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HISTORIA DE VIDA EN AVES DE AMBIENTES
FRAGMENTADOS**

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Por

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**FACULTAD DE CIENCIAS
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TESIS DE DOCTORADO**

Se informa a la Escuela de Postgrado de la Facultad de Ciencias que la tesis de Doctorado presentada por el candidato

RENZO VARGAS RODRÍGUEZ

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The image shows three handwritten signatures on dotted lines. The top signature is in black ink. The middle signature is in blue ink. The bottom signature is in black ink. To the right of the signatures is a circular stamp with the text "FACULTAD DE CIENCIAS" at the top, "BIBLIOTECA CENTRAL" in the middle, and "UNIVERSIDAD DE CHILE" at the bottom.

Introducción

Dedicado a:

Alejandra y Nataniel,

Por ser mi familia, mi vida y mi inspiración ...

A mis padres

Por darme todas las herramientas para llegar hasta aquí y seguir más allá ...



Autobiografía



Nací en Oruro, Bolivia (1974). Realicé mis estudios de pre-grado en la Carrera de Biología de la Universidad Mayor de San Simón en Cochabamba, Bolivia, donde obtuve el grado de Licenciado en Biología y título profesional de Biólogo en provisión Nacional. Comencé mis estudios sobre la ecología de aves y micromamíferos de los bosques de *Polylepis* siendo aún universitario. Durante este periodo también trabajé como auxiliar de investigación y posteriormente como investigador asociado en el Centro de Biodiversidad y Genética, lugar donde realicé mi tesis de grado sobre la variación poblacional de pequeños mamíferos en fragmentos de bosque de *Polylepis*. Además, participé en múltiples

proyectos de investigación sobre las consecuencias poblacionales y comunitarias de la modificación y fragmentación de estos bosques Altoandinos en aves y micromamíferos. En 2002, me trasladé a Santiago de Chile para realizar el curso de Ecología de Campo e incorporarme al laboratorio de Química Ecológica de la Universidad de Chile y realizar una estadía de investigación LANBIO sobre la ecología conductual de selección de hospedero en insectos fitófagos. Posteriormente (2003), me trasladé al laboratorio de Ecología Terrestre donde realicé una estadía para redacción de artículos científicos y finalmente (2005) me incorporé como investigador en postgrado al programa de Doctorado en Ecología y Biología Evolutiva de la Universidad de Chile, realizando mis estudios y múltiples investigaciones acerca de las consecuencias de la fragmentación del hábitat sobre la variación de interacciones ecológicas, en el marco de la biología de la conservación. Mi proyecto de investigación doctoral versó sobre las consecuencias de la fragmentación del hábitat sobre la modificación de síndromes de historia de vida en aves.

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INDICE DE MATERIAS



Índice de materias	viii
Lista de tablas	xi
Lista de figuras	xiii
Resumen	1
Abstract	2
Antecedentes generales	3
Referencias	6
Capítulo I:	9
Nest predation risk in <i>Polylepis</i> forests fragments and <i>Pinus radiata</i> plantations in the tropical Andes of Bolivia	
Abstract	10
Introduction	11
Materials and Methods	12
Results	14
Discussion	19
Acknowledgements	22
References	22
Capítulo II:	27
Reproductive life-history traits variation of birds in fragmented habitats: a review and meta-analysis	
Abstract	28



Introduction	29
Materials and methods	29
Results	31
Discussion	32
Acknowledgments	34
References	34
Capítulo III:	37
Habitat fragmentation, predation risk and reproductive life-history syndrome in <i>Leptasthenura yanacensis</i>	
Abstract	38
Introduction	39
Materials and methods	40
<i>Study species and study site</i>	40
<i>Evaluation of predator diversity</i>	40
<i>Nest searching and monitoring</i>	41
<i>Behaviour and manipulation of predation risk</i>	41
<i>Life-history trait measurements</i>	43
<i>Nest fate</i>	43
Results	44
<i>Predator diversity</i>	44
<i>Model selection</i>	44
<i>Induced antipredator behaviour</i>	44
<i>Life-history trait variation</i>	46
<i>Nest fate</i>	50
Discussion	50
<i>Response to increased predation risk within habitat fragments</i>	50
<i>Responses to predation risk across habitat fragments</i>	51
<i>Growth rate differences</i>	52

Main conclusions 54
Acknowledgments 54
References 55

Conclusiones generales 59
Referencias 64



LISTA DE TABLAS

Capítulo I.

Nest predation risk in *Polylepis* forests fragments and *Pinus radiata* plantations in the tropical Andes of Bolivia

- Table 1.** Vegetation structure of kewiña (*Polylepis besseri*) and pine (*Pinus radiata*) plantation at the Tunari National Park, Cochabamba, Bolivia 16
- Table 2.** Results from the factor analysis of the vegetation variables of pine plantations (*Pinus radiata*) and *Polylepis* forests summarized in the ranked rotated factor matrix 17
- Table 3.** Evaluation of vegetation of *Polylepis* forest fragments (from factor analysis), nest level and habitat type effects in an ANOVA-like design based on structural logistic regression analysis through Generalized Linear Models 19

Capítulo II:

Reproductive life-history traits variation of birds in fragmented habitats: a review and meta-analysis

- Table 1.** Sample sizes representation for each of the reproductive life history traits evaluated in publications related to habitat fragmentation 32
- Table 2.** Hedges' *d* effects of different life history traits in relation to clutch and brood size 33

Capítulo III:

Habitat fragmentation, predation risk and reproductive life-history syndrome in *Leptasthenura yanacensis*

Table 1. Bird raptor diversity differences among large and small fragments of <i>Polylepis besseri</i> highland forest fragments at Cochabamba, Bolivia	45
Table 2. Analysis of variance of the candidate models evaluated for tree behavioral variables through GLMMs	47
Table 3. Regression analysis of the effects of fixed and random factors evaluated for tree behavioral variables through GLMMs and the Linear Mixed Effect	47
Table 4. Life history traits and nest fate values of <i>Leptasthenura yanacensis</i> during nesting periods in birds of large and small <i>Polylepis besseri</i> highlands forest fragments at Cochabamba, Bolivia	49

LISTA DE FIGURAS

Capítulo I.

Nest predation risk in *Polylepis* forests fragments and *Pinus radiata* plantations in the tropical Andes of Bolivia

Figure 1. Artificial nest predation at two layer (ground and trees) in exotic pine (*Pinus radiata*) plantations of and in native Kewiña (*Polylepis subtusalvida*) forest fragments at Tunari National Park, Cochabamba, Bolivia 14

Figure 2. Number of plasticine eggs preyed by distinct predators at tree and ground layers at the Tunari National Park, Cochabamba, Bolivia 15

Figure 3. Graphical representation of factor analysis of the vegetation structure variables of pine plantations (*Pinus radiata*) and *Polylepis* forests of the Tunari National Park, Cochabamba, Bolivia 18

Capítulo III:

Habitat fragmentation, predation risk and reproductive life-history syndrome in *Leptasthenura yanacensis*

Figure 1. Comparison of bird predator species diversity between small and large fragments using rarefaction procedure 46

Figure 2. Nest parental care behaviour of *Leptasthenura yanacensis* during incubation periods in nest “With” and “Without” the presence of the predator simile in large and smaller *Polylepis besseri* highland forest fragments at Cochabamba, Bolivia 48

RESUMEN

La modificación y fragmentación del hábitat transforman el paisaje y son amenazas significativas para la biodiversidad. Sus efectos modifican las interacciones ecológicas en las que la biodiversidad participa y ello puede implicar la modificación de presiones selectivas y cambios en las dinámicas evolutivas de las poblaciones remanentes. Por ejemplo, en ambientes fragmentados los cambios en la abundancia y diversidad de depredadores tienen consecuencias en el riesgo de depredación de nidos de aves. Siendo la depredación la principal causa de falla reproductiva en las aves, ésta podría representar una presión selectiva capaz de producir cambios microevolutivos en rasgos asociados a las estrategias reproductivas antidepredatorias en las aves. En ese sentido, propongo que la modificación y fragmentación del hábitat modificará el escenario ecológico promoviendo alteraciones en las dinámicas microevolutivas que impliquen cambios en síndromes de historia de vida de los organismos remanentes. Para ello, primeramente evalúo el efecto de la modificación del hábitat sobre la variación del riesgo de depredación de nidos entre plantaciones forestales y remanentes de bosque nativo en los altos Andes de Bolivia. Además, evalúo la generalidad de este fenómeno mediante una revisión y meta-análisis sobre la variación en rasgos de historia de vida reproductivos en aves que habitan ambientes fragmentados. Identificamos y discutimos los principales patrones y efectos encontrados en la literatura científica (ISI) producida en los últimos 21 años. Finalmente, mediante un estudio de caso evalúo la variación de síndromes de historia de vida reproductivos de *Leptasthenura yanacensis* ante la modificación natural y experimental del riesgo de depredación de nidos en fragmentos de bosque de distinto tamaño.

ABSTRACT

Habitat loss and fragmentation are transforming the landscape and represents a significant threat to biodiversity. Its effects alter ecological interactions in which biodiversity participates and may involve the modification of selective pressures and evolutionary dynamics of remnant populations. For example, in fragmented habitats the changes in the abundance and richness of predators have an impact on the predation risk of nesting bird. Since predation is the main cause of reproductive failure in birds, it could represent an evolutionary pressure that may produce microevolutionary changes in traits associated with antipredatory strategies of reproduction. In this regard, I propose that habitat fragmentation alter the ecological scenario promoting changes in the microevolutionary dynamics involving changes in life history syndromes of remaining organisms. To do this, I first evaluated the effect of habitat modification on the variation of the risk of nest predation between forest plantations and native forest fragments in the high Andes of Bolivia. In addition, I assess the generality of this phenomenon through a review and meta-analysis of the variation in reproductive life history traits in breeding birds inhabiting fragmented landscapes. I identify and discuss the main patterns and effects found in the literature (ISI) produced in the last 21 years. Finally, through a case study I assessed the variation in life history syndromes of *Leptasthenura yanacensis* to natural and experimental changes in the risk of nest predation in forest fragments of different sizes.

ANTECEDENTES GENERALES

La pérdida y fragmentación del hábitat transforman el paisaje y son amenazas significativas para la biodiversidad (Fahrig 2003). Estos procesos pueden modificar la abundancia y riqueza de especies, y con ello también modificar la intensidad de las interacciones ecológicas (Murcia 1995; Simonetti et al. 2006). Por ejemplo, en paisajes fragmentados, los cambios en la abundancia de depredadores, en respuesta a la subdivisión y reducción de los parches remanentes, generan un mosaico variable de ambientes con distinto riesgo de depredación de nidos (Soderstrom 1999; Chalfoun et al. 2002; Batary and Baldi 2004; Stephens et al. 2004; Bergallo et al. 2005). Dado que la depredación de nidos es la causa más frecuente de fracaso reproductivo en aves (Ricklefs 1969; Skutch 1985; Martin 1992, 1993), este proceso es un mecanismo ecológico capaz de provocar cambios micro y macroevolutivos, influenciando la modificación de rasgos de historia de vida, además, de conductas de nidificación y cuidado parental en las aves (Martin 1988, 1995; Robinson et al. 1995; Soderstrom 1999). Esto debido a que la modificación del riesgo de depredación puede alterar el balance entre los costos y los beneficios asociados con la provisión de cuidado parental, produciendo diferencias entre poblaciones en la cantidad y tipo de cuidado que los padres proveen (Badyaev and Ghalambor 2001). Por ejemplo, en respuesta a la percepción de mayor riesgo de depredación, los individuos de muchas especies exhiben cambios fenotípicos que reducen la probabilidad de ser depredados (Werner et al. 1983; Lima and Dill 1990; Relyea 2001; Lima 2009). En aves reproductivas, ésta respuesta se esperaría que esté caracterizada por una integración particular de rasgos conductuales y de historia de vida propuesto recientemente como un "síndrome" anti-depredación (Ferretti et al. 2005).

En ambientes fragmentados, la variación del riesgo de depredación podría determinar la evolución de rasgos que confieran una mayor adecuación biológica correspondiente a las condiciones de los parches de hábitat locales, determinando la existencia de puntos cálidos o fríos y por lo tanto, de mayor o menor integración fenotípica (Pigliucci and Preston 2004; Thompson 2005). De esta manera, si la modificación y fragmentación del hábitat producen cambios en el riesgo de depredación, se producirían diferencias en los síndromes de historia de vida reproductivos antidepredatorios en las aves, generando un mosaico conductual y de historias de vida o promoviendo la evolución de plasticidad fenotípica necesaria para que los individuos puedan responder a la heterogeneidad ambiental a la que se ven expuestos. Por lo tanto, se esperaría que en ambientes espacialmente variables no exista un solo fenotipo

consistentemente óptimo (Ghalambor and Martin 2002). La comparación de rasgos conductuales y de historia de vida en subpoblaciones que difieren en el riesgo de depredación de nidos nos permitirá comprender como ocurre la evolución de los síndromes de historia de vida reproductivos y las estrategias reproductivas antidepredatorias de las aves en ambientes fragmentados.

Las respuestas de los rasgos de historia de vida y conductuales reproductivos de aves a los efectos del riesgo de depredación en ambientes modificados han sido escasamente estudiadas (Lima 2009). De hecho, son pocos los casos que estudian específicamente la modificación de rasgos de historia de vida a nivel intraespecífico en respuesta a la fragmentación del hábitat y usualmente estos se basan en la modificación del tamaño corporal (Schmidt and Jensen 2003; Lomolino and Perault 2007). Aún no se ha analizado como la modificación y fragmentación del hábitat, al ser determinantes de la variación del riesgo de depredación de nidos, pueden tener consecuencias en la modificación de síndromes de historia de vida reproductivos en aves. Si así fuera, deberíamos encontrar diferencias consistentes en los distintos rasgos conductuales y de historia de vida reproductivos en aves que habitan fragmentos de diferente tamaño y con distinto riesgo de depredación. En ese sentido, el objetivo general de esta tesis es evaluar el efecto que tiene la modificación y fragmentación del hábitat sobre el riesgo de depredación de nidos y sus consecuencias en la variación de síndromes de historia de vida reproductivos antidepredatorios en aves.

