Conducta Antidepredatoria y Territorial en el Rayadito (*Aphrastura spinicauda*): Comparaciones Interpoblacionales en Conducta Vocal y de Defensa

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A mi mamá, mi papá y mis hermanos
A Nolberto y Facundo
A los bosques y sus habitantes

RESUMEN BIOGRÁFICO

Silvina nació en el norte de la patagonia argentina y estudió Licenciatura en Ciencias biológicas en la Universidad Nacional del Comahue, en la ciudad de San Carlos de Bariloche (1996-2001). Sus primeras investigaciones sobre aves se desarrollaron en los hermosos bosques de lengas de la precordillera argentina, para luego continuar en los bosques subantárticos de la lejana isla de Navarino, en Chile. En esas latitudes, el trabajo de investigación (con aves, musgos y líquenes) se entrelazó con el de educación y conservación de los bosques. También desde allí, se gestó la idea de realizar un doctorado en ecología de aves, bajo la dirección del Dr. Rodrigo Vásquez, ingresando al programa de Ecología y Biología Evolutiva en el año 2004. Casi finalizando la presente tesis, en el 2009, nace Facundo…agregando la dimensión de la maternidad a la investigación en ecología.

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ABSTRACT

Nest and adult predation and the loss of nests to rivals are the most important factors determining breeding success in birds. Several behavioral strategies are thought to have evolved to counteract or avoid their associated costs. Those strategies can be named as defense behaviors, and they include *antipredator behavior, nest defense behavior* and *territorial defense behavior.* Generally, these three types of defense behaviors involve a set of visual and vocal behavioral displays, that can include physical atacks. Such displays also involve costs in breeding success and survival of parents. Defense behavior can exhibit intra-specific variation, such as, for example, the different responses to the same predator due to different histories of co-existence between prey and predator. A loss of antipredator behavior could occur in isolated populations, where no predators co-exist. In birds, vocalizations play an important role in defense behavior. Generally, birds emit alarm calls (i.e., short and simple sounds) when facing predators, while they emit songs (i.e., more complex and longer sounds), when facing conspecifics, frequently produced by males. Vocalizations can change between populations inhabiting structurally different habitats, because sound transmission can differ between habitats.

This study evaluated variation and possible differences in defense behavior (territorial and antipredator behavior) and in acoustical signals of the Thorn-tailed Rayadito or Rayadito (*Aphrastura spinicauda;* Furnariidae), in three populations across its geographic distribution. The Rayadito is a suboscine endemic to temperate forests of Chile and Argentina that nests in natural cavities. Because Rayaditos inhabit a wide

geographic distribution (30°S-56°S), they experience different ecological pressures due to different types of forests and assemblages of predators. Specifically, in this study, I analyzed the geographic variation of vocalizations and defense behavior, between distant populations of Rayaditos. Through experiments, I evaluated the antipredator behavior of Rayaditos facing an aerial predator, the Chuncho (*Glaucidium nanum*), and when facing a nest predator, the Monito del monte, an arboreal marsupial (*Dromiciops gliroides*). Additionally, I analyzed the territorial defense behavior when facing a conspecific male. As a control of these experiments, I used a passerine that do not represent a strong competitor for cavities nor for feeding resources, the Chincol (*Zonotrichia capensis*).

Studied vocalizations included mobbing/alarm calls, repetitive trills and loud trills. Trills were characterized only in a descriptive way, because no study of functionality has been conducted yet. Results suggest that there are no strong differences among vocalizations of five populations, although significant differences were detected in some acoustical variables among some populations in the repetitive trills.

No inter-populational differences were detected in defense behaviors, with the exception that antipredator behavior was more intense in Navarino Island. The most frequently recorded vocalization in all the experiments was the mobbing/alarm call. Calls emitted by Rayaditos when facing different stimuli were acoustically the same, although the time vocalizing when facing the Chuncho was much longer, and this behavior was expressed by both parents.

Nest defense behavior did not differ between Monito del monte and Chincol (control), neither in general behaviors nor in vocalizations. Likewise, no differences were detected between territorial defense when confronting a Rayadito male and a

Chincol male. Therefore, I suggest that Rayaditos express intra- and inter-specific territoriality during the breeding season.

The Rayadito have a unique behavior, the mobbing behavior, that includes alarm/mobbing calls, to confront different types of threats, such as nest predators or conspecific rivals. Additionally, they also use mobbing behavior to confront a stimulus that does not represent a threat, such as the Chincol. This last mentioned behavior could be a by-product of intra-specific territoriality, and although it seems costly, possibly it also has advantages, particularly when Rayaditos face previously unknown species.

Therefore, low geographic variability of vocalizations and defense behavior of Rayaditos, suggest that there is not behavioral divergence among the studied populations, possibly because of a high gene flow through dispersion or migration. Additionally, the results of this study suggest that high levels of indiscriminate aggressiveness expressed during the breeding season, and the mobbing behavior are the main components of defense behavior in Rayaditos and they could explain the success of this species across their geographic range.

