kattan et al. 1994) and the way as bird perceive habitat mosaic (Roldstad 1991). Chilean forest fragmentation is caused mostly by clear to pasture, pine substitution, urban development and logging. In Chiloé Island, southern Chile, a forest fragmented by pastures, forest birds are confined to use forest fragments, being the pasture matrix an unsuitable habitat (Willson et al. 1994). On the other hand, in landscape dominated by pine, pine matrix could be beneficial to some birds species, depending of the characteristics of the vegetation in the understory (Estades 1994, Estades and Temple 1999, Vergara Capítulo I). Many bird species nest commonly in pine plantations (Estades 1997b,c). Further, birds associated with temperate forests, including some nocturnal raptors (*Strix rufipes*) as an understory birds (*Pterotochos castaneus*) also nest in pine plantations (Estades pers. comunic., Vergara Capítulo II).

Fragmentation of deciduous forests has contributed to increase bird species abundance rather than a decrease. Insectivorous birds that forage in the understory or low forest stratum increased in pine as forest fragments, according to an increase of ground insects (Moreno 2001). Pine and fragment understories have complex and dense vegetation. Dense understory is an important variable in determining understory bird abundance (Sieving et al. 2000). Thus plantations with more heterogeneous understory could support more birds (Hanowski 1997). In this way, management prescriptions such as herbicide application, removal of native

stumps and roots, and other soil disturbances may reduce the habitat quality for these birds.

On the other hand, plantations of Monterrey pines in California (*Pinus radiata*) serve as an important foraging resource for certain birds during the breeding season (Kleintjes and Dahlsten 1994). Most Chilean bird species could use pine matrix independently of the forest canopy composition.

The reserve forest has a less complex understory than pine matrix and native forest fragments. However, In this habitat, Thorn-tailed Rayadito and White-throated Treerunner are forest specialist species (Vuilleumier 1985) that forage mostly on boles and occasionally on the ground (Schlatter and Vergara unpublished). Thus, insectivorous specialists in trunks and branches could be sensitive to land cover change because perturbation of continuous forests triggers an reduction of remnant forest and a loss of canopy structures such as large and decayed tree branches. Chilean Pigeon and Austral Pygmy-Owl are two forest specialist species, the first feed seeds and forest fruits and the second species nesting in tree holes. Fragmentation effects on mature continuous forest may reduce fruit availability and nesting structures. Finally, forest disturbance could be more important for birds that exploit trunk structures, like bark insect and holes to nest. These structures are more available in continuous forest than the pine matrix. Conservation programs of deciduous forest birds should be focused on species that depend on specific forest structures, which become less available when pine plantations replace the original forests. Therefore, forest management should consider to maintain patches of mature forest rather fragments with native second growth forests.

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## DISCUSIÓN GENERAL

La fragmentación de los bosques involucra una transformación del paisaje y del hábitat. Estas transformaciones generalmente son expresadas en cambios en la estructura y composición de la vegetación dominante que constituye el dosel de los bosques. Sin embargo, un cambio en la composición del dosel (por ejemplo de bosque nativo a plantación de pino) no significa que estas unidades sean comunidades discretas en el paisaje, si no que podrían existir gradientes entre estas unidades del paisaje. Específicamente, la estructura y la composición de la vegetación del sotobosque podría ser mayor en plantaciones de pino que en sectores de bosque nativo. Del mismo modo, áreas con bosque nativo podrían estar conformadas por matorrales, bosques de segundo crecimiento o bosque maduro. De esta forma, la fragmentación por pino Monterrey en la zona costera de Chile central ha creado un mosaico de variados hábitats para las aves, especialmente para aquellas asociadas con el sotobosque.

Esta transformación del paisaje, que implican un aumento en la diversidad de hábitats, podría afectar de diferentes formas a las aves. Sin embargo estos efectos no necesariamente son directos, sino que están siendo controlados por una serie de procesos autoecológicos de las especies y de orden bióticos. Entre estos habría que señalar aquellos que fueron estudiados por esta tesis: los atributos de las especies; la selección de hábitat de las aves; la habilidad para moverse entre hábitats; y la influencia del riesgo de depredación de nidos sobre el uso de los hábitats por las aves. Así estos cuatro factores y procesos estarían controlando el efecto de la fragmentación de los bosques y diversificación del paisaje sobre el



uso del espacio por las aves del sotobosque de Chile central. De esta manera, solo podríamos afirmar que este paisaje está realmente fragmentado, para las aves del sotobosque, en la medida que éstas perciban el paisaje como discontinuidades de hábitats y que estas discontinuidades sean provocadas por el efecto antrópico sobre el uso del suelo y la vegetación.