La validez de estas proposiciones las evalúo de la siguiente manera:

En el Capítulo I evalúo la variación del riesgo de depredación entre plantaciones forestales de pino y fragmentos de bosque nativo de *Polylepis* en la región Andina de Bolivia. La modificación y fragmentación de hábitat boscoso afecta a muchas especies dependientes de estos hábitats. Estos efectos negativos han sido reportados cuando los bosques son reemplazados tanto por áreas abiertas (Freemark and Merriam 1986; Blake and Karr 1987) como por plantaciones forestales (Enoksson et al. 1995; Jansson and Angelstam 1999). Dicho efecto es particularmente conocido para la avifauna de los bosques altoandinos de Bolivia, donde las poblaciones de aves han declinado en los remantes de bosques nativo producto del reemplazo de la vegetación nativa por plantaciones de pino y eucalipto (Fjeldsá and Kessler 2004; Balderrama 2006). Sin embargo, comparadas con las áreas abiertas, las plantaciones no son completamente inhabitables para muchos organismos dependientes de los bosques (Hartley 2002) y es importante determinar cuáles son los factores que determinan la persistencia o declinación de las especies en estos nuevos ambientes. Algunas causas próximas han sido sugeridas para la declinación, incluyendo

una mayor depredación de nidos en plantaciones forestales comparado con el bosque nativo (Carignan and Villard 2002; Vergara and Simonetti 2003). Al ser la depredación de nidos una de las principales causas de la falla reproductiva de aves, ésta puede afectar la viabilidad de las poblaciones al punto de provocar extinciones locales (Zanette and Jenkins 2000), pero hasta ahora no se ha documentado la existencia de riesgo diferencial de depredación de nidos en el bosque nativo y las plantaciones forestales en Bolivia.

En el Capítulo 2 evaluó la generalidad del efecto de la fragmentación del hábitat y sus consecuencias sobre la modificación de rasgos de historia vida reproductivos en aves. Para ello comparamos la variación de rasgos de historia de vida reproductivos de aves estudiadas en ambientes fragmentados. Sugiero que si la fragmentación del hábitat es un factor determinante de la variación del riesgo de depredación de nidos, entonces debería encontrar diferencias en rasgos conductuales y de historia de vida reproductivos entre poblaciones que habitan fragmentos de distinto tamaño. Identifico, y discuto los principales patrones y efectos encontrados en la literatura mediante una revisión y meta-análisis de publicaciones científicas ISI disponibles para los últimos 21 años.

En el Capítulo 3 evaluó el efecto de la variación del riesgo de depredación de nidos entre fragmentos de bosque de distinto tamaño sobre la modificación de síndromes de historia de vida reproductivos en *Leptasthenura yanacensis*. Esta es una pequeña ave insectívora especialista que nidifica y se alimenta exclusivamente en árboles de *Polylepis* (Fjeldsá and Krabbe 1990). En Bolivia, *L. yanacensis* es considerada como una especie amenazada (VU) debido a la degradación y fragmentación de su hábitat (Cahill et al. 2009). Estos bosques representan el hábitat altoandino más amenazado de Bolivia producto de la pérdida y fragmentación del mismo como consecuencia de diversas causas, entre ellas la introducción y reemplazo del bosque nativo por plantaciones forestales de pino *Pinus radiata*. *Leptasthenura yanacensis* sería más vulnerables al riesgo de depredación de nidos por aves (Capítulo 1), sin embargo, se desconoce si son capaces de reconocer a sus potenciales depredadores y si las posibles variaciones en la abundancia de depredadores producto de la fragmentación del hábitat promueve variaciones en sus rasgos de historia de vida reproductivos. Sugiero que en los fragmentos más grandes de los bosques de *Polylepis* la abundancia de depredadores y por tanto, el riesgo de depredación de nidos es mayor que en fragmentos más pequeños, entonces los individuos de *L. yanacensis* nidificando en fragmentos grandes expresarán el síndrome de historia de vida antidepredatorio (*sensu* Ferretti et al. 2005), al contrario de lo que ocurrirá en fragmentos pequeños donde estos mostrarán una desintegración del síndrome. Así mismo, si los síndromes conductuales

relacionados a la reproducción representan rasgos fenotípicos plásticos, y si la depredación puede modificar dichos rasgos conductuales, entonces al incrementar el riesgo de depredación de los nidos, los padres mostrarán ajustes conductuales acordes al síndrome antidepredatorio (*sensu* Ferretti et al. 2005). Específicamente, los objetivos son: 1. evaluar la expresión de plasticidad fenotípica conductual antidepredatoria en *L. yanacensis* durante el cuidado parental ante el incremento del riesgo de depredación de nidos en fragmentos de distinto tamaño y 2. Contrastar la hipótesis del síndrome anti-depredación en *L. yanacensis* comparando la variación de rasgos conductuales y de historia de vida en individuos parentales de fragmentos de distinto tamaño.

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CAPITULO I

NEST PREDATION RISK IN *POLYLEPIS* FOREST FRAGMENTS AND *PINUS RADIATA* PLANTATIONS IN THE TROPICAL ANDES OF BOLIVIA

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ABSTRACT

Nest predation is the main cause of reproductive failure in birds and accordingly, birds display behavioral traits to reduce nest predation risk such as the selection of safe breeding habitats. For example, vegetation cover directly over the nest is assumed to be a measure of nest concealment, and could reduce the risk of nest predation. Deforestation and afforestation with exotic species have increased world-wide modifying the patterns of vegetation cover and impacting on biodiversity. Thus, tree plantations are considered "biological deserts" since they hold depauperated original biota, and are discarded as suitable habitat for the local fauna. The higher nest predation in tree plantations than in native forests might account for this fact. We have tested if there are differences in nest predation risk between pine plantations and native *Polylepis* forests fragments through natural and field experiments in Cochabamba, Bolivia. Furthermore, we have evaluated the relation of microhabitat vegetation cover characteristics with artificial nest predation. A third of the nests were preyed. The probability of nest predation was significantly smaller in pine plantations than in *Polylepis* forests. The main predators identified were rodents, marsupials and canids, followed by birds and humans in smaller proportions. Understory structure of pine plantations and *Polylepis* forests were different. The percentage of cover of bushes, herbs, mosses and grass was significantly higher in *Polylepis* forests than in pine plantations. Nevertheless, ground and tree nest predation risk was not directly associated to microhabitat variables. Nests predation could not explain the reduced species diversity associated to pine plantations, thus other causes should be explored.

Key words: Predation, artificial nests, forest plantation, native forest, pine, *Polylepis*

INTRODUCTION

Nest predation is the main cause of reproductive failure in birds (Ricklefs 1969; Skutch 1985; Martin 1993). Nevertheless, nesting birds display behavioral traits to reduce nest predation risk, through the selection of safety sites to nest (Martin 1988; Wiens et al. 1993; Hanski et al. 1996). For example, vegetation cover directly over the nest is assumed to be a measure of nest concealment (Howlett and Stutchbury 1996), and 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 the nest could improve egg and nest survival rates (Huhta et al. 1996; Knutson et al. 2000). However, whether these nest site characteristics improve nest success remain controversial since they also could result of shelter for potential predators (Wilson and Cooper 1998; Schmidt and Whelan 1999).

Land-use change is one of the main causes of vegetation cover modification and is one of the most significant threats to biodiversity (Sala et al. 2000a; Foley et al. 2005). In fact, deforestation and afforestation with exotic species have increased world-wide impacting upon the composition, structure and functioning of biodiversity (Sala et al. 2000b). Currently, 3% of the arboreal mass of the planet are commercial plantations covering 60 million hectares in developed countries and 55 millions in developing countries (FAO 2005). Among them, plantations of *Pinus radiata* constitutes one of the economically more successful and widespread plantations (FAO 2005). Commercial plantations are usually considered "biological deserts" as they hold depauperated assemblages of the original biota, being discarded as a suitable habitat for the local fauna (Hartley 2002).

One of the groups best documented about the effects of habitat modification by forest plantations, are the birds (Estades 1999; Estades and Templeton 1999). Several causes have been suggested to explain the decline of birds in these environments; one such factor could be nest predation (Carignan and Villard 2002; Vergara and Simonetti 2003). Indeed, it has been reported that nest predation is higher in plantations than in adjacent native forests (Carignan and Villard 2002). High predation is translated in smaller bird reproductive success (Remes 2003), rendering nest predation one of the main causes of reproductive failure of birds, affecting the viability of the populations to the point of causing local extinctions (Zanette 2000).

In Bolivia, plantations of *P. radiata* and *Eucalyptus* spp. are increasing (CFB 2005; FAO 2005). Even within protected areas, pine plantations are promoted for increasing vegetation cover to enhance gulch protection and stop soil erosion (Fjeldså and Kessler 2004). However, the increase in plantations occurs at the expense of the native *Polylepis* forests, impacting

negatively on the native bird diversity due to the fragmentations and modification of the original habitat (Fjeldsá 2002, Balderrama 2006). These Andean tropical forest are important areas for the conservation of several endemic, forest-dependent and threatened birds (Soria and Hennessey 2005; Balderrama 2006) but they are being replaced by pine plantations, despite plantations maintain less bird diversity than *Polylepis* forests (Fjeldsá 2002). Although this pattern has been repeatedly confirmed (Jarsen, 1998; Fjeldsá 2002; Balderrama 2006), we still ignore the ecological causes responsible for the decline in bird diversity in pine plantations.

Since nest predation in pine plantations can be higher than upon nests placed in native vegetation (Vergara and Simonetti 2003), birds might avoid plantations as they could be insecure habitats for reproduction. Based on this evidence, we wonder if nest predation is higher in exotic forest plantations than in native *Polylepis* forest, triggering birds to avoid plantations, hence decreasing their richness and abundance. Furthermore, here we measure whether different nest level and vegetation cover in the landscape confer an advantage in reducing nest predation risk.

MATERIALS AND METHODS

We relied on an experimental approach appealing to natural experiments (pine plantations and *Polylepis* forests), and through manipulative experiments (artificial nest predation) at the Tunari National Park in Cochabamba, Bolivia. Nest predation experiments and vegetation evaluation were performed during November 24 and December 8 of 2006, dates corresponding with the reproductive period of birds in the study area. Nest predation intensity was evaluated through a manipulative experiment, using artificial nests baited with quail (*Coturnix japonica*) and plasticine eggs (Part and Wretenberg 2002). Although the use of artificial nests remains controversial (Major and Kendal, 1996; Moore and Robinson, 2004), they do allow experimental control over numerous confounding factors and provide an attractive, low cost and nondestructive system for examining nest predation risk (Esler and Grand, 1993; Whelan et al., 1994, Zuria et al. 2007). Artificial nests do provide an index of overall potential predation risk and are a valuable tool for answering comparative ecological questions regarding spatial variation on predation risk (Seitz and Zegers, 1993; Wilson et al., 1998; Thompson and Burhans, 2004).

We replicate nests of birds reported nesting in the study area, both in the ground, as the Andean tapaculo (*Scytalopus simonsi*), and birds nesting on trees as the Chiguanco (*Turdus chiguanco*). We simulated tree nests using Andean grass *Festuca ichu*, an abundant species in the area and commonly used by birds to build nests, following the protocol of similar studies

(e.g., Vergara and Simonetti 2003; Vergara and Simonetti 2004). Each nest was baited with three eggs: two of quails and one of plasticine simile of quail eggs in shape, size and aspect. Furthermore, both types of eggs were salved with olive oil to homogenize the scent among them.

Artificial nests were installed in four patches of *Polylepis* forests ($n = 100$) and in five patches of pine plantations ($n = 130$). Nests were separated by 50 m among them and at 25 m from the edge of the patch. Distance between nests varied a few meters depending on the availability of a suitable nest site; however, we maintain the same nest density in all forest patches, to avoid biases among predators, since predators increase their search intensity with increasing density of prey (Martin 1988). In each point, we installed two nest, one on the ground in cavities of 10 to 20 cm deep ($n = 115$), and the other on the trees between 70 to 250 cm high ($n = 115$). We review the nests after a week and registered the number of preyed nests and identified potential predator through plasticine eggs and the use of other predator signs around the nests when possible. The predation probability was estimated as the proportion of nests preyed of the total installed by habitat type (pine versus *Polylepis*) and strata (ground versus tree). Comparisons of the proportion were made through the z test with Yates correction for continuity (Zar 1999). Furthermore, we applied Bonferroni correction for multiple comparisons and significant results were below $P = 0.0125$ (Zar 1999).

To evaluate the effect of the vegetation cover on nest predation we measure the vegetation by strata. In each point where we install nests, the immediately surrounding understory stratum was evaluated in plots of 9 m^2 (*Polylepis* = 50; Pine = 65). We quantify the cover of bushes, grasses, mosses and straw inside the plots through a modification of the Cover Abundance Scale (CAS) method of Braun-Blanquet, whose covering categories were as follow: 5 = > 75%; 4 = 50-75%; 3 = 25-50%; 2 = 5-25%; 1 = < 5%; 0 = Absent (Ralph et al. 1996). Forest cover at nest site was measured with the mean canopy diameter method represented by the equation: $A = c * d^2$; where: A = Area; $c = 0.7854$ (constant) y d = mean diameter canopy of trees (TROPICO 2004). Furthermore, we characterized the tree stratum of each nest through: 1) tree structural variables (DBH, high and cover) and 2) tree density with Point-Centered Quarter Method (PCQM) (Rabinowitz 2003). To compare each of the structural variables between habitats types we used the Mann-Withney U test. A second exploratory phase consisted of a factor analysis using a varimax rotation procedure of all the habitat variables. This resulted in three factors, each grouping a set of variables that exhibited a high degree of correlation. Nevertheless, factor rotation enables us to obtain three orthogonal and uncorrelated factors that make a better representation of the variance among variables (Manly 2005). To determine the

effect of vegetation variables, plus the effect of habitat and nest level on the probability of nest predation we performed a factorial multiple logistic regression using generalized linear models for analyzing the effects of continuous and categorical predictor variables on nest predation. The design of the analysis included effects for continuous variables (Factors 1, 2, and 3) as well as categorical predictor variables (habitat and nest level) fitted as ANOVA-like designs. We use the three factors from the factorial analysis as continuous variables plus habitat type (pine or *Polylepis*) and nest strata (ground or trees) as factors (Manly 2005).

RESULTS

A third (70 of 230) of ground and tree nests was depredated. The probability of nest predation in pine plantations is significantly smaller than in *Polylepis* forest fragments. In pine plantation, 36% of the nest were preyed compared with 64% of nest predation in *Polylepis* fragments ($z = 3.14$; $P < 0.002$; $1-\beta_{0.0125} = 0.98$). Independently of habitat type, the probability of ground nest predation is not significantly different of tree nests (35 nests in tree and ground, respectively). Furthermore, in pine plantations 14% of tree nest were preyed versus 25% of ground nests ($z = 1.36$; $P = 0.17$; $1-\beta_{0.0125} = 0.25$; Figure 1). In the same way, in *Polylepis* forests fragments, nest predation probability is not significantly different between strata with 52% of preyed nests in trees and 36% on the ground ($z = 1.41$; $P = 0.16$; $1-\beta_{0.025} = 0.26$; Figure 1).

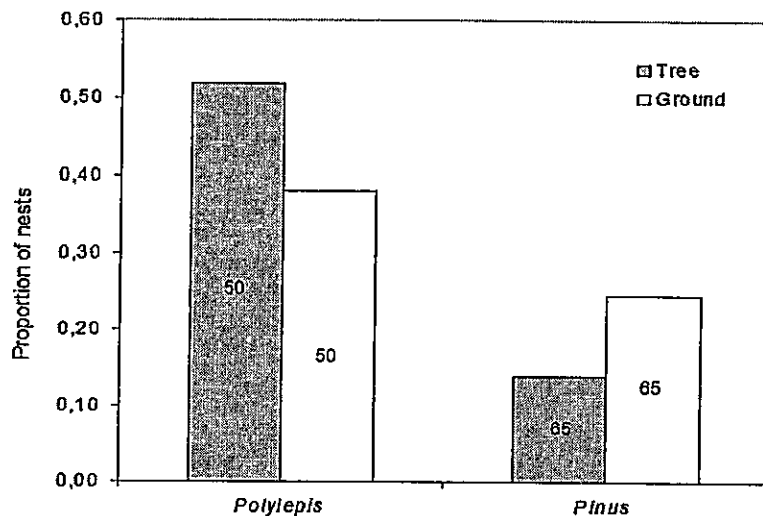


Figure 1. Artificial nest predation at two layer (ground and trees) in exotic pine (*Pinus radita*) plantations and in native Kewiña (*Polylepis subtusavida*) forest fragments at Tunari Nacional Park, Cochabamba, Bolivia. Values above the bars represent sample size ($n_{total} = 230$).

As assessed through plasticine eggs, the main nest predators are rodents, canids, marsupials and birds. The 46% of total eggs were attacked by small mammals (rodent and the marsupial *Thylamis venustus*) and 22% by canids (*Canis familiaris* or *Pseudalopex* sp.). Furthermore, 14% of the eggs were preyed by birds and a smaller proportion was preyed by humans (2%). The predators of 17% of attacked plasticine eggs were not identified. The relative frequencies of plasticine eggs attacked by different predators in pine plantations and in *Polylepis* forest fragments is homogeneous ($G = 8.96$; d.f. = 5; $P > 0.05$). With respect to nest level the relative frequency of egg predation shows that rodents and canids prey relatively more eggs on the ground ($G = 24.56$; d.f. = 5; $P < 0.001$), while marsupials and birds prey relatively more eggs on the trees ($G = 12.85$; d.f. = 4; $P < 0.025$; Figure 2). This heterogeneity is no longer significant when excluding rodents and birds of the analysis ($G = 8.54$; d.f. = 4; $P > 0.05$; Figure 2). This means that the rodents prey disproportionately more in the ground while birds do it more on the trees respect to all other predators.

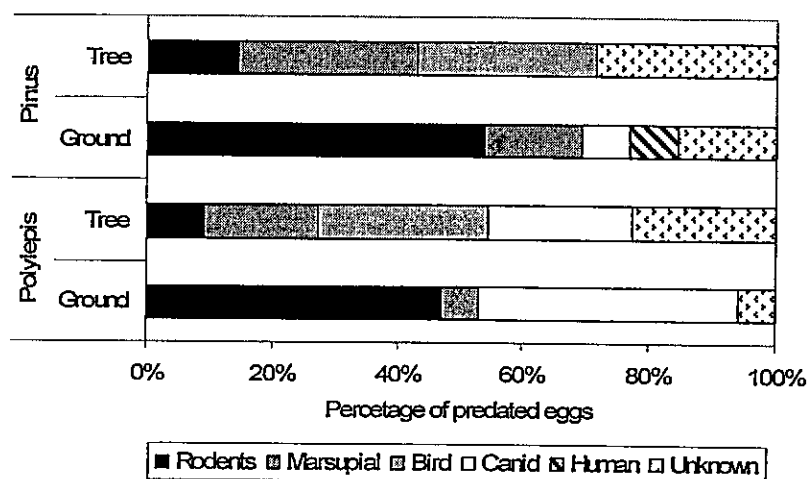


Figure 2. Number of plasticine eggs preyed by distinct predators at tree and ground layers of *Polylepis* and pine plantations at the Tunari Nacional Park, Cochabamba, Bolivia. NN = None identified predator.

Understory structure in pine plantation and *Polylepis* forest fragments was different. The percentage of cover by bushes, herbs, mosses and grass was significantly higher in *Polylepis* fragments than in pine plantation (Table I). In *Polylepis* fragments, median cover of bushes, herbs and moss was of 5-25% (Equivalent to 2 in the Cover Abundance Scale – Table I) and the grass cover was of 25-50% (3 in Table I). In pine plantations, vegetation cover by bushes varied

among zero and less than 5%, with a median of zero, representing a decrease of bushes in relation to *Polylepis* forest. In pine plantations, herbs and mosses were more abundant than bushes, but less abundant than in the *Polylepis* forest fragments with a median cover minor to 5%. In pine plantations the grass was the more abundant life-form with an average representation of 5-25% (2 in Table I); however, it was lower than cover in the *Polylepis* fragments where grass cover varies from 25 to 50% (3 in Table I).

Table 1. Vegetation structure of kewiña (*Polylepis besseri*) forest fragments and pine (*Pinus radiata*) plantation at the Tunari National Park, Cochabamba, Bolivia. Data shows medians and percentiles to 25% and 75%. *U* = Mann-Whitney Test and *P* = 0.05. The Cover Abundance Scale (CAS) represents the following vegetation cover categories: 5 = > 75%; 4 = 50-75%; 3 = 25-50%; 2 = 5-25%; 1 = < 5%; 0 = Absent.

	Kewiña	Pine	<i>U</i>	<i>P</i>
Understory				
Bushes	2.00 (2.00-2.00)	0.00 (0.00-1.00)	4064.00	<0.001
Herbs	2.00 (1.00-2.00)	1.00 (0.00-2.00)	3697.50	<0.001
Moss	2.00 (1.00-2.00)	1.00 (0.00-2.00)	3480.50	0.001
Grass	3.00 (2.00-4.00)	2.00 (1.00-2.00)	3862.00	<0.001
Canopy				
Tree cover [m ²]	11.64 (6.03-20.22)	16.69 (10.49-28.27)	2020.50	0.042
DBH [cm/Pi]	20.37 (15.12-31.03)	26.74 (17.19-32.47)	2391.50	0.264
High [m]	4.00 (3.18-4.95)	18.49 (14.50-21.00)	1154.50	<0.001
Density [ind/m ²]	0.06 (0.03-0.10)	0.06 (0.03-0.09)	3024.00	0.486

At arboreal level, the height and cover of tree canopy was significantly higher in pine plantations than in *Polylepis* fragments. In pine plantations the trees reached a median height of 18.5 m while in *Polylepis* fragments trees had a median height of 4 m. In the same sense, the median cover in pine plantations was of 16.7 m² per individual while in *Polylepis* it was of 11.6 m² (Table I). There are no differences among habitats in the density and DBH of trees. In pine as in *Polylepis* forest fragments the average density of trees was 0.06 individuals/m² and the average DBH was of 24.29 (Table I).

Table 2. Results from the factor analysis of the vegetation variables of pine plantations (*Pinus radiata*) and *Polylepis* forest fragments summarized in the ranked rotated factor matrix. All eigenvalues are greater than one, distinguishing the following characteristics: understory (factor 1), tree canopy (factor 2), and tree density (factor 3). The percentage of the variance explained by factor = Var%

	Factor 1	Factor 2	Factor 3
Bushes	0,841509	-0,077414	0,175834
Herbs	0,782810	0,135301	0,000173
Mosses	0,702772	0,281412	0,085638
Grass	0,569587	-0,401115	-0,344713
Tree density	0,084201	-0,141382	0,922979
DBH	0,097043	0,851328	-0,104477
Tree height	-0,656023	0,567972	0,047765
Cover	-0,026170	0,820571	-0,153804
Var%	0,323351	0,250633	0,130728

Results of the factor analysis of the vegetation variables are summarized in the ranked rotated factor matrix (Table 2). The matrix comprises three factors with eigenvalues greater than one, allowing us to distinguish three variable groups which can be referred to as habitat understory characteristics (factor 1), tree canopy characteristics (factor 2), and tree density (factor 3). Thus, shrubs, herbs and moss are positively and highly (>70%) correlated with factor 1, followed by grass with 60 % of correlation. We can also observe that tree height has also a large correlation (65%) with factor 1, but a negative one, thus while higher the trees, the fewer the understory. In relation to canopy characteristics, DBH and COVER are highly correlated (>80%) with factor 2, followed with tree height. Finally, tree density is the only canopy vegetation variables highly correlated (92%) with factor three (Table 2; Figure 3).

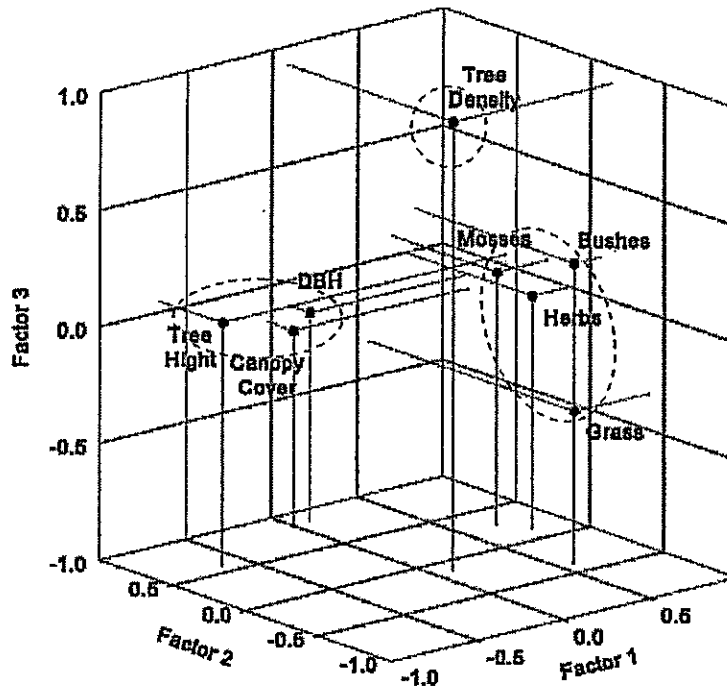


Figure 3. Graphical representation of factor analysis of the vegetation structure variables of pine plantation (*Pinus radiata*) and *Polylepis* forest fragments at the Tunari National Park, Cochabamba, Bolivia. Dotted circles distinguish the following habitat characteristics: understory (factor 1), tree canopy (factor 2), and tree density (factor 3). Factor loading in table 2.

The equations of the logistical regression incorporating the factors of vegetation (from factor analysis) and categorical predictor variables (habitat and nest level) effects in an ANOVA-like designs were statistically significant (Simplest model [Habitat]: d.f. = 1; Likelihood score = 13.49; $P = 0.0002$), and the statistic of Pearson χ^2 indicates that the regressions were adjusted well to the data (d.f. = 228; Stat = 230; Stat/d.f. = 1.009). Nest predation risk was not related with any variable of vegetation structure neither with the position of the nest (Table 3). However, there was a highly significant effect of the habitat type (Table 3; Figure 1), and there was a significant interaction between the habitat type and the nest level on nest predation risk (Table 3; Figure 1). This means that although nests predation risk is smaller in pine plantations than in *Polylepis* forests, it varies depending on the level of the nest. Thus, in pine plantation the risk of nest predation is smaller on the trees than in the ground, while in *Polylepis* fragments this relationship is opposite being higher on the trees than on the ground (Figure 1).

Table 3. Evaluation of vegetation of *Polylepis* forest fragments (from factor analysis), nest level and habitat type effects in an ANOVA-like design based on structural logistic regression analysis through Generalized Linear Models.

	d.f.	Estimate	SE	Wald	P
Inter.	1	0.861040	0.173944	24.50360	0.000001
F1=Understory	1	0.276709	0.279636	0.97917	0.322403
F2=Tree	1	0.150841	0.171333	0.77510	0.378644
F3=Tree density	1	-0.401508	0.205155	3.83023	0.050336
Level	1	0.037577	0.171277	0.04813	0.826342
Habitat	1	-0.763983	0.281858	7.34695	0.006718
Habitat*Level	1	-0.349303	0.171651	4.14106	0.041855

DISCUSSION

We proposed that higher predation risk could be the cause for bird declination in pine plantations compared to native *Polylepis* forest fragments. However, nest predation risk measured through artificial nests is lower in pine plantations than in *Polylepis* forest fragments. Therefore, nests predation would not explain the reduced species diversity associated to pine plantations.