Las diferentes especies de aves difieren en sus atributos de historia de vida. Bajo condiciones medioambientales adversas, como aquellas impuestas por la fragmentación antrópica de los hábitats, las especies de aves diferirán en su vulnerabilidad a la extinción. Esta variación será, en gran parte, explicada por ciertos atributos de historia de vida que hacen que algunas especies de aves sean más sensibles a la fragmentación. Los rinocriptidos no son la excepción a esta regla, al menos para las cuatro especies que coexisten localmente en el bosque deciduo fragmentado por pino de la Cordillera de la Costa de Chile central. Para estas especies, un aumento en la sensibilidad determina una reducción en su incidencia. Las especies más sensibles en general son menos abundantes y tienen una menor especificidad de hábitat.

Todas estas especies usan hábitat con abundante cobertura en el sotobosque y el suelo, por esta razón los fragmentos de bosque nativo remanente y algunas plantaciones de pino proporcionan estas condiciones. Las especies menos sensibles como el churrín y el churrín de la mocha, son más beneficiadas por las condiciones de hábitat que resultan de la fragmentación. En el otro extremo, las especies más sensibles como el chucao y el hues-hues castaño, usan una menor fracción del espacio debido a que algunos hábitats como las plantaciones de pino con poco sotobosque, podrían ser hábitats desventajosos para su persistencia.

Las aves, como muchos otros organismos, usan los hábitats en la medida que pueden acceder a ellos. Así podrían existir hábitats que actúen como barrera, limitando sus movimientos y la habilidad para colonizar hábitats convenientes. Los rinocriptidos en los bosques de pino tiene una gran habilidad para moverse entre diferentes tipos de hábitat e incluir estos como parte de sus ámbitos de hogar, a excepción de las plantaciones con escaso sotobosque. Esta situación podría ser diferente en bosques que han sido fragmentados con praderas, donde los individuos tendrían menor habilidad para dispersarse entre parches boscosos. De esta forma, la disponibilidad de hábitats con sotobosque complejo es un factor importante en la selección de hábitats y el movimiento de los rinocriptidos. El uso del paisaje por el componente humano, incluyendo tanto el manejo de las plantaciones de pino como la proporción del espacio dejado como protección, debieran incorporar como criterio la conservación de la diversidad de aves del sotobosque y otros organismos asociados al suelo. De este modo, sería importante dar prioridad a los planes de manejo que involucren sistemas interconectados de quebradas con vegetación nativa, así como una reducción en las perturbaciones del sotobosque durante las rotaciones efectuadas a las plantaciones de pino (por ejemplo mantener raíces y tocones de árboles nativos, junto con reducir el uso del fuego y herbicidas antes de una plantación). Con estas prescripciones en el manejo se busca incrementar la superficie de hábitats convenientes y capaces de mantener la dispersión de individuos entre subpoblaciones que sean proclives a quedar aisladas.

La depredación de nidos podría aumentar cuando las condiciones de hábitat favorecen un incremento en la abundancia de depredadores con dieta generalista.

La fragmentación de estos bosques ha cambiado la composición y abundancia de los depredadores de nidos, siendo más abundantes los depredadores generalistas en los fragmentos y plantaciones de pino (pequeños mamíferos y cánidos). Este hecho concuerda con una mayor depredación de nidos en los fragmentos con relación al bosque continuo. Además, los fragmentos donde la densidad de rinocriptidos es alta, podrían constituir trampas ecológicas para estas aves que anidan ahí. Por otro lado, la mayor cobertura alrededor del nido usada por los rinocriptidos no les proporciona una mayor protección con relación a sitios con menor cobertura.

De este modo, la fragmentación de los bosques deciduos aparece como beneficiosa, al menos para las especies menos sensibles, pero sin embargo, sus incrementos en densidad podrían no compensar la mortalidad por pérdidas de nidos. Por lo tanto en el largo plazo las poblaciones de estas aves podrían no persistir, al menos localmente.

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