This pattern is similar to other findings as in the coastal forest of the Central region of Chile, where nests predation is higher in forest fragments than in pine plantations (Vergara and Simonetti 2003), but is the opposite to findings in conifer plantations in a managed forest landscape of northwestern New Brunswick, Canada (Carignan and Villard 2002). A possible explanation for this pattern could be the variation in predator community structure between native forest fragments and forest plantation stands, since in Chile small mammals and raptors were more abundant in the forest fragments than in pine plantations (Vergara and Simonetti 2003), while in the conifer plantations in Canada, small mammals were the main predator and they also were more abundant compared to native forest (Carignan and Villard 2002). In the Tunari National Park of Bolivia, species richness of small mammals doesn't differ between pine plantations and *Polylepis* forest fragments; however its abundance is smaller in pine plantations

(Vargas et al. 2007). Considering that 46% of the eggs were preyed by small mammals, the decrease of nest predation in pine plantations could be associated with the minor abundance of small mammals in these habitats respect to native forests. Furthermore, birds also preyed near 28% of the nests on the trees and they also diminish in pine plantations compared with *Polylepis* forest (Fjeldså 2002; Balderrama 2006), reinforcing the idea that the decrease in nest predation risk observed in pine plantations, can be due to a decrease of the potential predator assemblage.

Furthermore, the significant interaction between the habitat type and the nest level reveals differences in the probability of nest predation between ground and tree nests depending on habitat type, reinforcing the idea that nest position could affect predation risk depending on the abundance and foraging strategies of potential predators (Martin 1988). This interaction is mainly due to a significant increase of tree nest predation in *Polylepis* forest fragments compared to pine plantations. This result partly agree with established patterns of nest predation noted in literature reviews and field studies with artificial nests who postulated that ground nest predation is minor than on trees (Yahner and Scott 1988; Santos and Telleria 1991; Martin 1993; Seitz and Zegers 1993; Martin 1995; Reitsma and Whelan 2000), and partly disagrees with some other authors who postulated that ground nests have higher rates of predation because of the presumed greater diversity of terrestrial predators (Ricklefs 1969; Wilcove 1985; Melampy et al. 1999). For example, in a study carry out in mature forest stands on a ruffed grouse (*Bonasa umbellus*) management area in central Pennsylvania, researchers have found that a higher number of nests from trees were preyed instead of ground nests, and that birds were the main predators (Yahner and Scott 1988). On the contrary, in a research in patches of Maulino Forest of Central Chile surrounded by pine plantation matrix, nest predation was higher on the ground than on off-ground nests (Vergara and Simonetti 2003). Coincidentally, in these environments the arboreal activity of small mammals would be reduced by the habitat modification, causing a higher foraging intensity in the ground (Meserve 1981; Gallardo-Santis et al. 2005). Thus, as suggested by Martin et al. (1993), nest risk predation is not necessarily higher in ground than on trees nests but depends on predators assembles more than the position in self.

Although, it has been suggested that nest risk predation could be related to nest concealment by vegetation cover and structure at understory and canopy levels (DeLong et al. 1995; Huhta et al. 1996; Hartley and Hunter 1998), in our study, vegetation cover was unrelated with nest predation patterns. Thus, although understory cover is higher in the native *Polylepis* forests, and could suggest a higher concealment of ground nests, the predation probability is similar in both habitats, therefore this habitat characteristic would not be conferring protection to

the nests in *Polylepis* forests, but the absence is not neither conferring higher predation risk in pine plantations.

A possible explanation for this pattern suggest that although several authors agree that birds nesting in dense understory, have greater protection from mammalian predators due to reduced predator foraging efficiency (Yahner and Scott 1988; Martin 1993; Seitz and Zegers 1993; Bayne et al. 1997) others suggested that a high understory covering in the nests doesn't confer them an antipredator protection, at least against the small mammals, which prefer to use the same microhabitat characteristics (Vergara and Simonetti 2004). This suggests that nest predation risk in relation to vegetation cover depends on predator community structure and its foraging strategies in a particular habitat. In our study, rodents were the main predators of ground nests and it is known that they prefer sites with greater vegetation cover, just like in *Polylepis* forests where understory is more abundant (Vargas et al. 2007) and produce more ground nest predation compared to pine plantations, according with the suggestion of Vergara y Simonetti (2004). Certainly, mammals are generally considered the main predators of ground nests (Baker 1980; Bowman and Harris 1980; Bayne et al. 1997; Hannon and Cotterill 1998). Similarly, birds are the main predators of nests in trees. Elevated nests should be less accessible to mammalian predators and be more easily detected by avian predators flying above or perching in trees (Joern and Jackson 1983; Yahner and Scott 1988; Bayne et al. 1997). Thus, the discovery of the nests in the *Polylepis* forests by predatory birds could be facilitated by the lower coverage of trees, compared to that of pine plantations (Table 1), which would make the nests more visible.

We envisage several problems that require taking actions to promote bird conservation in both native *Polylepis* forest and pine plantations. On one hand, if nest predation is not the cause of the decrease of bird diversity in pine plantations, it is necessary to study other possible ecological causes that can explain the pattern, since only knowing the direct causes that determine bird absence from pine plantation we will be able to take direct actions to solve the problem. The second issue is related with canids' presence as bird nest predators. As in many protected areas, inside the PNT, there are numerous human settlements dedicated to the breeding of sheep, which is usually accompanied by shepherd dogs during pasture. We have found a higher abundance and cover of understory vegetation in *Polylepis* forests, the main resource for sheep livestock, concentrating the shepherding and a higher activity of canids in *Polylepis* forests, which would explain the highest nest predation by canids in this habitat, regardless of the low abundance of dogs. It is possible that shepherd canids activity has been an undervalue

risk for the persistence of the birds until now, mainly in natives *Polylepis* forests. Nevertheless, is necessary to discern the effect of shepherd dogs from the effect of feral dogs and foxes (*Pseudalopex culpaeus*) to outline actions directed to bird conservation based on canids management at the PNT.

The different described patterns of nest predation risk emerge from a combination of predator assemblage structure and habitat characteristics; predation risk being higher in levels where predators assemble, or part of them, are more abundant, diverse, or active (Chalfoun et al. 2002; Zuria et al. 2007), in this case the native *Polylepis* forest. Thus, habitat type seems to be the final cause of the observed patterns since, habitat modification from a continuous native forest to a landscape mosaic of native fragments surrounded by pine plantations seems to have altered faunal composition of birds and mammals, and therefore potential predators assemble and the patterns of nest predation risk. From this study, it is clear that: 1) Habitat modification and fragmentation influence nest predation risk, making it to be higher in native *Polylepis* forest fragments than in pine plantations, 2) rodents are the main predators on the ground while birds are more on the trees and 3) those bird species that nest on forest fragments may be more vulnerable to the risk of nest predation than those nesting in pine plantations. It will be valuable to assess the effects of nest predation risk variation due to habitat fragmentation on the reproductive biology of breeding birds.

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CAPÍTULO II

REPRODUCTIVE LIFE-HISTORY TRAIT VARIATION OF BIRDS IN FRAGMENTED HABITATS: A REVIEW AND META-ANALYSIS

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ABSTRACT

Habitat fragmentation and birds are the most studied topics in conservation biology, but the information regarding reproductive life history traits and its variation on fragmented habitats is scarce. We reviewed the available literature on this subject through a quantitative assessment, using a meta-analysis. Only 8% of the 1433 studies regarding birds on fragmented habitats studied life history traits, but 1.3% provided appropriate data to perform statistics. There were neutral effects of fragmentation on clutch and brood size. However, we have found significant heterogeneity, which suggest that large-bodied, ground nesting, and precocial birds show a positive response in brood size. In 21 years, 15 species were studied, only one of conservation concern. Despite birds are the most studied vertebrate group, information regarding reproductive life history traits variation, and its consequences, is insufficient to make conclusions.

Keywords: Brood size; clutch size; life history traits; meta-analysis; review.

INTRODUCTION

Reproductive and survival success of birds can vary with habitat fragmentation (Lampila et al., 2005). Altered reproduction and survival compromise species' persistence in fragmented environments (Ewers and Didham, 2006). Birds, habitat modification and fragmentation are some of the most frequent subjects regarding conservation studies (Clark and May, 2002; Fazez et al., 2005). Therefore, a sound empirical baseline is expected to be available to assess the consequences of habitat fragmentation upon fitness components of birds to inform conservation management implications.

A plethora of studies related to habitat fragmentation literature associate variations in reproductive success and survival to life history traits of remaining species (Fahrig, 2003; Ewers and Didham, 2006). For example, habitat specialist, small-bodied, and ground nesting birds tend to decrease or become locally extinct in habitat remnants (Lees and Peres, 2008). Life history trait-mediated differences in species response to habitat fragmentation have been invoked to explain the apparently contradictory results found in the literature (Ewers & Didham, 2006). Nevertheless, the bulk of available information focuses on community and demographic change patterns, particularly on nest success as related to predation and parasitism (Batary and Baldi, 2004; Lampila et al., 2005), but few studies assess life history change patterns in fragmented landscapes. Life history traits are not invariant and they can change in a flexible fashion (Piersma and Drent, 2003) or as local adaptations (Kaweki & Ebert 2004). Thus, life history variation may illustrate how phenotypic changes can help us to unravel the way in which organisms solve problems of time and energy allocation to reproduction resulting from ecological demands related to habitat fragmentation (Ricklefs, 1991).

Within this framework, we quantitatively review supporting evidence regarding life history traits changes in response to habitat fragmentation. The understanding of the magnitude and direction of changes in birds' reproductive life history traits might inform conservation practices, pinpointing species whose suite of life history attributes render them more extinction prone in fragmented habitats. Herein, we analyze if there is information to determine how clutch and brood size change based on nest site, nest type, body size, trophic niche breadth, and development type in birds of fragmented habitats.

MATERIALS AND METHODS

We searched scientific publications using a hierarchical criteria, first recovering articles dealing with habitat fragment* or forest fragment*. This suite of papers were later refined by bird*, and further refined by clutch size, brood size, number of brood*, number of

chick*, number of egg*, egg size, or nest attempt* in the ISI Web of Science database for the period 1988-2009. We only considered studies explicitly comparing life history traits at fragmented and continuous habitats, excluding those restricting their analysis to potential edge effects. Each comparison of two populations of the same species inhabiting two habitats with greater and lesser degree of fragmentation represented an independent case. Whenever there were more than one species in the same study, each of them were considered an independent case. To assess variation in life history traits, studies reporting mean, standard deviation or standard error, and samples sizes were analyzed using Hedges' d unbiased standardized mean difference as the metric of effect size, which accounts for the effects of small sample sizes, working well for $n < 10$ and even as small as $n = 5$ (Rosenberg et al., 2000). An effect size is a statistical measure portraying the degree to which a given event is present in a sample (Cohen, 1969). This estimate range from $-\infty$ to $+\infty$, were "0" signifies no difference in effects between the experimental and treatment groups; negative values represent effects were the control group attains a greater value than the experimental group; and positive values represent effects were the experimental group attains a greater value than the control group (Rosenberg et al., 2000).

Hedges' d was calculated as:

$$d = \left(\frac{\bar{X}^E - \bar{X}^C}{S} \right) j$$

Where \bar{X}^E and \bar{X}^C are de means of the experimental and control treatments respectively; " j " is a correction factor and " S " is the pooled standard deviation represented by:

$$s = \sqrt{\frac{(N^E - 1)(s^E)^2 + (N^C - 1)(s^C)^2}{N^E + N^C - 2}}$$

Where N^E y S^E and N^C y S^C are sample sizes and standard deviations of the experimental and the control treatments, respectively.

Furthermore, " j ", the correction factor is represented by:

$$j = 1 - \frac{3}{4(N^C + N^E - 2) - 1}$$

And the variance " v " of Hedge' d is found as:

$$v_d = \frac{N^C + N^E}{N^C N^E} + \frac{d^2}{2(N^C + N^E)}$$

Confidence intervals (CI) of effects sizes were estimated from the effect sizes and its variances, through bootstrap re-sampling procedures (using 999 permutations), for which we used a random effects categorical model (Rosenberg et al., 2000). If one of the branches of the CI exceeds the "0.0" coordinate then size effects are not statistically significant. Heterogeneity of effect sizes were examined using the Q -statistics (Rosenberg et al., 2000). Variation in clutch and brood size due to other life history traits was analyzed in relation to body size (small [11-22,5 cm]-large [22,6-90 cm]), nest type (open-closed), nest position (ground-elevated), diet breadth (generalist-specialist), and development type (altricial-precocial), when sample size ≥ 5 . Complete database is available upon request.

Publication bias was assessed through Kendall's Tau and Spearman rank correlation tests. Finally, we conducted a Rosenthal's fail safe calculation with an alpha value of 0.05 and an Orwin's fail-safe calculation with a negligible effect of 0.20 (following Rosenberg, 2005). All analysis were performed in the meta-analytic software *MetaWin* V.2.0 @ (Rosenberg et al., 2000).

RESULTS

A total of 5,754 ISI articles were published regarding habitat fragmentation from 1988 to 2009. Almost 25% (1,433) of them were about birds; nevertheless, only small fractions of this studies deal directly with reproductive life history traits (clutch size = 3.3%; brood size = 3.5%; egg size = 3.1%; nest attempt = 1.2%). Moreover, just 1.3 % (18 articles) of these publications met our criteria, comprising 69 independent cases: 28 for clutch size (from 11 articles), 39 for brood size (from 10 articles), two for nest attempt (from two articles), and no article provided comparative information about egg size (Table 1). Nest attempt had not enough sample size to run any statistical analysis. Eighteen studies reported only means but no data on dispersion and sample size, precluding their inclusion in the analysis.

Neither clutch size nor brood size varied in fragments compared to continuous habitats ($d = -0.12$, $CI = -0.36$ to 0.11 , $n = 26$; and $d = -0.02$, $CI = -0.16$ to 0.13 , $n = 23$, respectively). No significant effects were observed for clutch size due to other life history traits; nevertheless, large bodied, ground nesting, and precocial birds exhibited larger brood size in fragmented habitats (Table 2). No publication bias was detected for clutch size (Kendall's Tau = -0.05 , $p = 0.74$; Spearman $R_s = -0.08$, $p = 0.71$) or brood size (Kendall's Tau = 0.03 , $p = 0.85$; Spearman $R_s = 0.01$, $p = 0.97$). Small sample sizes precluded performing further statistical analyses, considering that the 69 study cases gathered

represented 15 species of 10 families (Table 1). Only one of the studied species (*Tympanuchus pallidicinctus*) is of conservation concern (VU, BirdLife-International, 2008).

Table 1. Sample sizes representation for each of the reproductive life history traits evaluated in publications related to habitat fragmentation. Number of cases and species per family, recorded for clutch, brood, and nest attempt traits.

Family	Clutch size		Brood size		Nest attempt	
	Cases	Species	Cases	Species	Cases	Species
Climacteridae	0	0	3	1	1	1
Muscicapidae	0	0	2	2	0	0
Paridae	20	2	15	2	0	0
Parulidae	2	2	1	1	0	0
Petroicidae	1	1	0	0	0	0
Picidae	2	1	0	0	0	0
Rhyncoptidae	1	1	0	0	0	0
Sittidae	0	0	1	1	0	0
Tetraonidae	1	1	17	3	1	1
Turdidae	1	1	0	0	0	0
TOTAL	28	9	39	10	2	2

DISCUSSION

Despite research being conducted on habitat fragmentation is exponentially increasing (Lampila et al., 2005), research on reproductive life history trait variation is noteworthy scarce, with 1.3 % of articles regarding birds and 0.3% of all papers regarding fragmentation studies, despite its direct bearing on population management. Several articles deals with just one fragment (e.g., Brown and Roth, 2002; Brown and Roth, 2004), or did not compare reproductive life history traits with continuous habitat (e.g., Möller, 1991) and just one deals with an endangered species. Clearly, the lack of adequate controls in fragmentation studies is a significant problem and research is ignoring endangered species.

The scarce evidence available suggest that fragmentation has no effect on clutch and brood size, implying that no action would be required at this level for managing birds in fragmented forests. Nevertheless, large bodied, ground nesting, and precocial birds, as represented by *Tetrao tetrix*, *T. urogallus*, and *Tympanuchus pallidicinctus* has larger brood size in forest fragments.

Table 2. Hedges' *d* effects of different life history traits in relation to clutch and brood size. Sample sizes shows number of cases / number of species analyzed. Variables with sample size lower than 5 were not evaluated (N/E). * = $Q_{between}$ significant at $p < 0.05$.

Trait	Level	Clutch size		Brood size	
		Sample size	Effect	Sample size	Effect
Body size	Small	23 / 5	Neutral	18 / 5	Neutral
	Large	3 / 2	N/E	5 / 2	Positive
Nest type	Open	22 / 4	Neutral*	23 / 7	Neutral
	Closed	4 / 3	N/E	0 / 0	N/E
Nest position	Elevated	23 / 4	Neutral	18 / 5	Neutral
	Ground	3 / 3	N/E	5 / 2	Positive
Diet breadth	Generalist	15 / 3	Neutral	12 / 3	Neutral
	Specialist	11 / 4	Neutral	11 / 4	Neutral
Development	Altricial	25 / 6	Neutral	18 / 5	Neutral
	Precocial	1 / 1	N/E	5 / 2	Positive

Although this evidence seems to contradict the fact that large-bodied taxa seems more vulnerable to habitat fragmentation (Gaston and Blackburn, 1995; Ewers and Didham, 2006), current evidence suggests that adult survival in fragmented habitats decreases coupled with increased clutch or brood sizes (Lampila et al., 2005; Patten et al., 2005), which might reflect a trade-off between reproductive effort and survival (Roff, 1992; Stearns, 1992). Therefore, to have more offspring might imply a decrease in adult survival. In addition, if the survival of juveniles would be compromised (e.g. Patten et al. 2005), this would increase the risk of extinction of bird populations in fragmented habitats. However, given that only three species of large body sizes have been studied so far, all from the order Galliformes, it is clear that this statement lacks generality due to the small sample size and because we cannot rule out phylogenetic inertia. This is because the organisms are interrelated in a hierarchical manner, which brings as a main consequence that related species tend to resemble, preventing us from ruling out the possibility that these traits have evolved independently, affecting the inferences derived from comparative studies between species, since a hierarchical relationship between them violates the statistical assumption of independence (Rezende and Garland, 2003; Adams, 2008; Lajeunesse, 2009). To correctly analyze comparative data between multiple species and to infer evolutionary patterns from them is necessary to consider explicitly the evolutionary history of the species in question (Rezende

and Garland, 2003). Although recently has been proposed a couple of approaches that consider the phylogenetic effect (Adams, 2008; Lajeunesse, 2009), they have not been included in this meta-analysis. Whether the observed increased reproductive effort is a general phenomenon, is yet to be assessed in order to determine if reproductive life history traits plays a role in the decline of large bodied birds in fragmented habitats. Furthermore, we have no information to confirm or reject the possibility that the observed changes in life history traits are due to local adaptations or phenotypic plasticity. In the future, the development of studies to identify the variation of these traits in birds should include the assessment of these issues and the heritability of traits to determine if there really is an evolutionary change.

Despite claims regarding the need for evidence-based conservation, and to incorporate micro-evolutionary aspects in the management of endangered biota (Ashley et al., 2003; Sutherland *et al.*, 2004), the scarcity of available information renders such an approach unfeasible with birds of fragmented habitats. This finding is particularly distressing considering that birds are affected by habitat fragmentation and are a common subject in fragmentation studies. Clearly the call to generate and share relevant information (Milner-Gulland, 2009) is supported by birds in fragmented habitats in order to improve our understanding regarding if and how changes on reproductive life history traits impinge upon both birds persistence in fragmented habitats and microevolutionary changes they might bring. To focus habitat fragmentation research on behavioural ecology and life history trait variation of conservation-concern species is urgently needed.

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CAPÍTULO III

HABITAT FRAGMENTATION, PREDATION RISK AND REPRODUCTIVE LIFE-HISTORY SYNDROME IN *LEPTASTHENURA YANACENSIS*: AN EXPERIMENTAL APPROACH

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ABSTRACT

Nest predation is the main cause of reproductive failure in birds, and shapes both behavioural and life history traits. Habitat fragmentation changes the risk of nest predation by modifying the abundance of local bird nest predators. We test if habitat fragmentation modifies the antipredator behaviours and life history traits related to reproduction of *Leptasthenura yanacensis*, an Andean threatened Furnariidae and *Polylepis* forest specialist of Bolivia. We performed natural and field experiments to compare parental care behavioural and life history traits by means of video recording of nests and monitoring of egg and chick in large and small fragments. Furthermore, bird raptor diversity, nest predation and nest success were assessed. Visitation rate and incubation time were smaller and foraging time was higher when predators were near the nest. Although predators are fewer in the small fragments, there were no differences in parental care behaviours when compared small to large fragments. There weren't neither differences in egg, clutch, nor brood size; nevertheless body growth rate is higher in large fragments. No differences in the risk of predation or nesting success were found. *L. yanacensis* is able to modify its parental care behaviour against predation risk. Despite the differences in predator diversity due to habitat fragmentation, the absence of differences in mortality due to nest predation is reflected in the absence of differences in antipredator behaviour and reproductive life history traits.

Keywords. Fragmentation, predation, life-history, behaviour, syndrome, *Polylepis*, Andes, Bolivia.

INTRODUCTION

The evolution of parental care strategies results from a trade-off between the costs and benefits associated with reproduction and survival of adults and young (Roff 1992). Different environmental conditions can alter these fitness trade-offs and lead to variation among populations or species in the amount or type of parental care provided and reproductive life history traits expressed (Badyaev and Ghalambor 2001). Frequently, incubating parents are faced with changes in the immediate risk of nest predation (Lima and Dill 1990; Martin 1992). Nest predation can be enhanced with increasing parental activity near the nest (Martin et al. 2000a; Martin et al. 2000b). Parents faced with an increased immediate risk are expected to decrease visitation rates to the nest in order to reduce drawing attention to the location of the nest (Ghalambor and Martin 2000, 2001; Ferretti et al. 2005). Since environments tend to be spatially variable, no single behavioural phenotype is consistently optimal. Such dynamic conditions require plasticity in behaviour as a means of tracking environmental change (Ghalambor and Martin 2002). Such behavioural plasticity in response to an immediate predation threat is under stronger selection in species more vulnerable to nest predation from visually oriented predators (Ghalambor & Martin 2002). Thus, the costs of reduced food delivery are offset by the benefits of reduced predation risk, and differences among species and populations in the risk of nest predation should alter this cost benefit trade-off (Ghalambor & Martin 2002).

Habitat fragmentation is one of the main agents of change in the modern landscape and is considered a major threat to biodiversity (Fahrig 2003). This may modify species abundance and richness, and alter the intensity of ecological interactions (Simonetti et al. 2006). The modification of ecological processes in turn may represent a change in selective pressures on organisms in the remaining fragments (Herrera 2000; Kokko and Sutherland 2001; Simonetti et al. 2006). Therefore, there is a need to study how species respond to environmental changes in order to understand the effects of natural selection imposed by variation in predation risk in fragmented landscapes. The comparison of life-history syndrome between populations that differ in their risk of nest predation can therefore provide insight into the degree to which parental decision making evolves and adapt to the new conditions imposed by processes of habitat modification (Martin 2004; Ferretti et al. 2005). Theory predicts that individual mean incubation and foraging time should increase and mean visitation rate to the nest should decrease when the perceived risk of predation increases near the nest. Furthermore, greater nest predation

also favours smaller clutch and brood sizes, young should grow faster to reduce accumulating daily risk of predation as a strategy to minimize drawing the attention of predators to the nest (Ferretti et al. 2005). Here, we use natural and field experiments in fragmented landscapes to test whether nesting parents can perceive changes in predation risk and modify their behaviour and life history traits accordingly. We tested two predictions within and across habitat fragments. First, we tested whether individuals exhibit plasticity in their parental care behaviours when faced with increased predation risk. Second, we tested whether parental care behaviour and reproductive life history traits varies in large fragments with higher diversity of nest predators compared to small fragments, which presumably reflects greater selection intensity on phenotypically plastic traits in larger fragments (see Ferretti et al. 2005).

MATERIALS AND METHODS

Study specie and study site. We focused on *Leptasthenura yanacensis* (Furnariidae), a small insectivore bird that nests and forages exclusively on *Polylepis* trees (Fjeldså and Krabbe 1990). This species is Vulnerable due to loss and fragmentation of their habitat (Cahill et al. 2009). Its breeding season runs from November to March (Huanca 2005). The nest is dome-shaped and is built mainly of grasses (Poaceae: *Festuca* sp., *Stipa* sp., and *Calamagrostis* sp.). The eggs are white and are small (length = 18.8 ± 0.55 mm, diameter = 15.03 ± 0.64 mm, weight = 2.16 ± 0.23 g; Huanca 2005). The clutch size is of two eggs in 90% and of one egg in 10% of cases. Time to hatching of the chicks is of 21 to 24 days, and the fledgling period is 15 to 21 days. There is no sexual dimorphism and both parents participate in parental care during incubation and feeding of the chicks (Huanca 2005). The study was conducted in two localities at Mizque province, Cochabamba, Bolivia. A set of large forest patches is the locality of Sacha Loma and has three large fragments (55 ± 12.8 ha [mean \pm SE]). A second set of small patches is located in Coturi, approximately 3.5 km from Sacha Loma, with fourteen small fragments of an average size of 1.05 ± 0.8 ha [mean \pm SE]. In both locations fragments are surrounded by grassland and spread on altitudinal range between 3710 to 3880 m.a.s.l. A detailed description of the vegetation is provided in Fernandez *et al.* (2001). In *Polylepis* forests, rodent, marsupial, birds and canids have been identified as potential nest predators (Annex 1).

Evaluation of predator diversity. During nest searching and monitoring in all sampling campaigns we assessed the diversity of predatory birds (Aves: Falconidae, Accipitridae, Strigidae and Icteridae) through a *list method*, standardizing the effort to day units (Sutherland et

al. 2004). Registered species in the lists ($n_{\text{small}} = 21$; $n_{\text{large}} = 46$) and individual counts were accumulated daily for both large and small fragments. To evaluate differences in bird raptor diversity among large and small fragments we compared the richness and abundance of registered individual using a random subsample of the large fragment's lists of species to balance sample sizes differences between large and small fragments. Furthermore, we performed comparisons with complete samples for both habitat types and diversity patterns remain the same so we report complete sample comparisons. For both variables statistical comparisons were performed through a Mann-Witney U test. Furthermore, we used a rarefaction analysis to compare bird predator diversity among localities when all samples are scaled down to a same number of samples allowing to assess expected species richness in random of similar sampling effort. Rarefaction was performed for each sample size separately based on the count of individuals per sample. For rarefaction procedure we used 1000 permutations and corresponding standard deviation. In the graphical plot, the standard deviations are converted to 95 percent confidence intervals (Oksanen et al. 2011).

Nest searching and monitoring. At both localities nests were searched from September 2008 to February 2009. Nests were located by using systematic search and behavioural cues of the adults, for later monitoring of chick development, nest success and causes of mortality of eggs and chicks (Ralph et al. 1996; Sutherland et al. 2004; Ferretti et al. 2005). A nest was considered successful if at least one chick left the nest as a fledgling. Nests were considered preyed when recorded eggs or young per nest disappeared during the nesting period and before the fledging stage or if we found any evidence of predation on the nest or its surroundings such as destroy nests, perforation or faeces (Ferretti et al. 2005). Monitoring of the nests began after a preliminary observation to ensure that parents were away from the nest, after this eggs and hatchlings were removed from nests for measurements and returned to the same nest as soon as possible and before parents return to the nest abandoned by the parents. We found 47 active nests, most of them (70%) in the large forest fragments of *Polylepis* at Sacha Loma.

Behaviour and manipulation of predation risk. To test effects of increased predation risk on parental care behaviour, we presented a taxidermic model of a common nest predator. The goal of model presentations was to increase the perceived risk of nest predation near the nest (Ghalambor and Martin 2002). We chose to present a taxidermy model of the Bolivian tiny owl *Glaucidium bolivianum*, a known predator of *L. yanacensis* which has been observed using parental activity as a cue to finding nests (Herzog et al. 2003; Cahill and Matthysen 2007;

personal observations). Depending on the position of the nest, the model was attached to nearby tree branches and placed 1.5–2.5 m from the nest in the same tree. In addition, we played vocalizations of the Bolivian tiny owl from a sound system placed at the base of the tree where the model was perched to increase detectability of the models (Martin and Ghalambor 1999). Use of vocalizations with the model is particularly effective in preventing habituation to the model alone (Ghalambor and Martin 2000, 2001). Behavioural responses to the predator model were compared to a control nest under natural condition: We evaluated the behavioural traits of *L. yanacensis* considering the following variables: mean time on- and off-bouts and mean visitation rate to the nests. These variables were assessed only in nests in egg stage to avoid differences in behaviour due to nestlings' maturation during 2008-2009 breeding season, considering each of the nests as sample units. The total number of nests for the behaviour evaluation was 25, of which 17 were in large fragments ($n_{\text{experimental}} = 8$; $n_{\text{control}} = 9$), and 8 occurred in small fragments ($n_{\text{experimental}} = 3$; $n_{\text{control}} = 5$). Behavioural evaluations were made through video recording of each nest during an hour (Martin and Ghalambor 1999; Martin et al. 2000a; Ferretti et al. 2005). Bird monitoring and measurements were made after video recording to avoid behavioural alteration of the parents. The recordings were reviewed at the laboratory and data were extracted to evaluate the mean time of on- and off-bouts and mean visitation rate with the aid of the software J-Watcher ® (Blumstein and Daniel 2007).

Behavioural variation analysis were performed through Generalized Linear Mixed Models (GLMMs) which accounts for a more flexible approach to analyzing nonnormal data when random effects are present (Bolker et al. 2009). The analysis of the effects of fixed factors (presence of predator simul, fragment size class, location and size of the fragment) and random (identity of the fragment) of the model were evaluated using generalized linear mixed models and the Linear Mixed Effect "lme" function in the "nlme" library (Fox 2002). Given the unbalanced design and small sample size, for the adjustment of the estimated parameters we used a Restricted Maximum Likelihood procedure using the package REML. For each variable of behavioral response we evaluated two models defined *a priori*, a full one including the interaction between experimental treatment with fragment size and a simpler model that did not include this interaction, in addition to the factors already mentioned. The fit of the models was evaluated using the Akaike Information Criterion (AIC) and an Analysis of Variance between the models allowed us to evaluate the difference in the level of fit and explanation of the data between different models. All tests were performed in the program R (Venables et al. 2010).

Since, all simplest models have a better performance compared to full models, based on AIC values and ANOVA we only report those regression results.

Life-history trait measurements. Clutch size was determined when the number of eggs in the nest did not change between two consecutive visits (Ferretti et al. 2005). Brood size was determined through consecutive evaluation of the nests and always regarded as the number of chicks fledged per nest, excluding those chicks that died during the nesting period (Donazar 1989). Eggs were extracted from the nest and the size was measured directly with a calliper or with scaled photographs to prevent damage due to manipulation. Measurements were later extracted from the photographs with ImageJ ® v. 1.40g measurement software (Rasband 2010). To analyze the egg size variation between fragments we used the Mann-Witney U test. Furthermore, since length, wide and weight of the eggs are correlated, we used a factor analysis to generate a single dimension factor and compared between fragments (Manly 2005). We examined body growth rates of nestlings in all recorded nests in large and small fragments. We weighed nestlings and measured the length of their tarsi at every development stage whenever possible. Measurements were made directly with callipers and when chicks were too small we used scaled photographs to prevent damage due to manipulation. Measurements were later extracted with ImageJ ® v. 1.40g (Rasband 2010). We calculated growth rates for measures of mass and tarsus through the difference between stage $X_{t+1} - X_t$ measurements, where X represents the mass or the tarsus length at each stage. To assess the variation in the rate of growth of body size of chicks from large and small fragments we compare tarsus and weight changes between first and second development stages only from individuals of control nests to avoid variation due to increased predation risk. Comparisons were made through the Mann-Witney U-test analysis, with individuals as the sampling units. Furthermore, due to small sample sizes we performed a Two Sample Permutation Analysis through a resampling probability estimates for the difference between the means of two independent samples based on 10000 permutations (Lowry 2010; Vassarstats ®). All sample sizes of life history trait comparisons are reported (Table 2).

Nest fate. Nest success and causes of mortality of eggs and chicks were assessed through monitoring (Ralph et al. 1996; Sutherland et al. 2004; Ferretti et al. 2005). A nest was considered successful if at least one chick left the nest as a fledgling. Nests were considered preyed when recorded eggs or young per nest disappeared during the nesting period and before the fledging stage or if we found any evidence of predation on the nest or its surroundings such as destroy

nests, perforation or faeces (Ferretti et al. 2005). Differences in nest success and nest predation between small and large fragments were assessed through a z-test for proportions, respectively (Zar 1999). Other causes of mortality were recorded and are reported. All sample sizes of the nest destiny comparisons are reported. Comparisons of the proportion were made through the z test with Yates correction for continuity (Zar 1999). Furthermore, we applied Bonferroni correction for multiple comparisons and significant results are accepted below $P = 0.017$ (Zar 1999).

RESULTS

Predator diversity. A total of 12 bird predator species were found in the study area and four species were shared between localities. Furthermore, 87% of the records were made in the large fragments (Table 1). Raptor diversity was higher in large fragments and both the abundance and richness of birds of prey was significantly higher in large compared to small fragments (Abundance: $U = 328.0$; $n_{\text{small}} = 21$; $n_{\text{large}} = 46$; $P = 0.02$; Richness: $U = 230.5$; $n_{\text{small}} = 21$; $n_{\text{large}} = 46$; $P = 0.02$; Table 1). In addition, the 95% confidence limits of rarefaction curves of bird raptor diversity from large and small fragments do not overlap with each other, except when samples are less than 14 samples indicating that bird predator species diversity is higher in large than in small fragments (Fig. 1).

Model selection. The values of AIC and the number of factors in the model indicate that the simplest model is the one that best adjusted to the data of the three behavioural variables (Table 1). In addition, there were no differences in the variance explained between the full and simplest models (Table 1), therefore, the latter model was selected for the evaluation of the effects on behavioral variables.

Induced antipredator behaviour. The presence of a potential predator near the nest triggered anti-predator behaviour in the parents, regardless of the size of the fragment, in which they were (Table 3). When the predator was present, parents spent less time inside and more time outside the nest (Table 3; Figure 2). Although there is a decreasing visitation rate in relation to the presence of the predator, this is not statistically significant (Table 3; Figure 2). Furthermore, the time that the parents spend inside and outside the nest, were not related to fragment size (Table 2). Although there is a positive relation between visitation rate and the area of the fragment, this is not statistically significant (Table 3).

Table 1. Bird raptor diversity differences among large and small fragments of *Polylepis besseri* highland forest fragments at Cochabamba, Bolivia. Reported the total number of individuals and species recorded in large and small fragments, the *Simpson* diversity index (C_{inv}), the median values and the two percentiles that define the upper and lower limits of the observed abundance and species richness daily recorded in the forest fragments.

Species	Small	Large
<i>Buteo brachiurus</i>	0	3
<i>Buteo poecilochrous</i>	2	11
<i>Buteo polyosoma</i>	0	1
<i>Buteo sp</i>	0	3
<i>Catarthes aura</i>	4	6
<i>Circus scinereus</i>	0	4
<i>Falco femoralis</i>	0	3
<i>Falco sparverius</i>	4	7
<i>Falco sp.</i>	0	12
<i>Falco boeufi</i>	2	27
<i>Geranoetus melanoleucus</i>	0	4
<i>Glaucidium bolivianum</i>	0	2
Sample size	21	46
Total individuos	12	83
Total especies	4	12
C_{inv}	3,60	6,17
Median abundance	0,0 (0,0-0.25) [21]	1,5 (0,0-3.0) [46]
Median richness	0,0 (0,0-0.25) [21]	1,5 (0,0-3.0) [46]
Rarefaction diversity	4 (0-0) [1000]	10, 49 (1,51-1,86) [1000]

* medians differ significantly $P \leq 0.05$

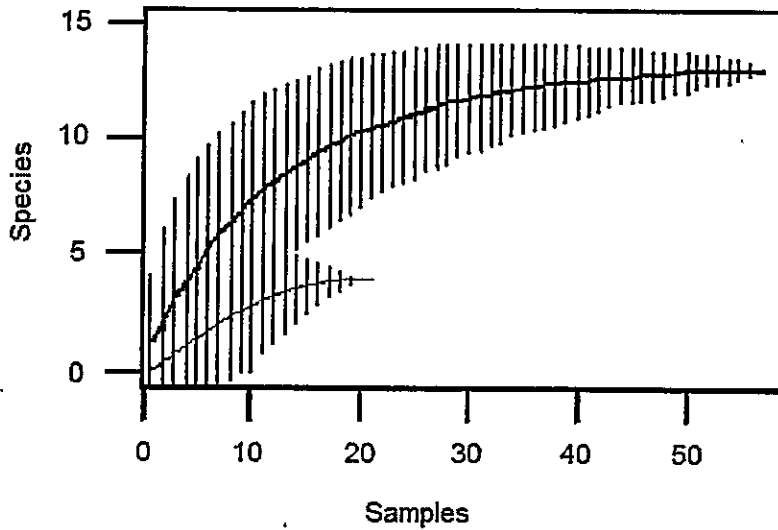


Figure 1. Comparison of bird predator species diversity between small and large fragments using rarefaction procedure. The extreme of the lines at each point depict the 95% confidence limits ($\pm 1.96 \text{ Var}^{1/2}$).

Life-history trait variation. Egg size between populations of large and small fragments is not significantly different (Table 2). Egg size varied from 18.2 to 24.7 mm in length and from 13.9 to 20.5 mm in width. Furthermore, the weight varied from 1.5 to 2.6 g. Egg size differences between nests of large and small fragments were not significant for each of the variables considering the egg mean size by nest, or all eggs independently (table 2). Clutch and brood size varied from one to two eggs or chicks per nest, with a highly significant proportion having two (Test of proportions: two eggs = 91% $z= 6.519$; $P = <0.001$; Two chicks = 77%; $z= 3.617$; $P = <0.001$, respectively). Furthermore, there are no significant differences between fragments in the number of eggs and chicks per nest (Table 1). Despite the lack of significant differences between the different life history traits evaluated, the power of the tests varies between 7% and 26% and are below the desired value of 80%, thus conclusions must be cautious.

Table 2. Analysis of variance of the candidate models evaluated for tree behavioral variables through GLMMs. Model 1 represents the full model with interaction term and Model 2 represents the simplest model without interaction term. Hypotheses are rejected below $P < 0.05$.

Model	df	AIC	Test	L. Ratio	p-value
Time on-bouts					
<i>Full model</i>	6	100.7821	1 vs 2	0.0348	0.852
Simple model	5	98.8169			
Time off-bouts					
<i>Full model</i>	6	74.9169	1 vs 2	0.3273	0.5673
Simple model	5	72.5897			
Frequency of visits					
<i>Full model</i>	6	82.55163	1 vs 2	0.8415	0.359
Simple model	5	79.71016			

Table 3. Regression analysis of the effects of fixed and random factors evaluated for tree behavioral variables through GLMMs and the Linear Mixed Effect.

Variable/Factor	Coef. Value	Std. Error	df	t-value	p-value
Time on-bouts					
(Intercept)	-0,0164	0,6765	14	-0,0243	0,9810
log(Area)	0,2782	0,1858	8	1,4970	0,1728
Trat S	1,3970	0,6030	14	2,3166	0,0362
Time off-bouts					
(Intercept)	3,7234	0,5007	14	7,4371	< 0,0001
log(Area)	0,0733	0,2151	8	0,3409	0,7420
Trat S	-0,7683	0,3036	14	-2,5308	0,0240
Frequency of visits					
(Intercept)	-0,1470	0,4382	14	-0,3355	0,7422
log(Area)	0,2692	0,1204	8	2,2364	0,0557
Trat S	0,7864	0,3906	14	2,0132	0,0637

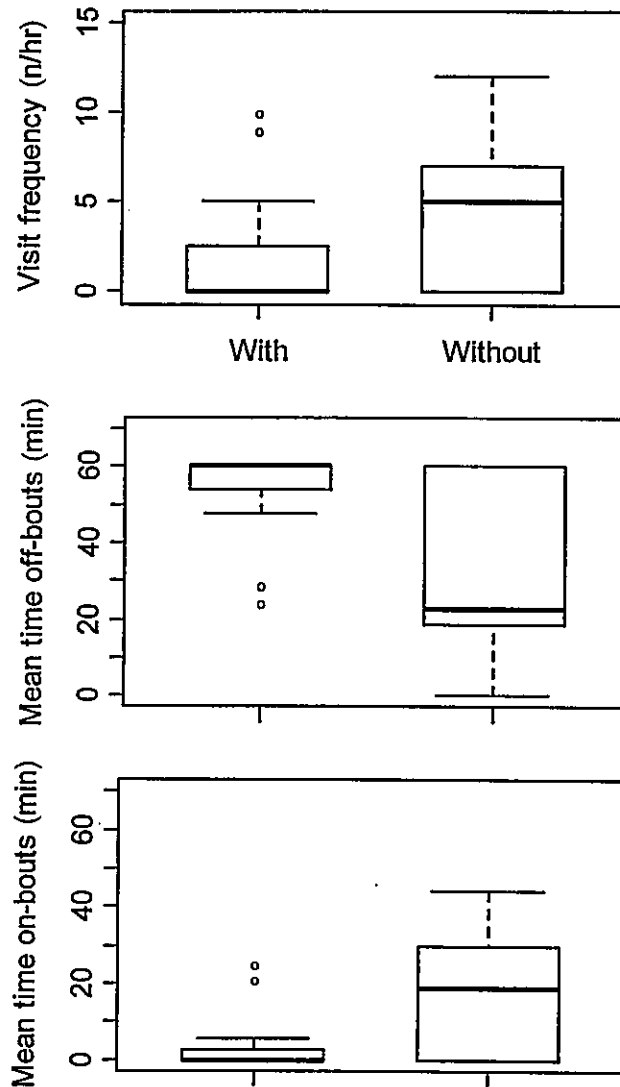


Figure 2. Nest parental care behaviour of *Leptasthenura yanacensis* during incubation periods in nest “With” and “Without” the presence of the predator simile in large and smaller *Polylepis berterii* highland forest fragments at Cochabamba, Bolivia. A) Duration of incubation on-bouts (i.e. time that parents spent inside the nest during an hour). B) Duration of incubation off-bouts (i.e. time that parents spent outside the nest during an hour). C) Parental activity during incubation (number of visits per hour). All represents median \pm Interquartile ranks.

Body growth rate measured through the body mass of individuals between populations is higher in large fragments (Two sample permutation analysis: Permutations = 10000; P = 0.002) but there were no differences in tarsi growth (Two sample permutation analysis: Permutation = 10000; P = 0.06).

Table 4. Life history traits and nest fate values of *Leptasthenura yanacensis* during nesting periods in birds of large and small *Polylepis besseri* highlands forest fragments at Cochabamba, Bolivia. Values represent: median (interquartile range) and [sample size]. Hypothesis are rejected when $P \leq 0.05$. Power of performed tests ($1-\beta$) is shown in the corresponding column.

	Large fragments	Small fragments	Statistics	Probability	Power
Egg size					
Large	20.0 (19.2-21.6) [12]	19.6 (19.3-22.2) [9]	<i>U</i>	0.72	0.07
Wide	15.5 (15.1-16.6) [12]	14.7 (14.6-16.7) [9]	<i>U</i>	0.30	0.09
Weight	2.1 (1.9-2.2) [12]	2.0 (1.9-2.3) [9]	<i>U</i>	0.75	0.06
Clutch size	2 (2-2) [23]	2 (2-2) [11]	<i>U</i>	0.23	0.26
Brood size	2 (2-2) [18]	2 (2-2) [7]	<i>U</i>	0.69	0.07
Body growth rate					
Weight	5.6 (4.6-7.0) [5]	2.8 (0.1-3.8) [5]	<i>TSP</i>	0.002	
Tarsi	8.8 (7.2-9.8) [4]	3.5 (0.4-8.3) [5]	<i>TSP</i>	0.06	
Nest success	0.58 [33]	0.57 [14]	<i>z</i>	0,80	0.05
Nest predation	0.24 [33]	0.36 [14]	<i>z</i>	0,63	0.07
Other losses	0.18 [33]	0,07 [14]	<i>z</i>	0,60	0.05

Nest fate. Nest predation is the main cause of nest failure of *L. yanacensis* in *Polylepis* forest fragments but other causes also occur (abandonment, nest fall, non-viability). The proportion of successful and preyed nests among large and small fragments is not significantly different (Table 2). Furthermore, experimental manipulation didn't have a pervasive effect on nest predation since we have not found any relationship between the predator model presence and nest fate (Fisher exact test: d.f. = 1; P = 0.58). Other causes of nest failure were: fallen nests (6% only in large fragments), abandoned (9% only in large fragments) and stolen (we registered only one nest of *L. yanacensis* that was evicted during the final stage of construction by a giant conebill *Oreomanes fraseri*) (Table 2). Despite the lack of significant differences between the proportions of nest fate, the power of the tests varies from 5% to 7% and are below the desired value of 80%, thus conclusions must be cautious.

DISCUSSION

Adaptive changes in traits that affect fitness often depend on the ability of an individual to monitor changes in the environment, mainly on those factors that directly affect survival (Moran 1992). Since predation is a major mortality risk for prey populations in both terrestrial and aquatic ecosystems (Lima and Dill 1990; Lima 2009), changes in predation rates may impose directional selection on traits that reduce mortality risk, and when migration between populations is restricted this may result in local adaptation to the prevailing predation regime. However, even modest migration between populations may instead favour the evolution of phenotypic plasticity (Sultan and Spencer 2002). Evidence suggest that prey exposed to spatially or temporally variable predation pressure have evolved inducible predator defences and thus show a high degree of phenotypic plasticity in these traits (Abjörnsson et al. 2004). Thus, to understand variation between populations in a trait we need to carefully evaluate if it is a result of local adaptation or phenotypic plasticity in response to environmental heterogeneity, such as differences in predation regime. Here we have tested whether increase predation risk, near the nest of *L. yanacensis* induces antipredator responses in parental birds and if antipredator life-history syndromes in *L. yanacensis* differ between local populations of habitat fragments of different sizes and with different predator diversity.

Response to increased predation risk within habitat fragments. Parents of all forest fragments recognize a potential nest predator and respond by modifying parental care behaviour, independently of the size of the nesting fragment. Based on our results it appears that parents'

accounts for the probability that nest visitation could reveal the location of the nest to potential predators and modify its behaviour to reduce this risk. These results are consistent with current evidence which shows that rate of nest visit decline as the presence of a predator becomes more evident near the nest (Ghalambor and Martin 2002; Eggers et al. 2005; Ferretti et al. 2005; Eggers et al. 2008). This behavioural modification is assumed to be an adaptive strategy that reduces the risk of drawing attention of visually oriented predators to the nest (Ghalambor and Martin 2000; Martin et al. 2000b; Ghalambor and Martin 2001). Furthermore, no attacks to the predator model by *L. yanacensis* were observed but they remained near the nest emitting alarm calls and jumping between branches, suggesting that parents sought to draw attention of the predator towards them and away from the nest. First, this suggests that parents balance the benefits of providing care to the nest against the cost of attracting the attention of the predator to the nest, and solve this trade-off by reducing visits to the nest in the presence of potential nest predator. However, the fact that parents remain near the nest and the predator in an attitude of alarm, suggests that parents could threaten their survival for the sake of keeping alive the progeny.

Responses to predation risk across habitat fragments. Our findings demonstrate that habitat fragmentation reduces the diversity of potential predator birds, but this seems not to alter nest predation risk of *L. yanacensis* at *Polylepis* forest fragments. Nevertheless, this last assertion must be cautious since the power of the tests for differences in nest predation between fragments of different size were below the desired level (table 2). Considering that the pattern of nest predation remains consistent, we suggest that this is the main reason why we did not detect differences in parental care behaviour and life history traits according with the hypothesis we proposed of reproductive antipredator syndrome based on Ferretti et al. (2005). Thus, individuals of different fragment sizes express similar antipredator behavioural syndromes as described before and a similar set of life history traits. Based on our results we reject our hypothesis of antipredator syndrome differences among populations in fragmented habitats with different predator regimens.

We suggest also as a possible cause an inter-population gene flow. As mentioned before, even modest migration between populations of different predation regimens may favour the evolution of phenotypic plasticity (Sultan and Spencer 2002). There have been detected ringed individuals of *L. yanacensis* moving between the different fragments which are separated by an average distance of 3.5 km, indicating that this distance could be overcome and promote genetic flow

between subpopulations. Thus, the movement of individuals between forest fragments may allow the interchange and establishment of individuals that are able to exhibit flexible antipredator behaviours. *Oreomanes fraseri*, another sympatric specialist bird species of *Polylepis* forests, nearly twice the size of *L. yanacensis*, is also able to move between patches (Cahill et al. 2009; De Coster et al. 2009). Individual's movement between fragments of different sizes avoid the possibility of establishing phenotypic forms locally adapted to different environments despite the differences that can be found in selective pressures such as predator diversity (Abjörnsson et al. 2004). On the contrary, Ferretti et al. (2005) found consistent differences of life-history syndromes between population in Argentina of a Neotropical thrush with different predation risk, that were separated by more than 1200 km, minimizing the possibility of gene flow. Therefore, it is necessary to study the effects of habitat fragmentation through a perspective of large scale isolation to elucidate the effect of proximity and gene flow in restricting the evolution of phenotypic plasticity in these landscapes. That is, all individuals within a certain prey species respond irrespective of whether they have been previously exposed to a predator or not (Abjörnsson et al. 2004).

Growth rate differences. The only life history trait that shows differences between large and small fragments was the rate of body growth of nestlings. The highest rate of body growth observed in the larger fragments would agree with the proposed predictions when predation risk is prevalent in predator-rich environments (Martin et al. 2000b; Ferretti et al. 2005). However, not only the risk of predation could favour a higher rate of body growth but also the availability of food and energy in the environment. If diet quality limits growth rate, it should prove difficult to select for increased growth rate without improving the nutritional level in the diet (Ricklefs et al. 1998). Thus, although both factors may influence body growth rates, these are not mutually exclusive and can actually co-occur since, for a higher rate of body growth to be favoured by natural selection (in this case, by nest predation), it is required a nutrient-rich environment (Ricklefs et al. 1998). Indeed, large fragments of this *Polylepis* forests have greater biomass of insects than smaller fragments (Cahill pers. com.) and we have found a higher prevalence of potential predators in the same fragments. Thus, although both factors may promote higher rates of body growth, it was expected that the risk of nest predation favours a different incubation pattern (on- and off-bouts and visitation rates to the nests) (Ferretti et al. 2005; Eggers et al. 2008). Consequently, the life-history syndromes are expected to differ under different food limitation versus nest predation regimes, allowing the differentiation of these alternatives. In our

study, we have not detected significant differences in the behavioural patterns of parental care of *L. yanacensis* during incubation between fragments of different sizes. Moreover, the risk of predation and nesting success are not significantly different between fragments. Therefore, this suggests that increased food availability in large fragments may be the determining factor that would favour a higher rate of body growth in chicks. Nevertheless, this chick's higher rate of body growth means less time exposed to predation risk (Martin 1995; Martin et al. 2000a). Therefore, the loss of *Polylepis* forests, either by attrition or fragmentation may promote a lower growth rate of chicks and increased predation risk due to exposure time in smaller fragments. Although our analyses show no significant difference in nest predation between fragments, the power of the test is below the desired level and predation is numerically higher in smaller fragments. Therefore it is necessary to do further study to rule out that predation is actually higher or not in smaller fragments.

Studies of phenotypic plasticity have historically been limited to environmentally induced changes in morphology and life histories, while plasticity in behavioural traits has been relatively understudied (Carroll and Corneli 1999). Understanding the factors that influence plasticity may play an essential role in understanding the selective pressures creating variation in parental care strategies within and across populations and species in variable environments (Ghalambor and Martin 2002). Behavioural traits, like other phenotypic traits, vary as a function of the interaction between genes and the environment (see Carroll and Corneli 1999). The norm of reaction or set of phenotypes expressed across a range of environments by a single genotype is the conceptual framework most often used in studies of plasticity (e.g. Stearns 1989). However, reaction norms can also be considered properties of any genetically related group of individuals, such as clones, populations or species (Ghalambor and Martin 2002). To the extent that reaction norms are heritable, comparison of the slopes of reaction norms provide insight into the evolution of plastic traits (Scheiner 1993; Gotthard and Nylin 1995). Nonparallel norms of reaction can be used as evidence for the evolution of phenotypic plasticity to different selective environments (Blouin 1992; Gotthard and Nylin 1995; Carroll and Corneli 1999; Thompson 1999; Ghalambor and Martin 2002). We haven't found evidence for non parallel norms of reaction of nest parental care behaviour (visitation rate and on-and off- bouts) among individuals of *L. yanacensis* in *Polylepis* forest fragments of different size and with different diversity of potential predators. Since the slopes for incubation behaviour are parallel our results suggested that the behavioural response to potential predators was similar among fragments and predation

has a strong effect on parental behaviour. The same applies to life history traits like egg, clutch and brood size which show no significant differences in the expression of these traits between fragments of different sizes. Greater attention to other selection pressures is needed, and we believe that examination of multiple life-history traits, in the form of life-history syndromes, among populations adds significant strength to understanding life-history variation that is not provided by the study of a single trait in one population, or single traits in different population (Ferretti et al. 2005).

In synthesis, although habitat fragmentation reduces raptor diversity in smaller fragments, they still persist and it seems that have a functional effect, similar to that of large fragments. Thus, the decrease in the richness and abundance of predators due to habitat fragmentation does not necessarily translate into a functional decline of an ecological process, in this case in nest predation. Additionally, the distance between fragments might allow the biological connectivity through individual dispersal and gene flow, probably homogenizing gene and phenotypic expression in near subpopulations.

Main conclusions. *L. yanacensis* is able to modify its parental care behaviour against predation risk. Despite the differences in predator diversity due to habitat fragmentation, the absence of differences in mortality due to nest predation is reflected in the absence of differences in antipredator behaviour and reproductive life history traits between large and small fragments. Thus, we reject our hypothesis of differential life history syndromes between subpopulations inhabiting fragments of different size. To the extent that habitat fragmentation does not alter the functional dimension of biodiversity in the remaining fragments the evolutionary dynamics will remain the same and no differences may evolve in reproductive life history syndromes on the remaining birds.

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CONCLUSIONES GENERALES

Los cambios adaptativos o estratégicos en rasgos que afectan la adecuación biológica a menudo dependen de la habilidad de un individuo de monitorear los cambios en el ambiente (Moran 1992). Al ser la depredación la principal causa de mortalidad para las poblaciones presas tanto en ecosistemas acuáticos como terrestres (Lima 2009; Lima and Dill 1990), los cambios en las tasas de depredación podrían imponer selección direccional sobre rasgos que permiten detectar y reducir el riesgo de mortalidad y cuando la migración entre poblaciones es restringida, esto puede resultar en adaptaciones locales al régimen de depredación predominante (Abjörnsson et al. 2004). Sin embargo, incluso una modesta tasa de migración entre dos poblaciones podría al contrario favorecer la evolución de plasticidad fenotípica (Sultan and Spencer 2002). En ese contexto, entender la forma en que las poblaciones evolucionan ante las nuevas condiciones impuestas por la modificación del ambiente podría ser muy útil ya que estos conocimientos podrían aplicarse en estrategias de manejo y conservación de especies en ambientes cambiantes.

En años recientes, algunos estudios han mostrado que las especies expuestas a presiones de depredación variables, espacial o temporalmente, responden de formas distintas ante dichas condiciones, algunas evolucionando adaptaciones locales que incluso los han llevado a perder la capacidad de reconocer a sus potenciales depredadores en ausencia de estos (Blumstein and Daniel 2005; Reznick et al. 2008), mientras que otras han evolucionado defensas antidepredatorias inducibles y por lo tanto muestran un alto grado de plasticidad fenotípica en esos rasgos (Abjörnsson et al. 2004; Gosline and Rodd 2008). Así, para comprender los patrones de evolución entre poblaciones en los rasgos conductuales y de historia de vida antidepredatorios, necesitamos evaluar si estos cambios son posibles y si son producto de adaptaciones locales o plasticidad fenotípica en respuesta a la heterogeneidad ambiental, en este caso impuesta por diferencias en el riesgo de depredación de nidos producida por la modificación de la diversidad de depredadores de nidos en hábitats fragmentados (Chalfoun et al. 2002).

En Bolivia los bosques de *Polylepis* representan el hábitat más amenazado producto de la pérdida y fragmentación del hábitat como consecuencia de varias causas, entre ellas la introducción y reemplazo del bosque nativo por plantaciones forestales de pino *Pinus radiata*. Esta modificación del hábitat ha provocado un empobrecimiento de la diversidad de aves en las

plantaciones y también en el bosque nativo (Balderrama 2006; Fjeldsá and Kessler 2004). Aunque consideré que una mayor depredación de nidos podría ser la causa fundamental de dicha declinación en las plantaciones de pino, descubrí que no es así y que el riesgo de depredación de nidos es mayor en los fragmentos de bosque nativo de *Polylepis* que en las plantaciones forestales (Capítulo I). Este patrón es similar al encontrado en la región central de Chile, donde la depredación de nidos es menor en plantaciones de pino que en fragmentos de bosque nativo (Vergara and Simonetti 2003). Además, en concordancia a hallazgos realizados sobre depredadores en ambientes fragmentados (Chalfoun et al., 2002; Zuria et al., 2007), concluyo que los diferentes patrones de riesgo de depredación de nidos entre hábitats de distinto tipo resultan de un balance entre la estructura de la comunidad de depredadores, sus estrategias de forrajeo, los niveles de los nidos y el tipo de hábitat; siendo el mayor el riesgo de depredación de nidos donde el ensamble de depredadores, o parte de este, son más abundantes, diversos o activos (Chalfoun et al., 2002; Zuria et al., 2007). Así, el tipo de hábitat parece ser la causa final del patrón observado ya que el reemplazo y fragmentación del bosque de *Polylepis* por plantaciones de pino parecen haber alterado el ensamble de aves y mamíferos depredadores y en consecuencia el patrón de riesgo de depredación de nidos, incrementándolo en los fragmentos de bosque de *Polylepis*. Cabe recalcar que la variación del riesgo de depredación de nidos y la respuesta de los depredadores a la fragmentación es compleja, taxón específico y contexto dependiente. Por tanto, los esfuerzos de conservación de especies de aves en declinación necesitan ser diseñados de acuerdo a las principales especies depredadoras de nidos que sean responsables de la mortalidad local de nidos y de la naturaleza del mosaico de paisaje (Chalfoun et al., 2002)

Aunque la declinación de muchas especies de aves en ambientes fragmentados ha sido a menudo atribuida al incremento de las tasas de depredación de nidos (Chalfoun et al. 2002), pocas veces se han analizado las consecuencias de estos procesos sobre la modificación de rasgos de historia de vida. A tiempo de indagar por una mayor generalidad de las consecuencias de la fragmentación del hábitat sobre la modificación de rasgos de historia de vida en aves, busqué en la literatura patrones de variación de rasgos de historia de vida reproductivos en aves que habitan ambientes fragmentados, esperando que los estudios mostraran diferencias en dichos atributos entre poblaciones locales en función del grado de fragmentación (Capítulo II). La revisión que realice me mostro que aunque las aves, y la fragmentación del hábitat se encuentran entre los tópicos más estudiados en el ámbito de la conservación (Clark and May 2002; Fazey et al. 2005), el conocimiento sobre los rasgos de historia de vida en aves y sus variaciones en ambientes fragmentados, es notablemente escaso. Sin embargo, la evidencia disponible sugiere

que en general la fragmentación del hábitat no tiene un efecto sobre los tamaños de nidada y pollada pero principalmente provoca una heterogeneidad significativa en cuanto a la respuesta, indicando que ésta varía en función de los distintos rasgos de historia de vida de las especies. Así, aquellas que cuentan con tamaños corporales grandes, nidifican en el suelo y son precociales, tendrían un incremento en el tamaño de pollada. Además, la información sobre especies estudiadas en ambientes fragmentados indica que la sobrevivencia de los adultos disminuye con el incremento en tamaño de nidada o pollada (Lampila et al. 2005; Patten et al. 2005) en concordancia con los compromisos entre sobrevivencia y reproducción de la teoría de historias de vida (Roff 1992; Stearns 1992). Por lo tanto, tener más crías no necesariamente debería ser visto como algo positivo, ya que esto podría representar una disminución en la sobrevivencia de los adultos. Además, si es que la sobrevivencia de los juveniles estaría comprometida (p.e. Patten et al. 2005), esto incrementaría el riesgo de extinción de las poblaciones locales en ambientes fragmentados.

Sin embargo, dado que solo tres especies de tamaño corporal grande fueron estudiadas, todas ellas del orden Galliformes, es evidente que esta afirmación carece de generalidad debido al pequeño tamaño muestral y a que no se puede descartar inercia filogenética. Esto último debido a que los organismos se relacionan entre sí de forma jerárquica, lo que trae como principal consecuencia que especies emparentadas tienden a parecerse, impidiéndonos descartar la posibilidad de que dichos rasgos hayan evolucionado de forma independiente afectando las inferencias derivadas de la comparación entre especies dado que se viola el supuesto estadístico de independencia (Adams 2008; Lajeunesse 2009; Rezende and Garland 2003). Para analizar correctamente datos comparativos entre múltiples especies, así como inferir patrones evolutivos a partir de ellas es necesario considerar de forma explícita la historia evolutiva de las especies en cuestión (Rezende & Garland 2003). Aunque recientemente se han propuesto un par de aproximaciones que consideran el efecto filogenético (Adams 2008; Lajeunesse 2009), no las he incorporadas en este meta-análisis. Si es que el incremento en esfuerzo reproductivo es un fenómeno general en algunas aves que habitan ambientes fragmentados, todavía necesita ser evaluado con mayor consistencia. Por otra parte, de los 21 años de producción científica analizados, 15 especies contaron con información apropiada para realizar el meta-análisis pero solo una se encuentra amenazada y es prioridad para la conservación. A pesar que las aves son el grupo de vertebrados más estudiados, la información respecto a las consecuencias de la fragmentación del hábitat sobre la modificación de rasgos de historia de vida reproductivos en aves es insuficiente para ser concluyente, así como para proponer estrategias de conservación basados en estas evidencias.

Dada la escasez de información mencionada, me propuse evaluar empíricamente las consecuencias de la modificación del riesgo de depredación de nidos, producto de la fragmentación del hábitat, sobre las estrategias reproductivas de las aves. En particular, me enfoque en *Leptasthenura yanacensis*, una pequeña ave insectívora, especialista de bosques altoandinos de *Polylepis*, que solo nidifica en ellos y que en Bolivia se encuentra amenazado (VU) por la fragmentación y pérdida de su hábitat (Cahill et al. 2009).

La evidencia empírica y teórica disponible indica que las aves de poblaciones que habitan lugares con mayor riesgo de depredación son capaces de ajustar sus rasgos conductuales y de historia de vida reproductivos para disminuir dicho riesgo y maximizar su adecuación biológica (Ferretti et al. 2005; Lima 2009; Lima and Dill 1990; Martin et al. 2000a; Martin et al. 2000b; Skutch. 1949). En consecuencia se espera que los organismo ajusten sus rasgos conductuales y de historia de vida según una combinación denominada síndrome antidepredatorio (Ver capítulo III). Sin embargo, las poblaciones de *L. yanacensis* que habitan fragmentos de bosque de *Polylepis*, de distinto tamaño y con distinta diversidad de aves rapaces, no muestran diferencias en los rasgos conductuales de cuidado parental y de historia de vida reproductivos durante la nidificación, a excepción de la tasa de crecimiento corporal. Dado este resultado, evalué como los rasgos de las aves de los distintos fragmentos en su conjunto se comportan en relación a lo esperado según lo predicho por el síndrome de anti-depredación (Ferretti et al. 2005) y encontramos un ajuste cualitativo del 50% entre lo observado y los esperado, sin embargo, este ajuste ocurre tanto en aves de fragmentos pequeños como grandes. A juzgar por la evidencia con que contamos, rechazamos nuestra hipótesis planteada y concluimos que no existe una expresión diferencial del síndrome antidepredatorio entre las subpoblaciones de fragmentos de distinto tamaño.

Sugerimos que la ausencia de diferencias en el riesgo de depredación de nidos podría ser una de las causas por la que no existen diferencias en los síndromes de historia de vida reproductivos de *L. yanacensis* entre fragmentos de distinto tamaño. Además, es posible que la distancia que existe entre los fragmentos grandes y pequeños sea la suficiente para permitir el flujo y establecimiento de individuos de *L. yanacensis* entre fragmentos ya que esto se ha observado en *Oreomanes frasieri* especialista de este tipo de bosques pero de mayor tamaño (Cahill et al. 2009), lo cual permitiría que dichos rasgos se mantengan en las poblaciones favoreciéndose la plasticidad fenotípica de la forma sugerida por Sultan y Spencer (2002).

Sin embargo, esto no quiere decir que el riesgo de depredación de nidos en los bosques de *Polylepis* sea irrelevante para *L. yanacensis*. Queda demostrado a partir de nuestros

experimentos, que los individuos parentales de esta especie son capaces de reconocer un incremento en el riesgo de depredación cerca de sus nidos y modificar significativa y drásticamente su conducta de cuidado parental durante la incubación, mediante la disminución del tiempo que pasan dentro del nido, el incremento de tiempo que pasan fuera de él y aunque no significativamente, una disminución de las tasas de visita a los mismo. Este patrón conductual se ajusta a lo predicho cuando la mortalidad por depredadores orientados por la visión selecciona en contra de una elevada actividad cerca al nido (Martin et al. 2000a; Martin et al. 2000b; Skutch. 1949) y se expresa de forma flexible *sensu* Piersma y Drent (2003).

La determinación de los patrones de variabilidad interpoblacional de la expresión de rasgos de historia de vida y conductuales reproductivos, los cuales son completamente relevantes para el entendimiento de cómo los organismos evolucionan ante la modificación del ambiente, junto con la evaluación de los cambios en las presiones selectivas, son fundamentales para establecer planes de manejo evolutivamente informados (Ashley et al. 2003). Más aún considerando que actualmente se reconoce que las poblaciones tienen el potencial de sufrir evolución contemporánea en breves plazos de tiempo y que las modificaciones antropogénicas del paisaje juegan un rol primordial en dicho proceso (Kettlewell 1955; Palumbi 2001; Patten et al. 2005; Stockwell et al. 2003).

En síntesis, la modificación y fragmentación del paisaje modifica el riesgo de depredación en los fragmentos remanentes, provocando un mayor riesgo de depredación de nidos en bosques de *Polylepis* que en plantaciones de pino. Como consecuencia de la fragmentación del hábitat, no se detectaron cambios significativos en los rasgos conductuales y de historia de vida reproductivos entre aves de ambientes con mayor o menor grado de fragmentación, tanto, a través del meta-análisis como del estudio experimental de campo. Sin embargo, en el meta-análisis encontramos una respuesta heterogénea cuando los datos fueron analizados en base a rasgos de historia de vida secundarios. Así, se detectó que el tamaño corporal, el hábito de nidificar en el suelo, y ser precociales podrían hacer a las aves más sensibles, aumentando el tamaño de pollada en ambientes más fragmentados. Esto sugiere que podría existir una elevada heterogeneidad en la respuesta de distintas especies a la fragmentación del hábitat, producto de distintos grados de sensibilidad de las mismas en función de sus rasgos de historia de vida, lo cual podría enmascarar patrones más complejos de respuesta a la fragmentación. Sin embargo, dado que pocas especies respaldan este patrón y que estas se encuentran emparentadas filogenéticamente, la generalidad de este fenómeno todavía debe ser evaluada con mayor robustez con el fin de determinar si los rasgos de historia de vida juegan un

rol en la declinación de las aves de gran tamaño corporal en ambientes fragmentadas. Para ello son necesarios más estudios que evalúen la variación de síndromes de historia de vida reproductivos en aves de ambientes fragmentados, como también determinar las posibles causas que los provocan. Además, la similitud de la expresión de rasgos conductuales y de historia de vida reproductivos en aves de ambientes con distinto grado de fragmentación podría deberse a la resiliencia funcional de la depredación presente en ambientes fragmentados y el flujo génico entre poblaciones locales. Así, en ambientes fragmentados una declinación en biodiversidad composicional y estructural no necesariamente se traduce en una declinación funcional. En la medida que la fragmentación no altere los niveles de depredación y el flujo génico entre poblaciones persista, las dinámicas microevolutivas se mantendrán y podrían no evolucionar diferencias en síndromes de historia de vida entre aves de ambientes fragmentados.

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