RESUMEN

La depredación o destrucción del nido y la depredación de la pareja reproductiva son los factores más importantes en determinar el éxito reproductivo de las aves. Por esta razón, se han desarrollado numerosas estrategias conductuales para contrarrestar o evitar sus costos. Dichas estrategias se pueden denominar globalmente como conductas de defensa, y entre ellas se pueden distinguir la *conducta antidepredatoria*, la *defensa del nido* y la *defensa territorial*. En general, estos tres tipos de conductas de defensa consisten en un conjunto de despliegues conductuales, tanto visuales como vocales, que pueden incluir ataques directos y que también implican riesgos y costos, tanto reproductivos como de sobrevivencia. La conducta de defensa puede exhibir variaciones dentro de una misma especie, como por ejemplo, las que se producen en relación a la historia de coexistencia entre la presa y un depredador. Esta situación puede desembocar en la pérdida de la conducta antidepredatoria en poblaciones aisladas, donde no existen determinados depredadores. En las aves, las vocalizaciones juegan un papel preponderante en la conducta de defensa. Generalmente, las aves emiten llamadas de alarma (i.e., sonidos breves y simples) frente a los depredadores, mientras que ante los conespecíficos se emiten cantos (i.e., sonidos más complejos de distinta duración), frecuentemente producidos por machos. Las vocalizaciones pueden sufrir modificaciones en poblaciones de la misma especie que habitan hábitats estructuralmente distintos, dado que la propagación del sonido en ellos puede ser diferente.

Este estudio se enfocó en evaluar la variación y las posibles diferencias en la conducta de defensa (territorial y antidepredatoria) y en las señales acústicas del rayadito (*Aphrastura spinicauda;* Furnariidae), en tres poblaciones a lo largo de su distribución geográfica. El rayadito es un suboscino endémico de Chile y Argentina, especialista de hábitats con alta cobertura vegetal y que nidifica en cavidades naturales. Su amplia distribución geográfica (30°S-56°S) lo sitúa en escenarios ambientales muy diferentes en cuanto a la estructura del hábitat y en relación a distintas faunas de depredadores, lo que puede derivar en diferentes presiones ecológicas. Específicamente, en este estudio se analizó la variación geográfica de la conducta de defensa y de sus vocalizaciones, en poblaciones distantes una de otra. Experimentalmente, se evaluó la conducta antidepredatoria frente a un depredador aéreo de adultos, el chuncho (*Glaucidium nanum*) y frente un depredador de nidos, el monito del monte, un marsupial arborícola (*Dromiciops gliroides*), y además se evaluó la defensa territorial frente a un conespecífico macho. Se utilizó como control de estos experimentos un paseriforme que no compite por cavidades ni por recurso alimenticios, el chincol (*Zonotrichia capensis*).

Las vocalizaciones estudiadas del rayadito fueron las llamadas de alarma/acoso, trinos repetitivos y trinos fuertes. La clasificación de los trinos tiene un carácter puramente descriptivo, ya que no se ha evaluado su funcionalidad. Los resultados obtenidos indican que no existen diferencias marcadas en las vocalizaciones de los rayaditos provenientes de las cinco poblaciones estudiadas, si bien se detectaron diferencias significativas en algunas variables acústicas entre algunas poblaciones en los trinos repetitivos.

No se detectaron diferencias en la conducta de defensa entre las poblaciones estudiadas, excepto que la conducta antidepredatoria fue más intensa en la población más sureña (isla Navarino). Las llamadas de alarma/acoso fueron las más usadas frente a todos los estímulos. Tampoco se detectaron diferencias acústicas entre las llamadas emitidas frente a distintos estímulos, aunque la respuesta antidepredatoria frente al chuncho provocó un respuesta vocal mucho más extensa en el tiempo, expresada por ambos padres.

Tanto en la conducta general como en las vocalizaciones no existieron diferencias entre la defensa del nido frente al monito del monte y frente al chincol. De la misma forma, no se registraron diferencias entre las respuestas conductuales al macho rayadito y al macho chincol. Por lo tanto, se sugiere que el rayadito demuestra tanto territorialidad intra como interespecífica.

El rayadito posee un único comportamiento, el comportamiento de acoso, que incluye las llamadas de alarma/acoso, para enfrentar distintos tipos de amenazas, como pueden ser depredadores de nidos o rivales conespecíficos. Adicionalmente, también utilizan el comportamiento de acoso para enfrentarse a estímulos que no representarían ningún tipo de amenaza, como el chincol. Es posible que esta conducta pudiera haberse adquirido como un subproducto de la territorialidad intraespecífica y, aunque en principio aparenta ser un rasgo costoso, es posible que también tenga beneficios a la hora de enfrentar especies desconocidas.

Por lo tanto, la baja variabilidad geográfica de las vocalizaciones y de la conducta de defensa del rayadito, sugieren que no existe una divergencia conductual entre las poblaciones, eventualmente impedida por un flujo génico alto a través de dispersión o migración. Los resultados de esta tesis sugieren que una elevada agresividad desarrollada indiscriminadamente durante la época reproductiva, y la conducta de acoso, son componentes fundamentales de la conducta de defensa del rayadito y que podrían ser claves en el éxito de esta especie a lo largo de su rango geográfico.

INTRODUCCIÓN

En aves, la depredación de adultos, polluelos y/o huevos, así como la pérdida de un nido o territorio por causa de competidores, son las interferencias más relevantes en el curso normal de cada evento reproductivo y, por lo tanto, en la determinación de su éxito reproductivo (Lack 1954, Martin 1995, Martin et al. 2000). La depredación puede ir dirigida al contenido del nido (huevos o polluelos) o a los mismos adultos reproductivos. Por esta razón existen diferentes estrategias para contrarrestar estas amenazas, las cuales constituyen *estrategias de defensa.* En la literatura, normalmente se define "defensas" como un conjunto de caracteres principalmente conductuales y morfológicos que evitan la depredación (Caro 2005). Esta tesis se focaliza exclusivamente en las estrategias conductuales de defensa del nido, incluyendo defensa antidepredatoria y defensa contra competidores, ya que estos últimos también pueden ocasionar daños similares a los causados por la depredación, aunque con distinto objetivo. Por ejemplo, machos de la misma o diferente especie pueden destruir los huevos y/o el nido de otro macho, con el fin de obtener un recurso que puede ser el territorio, la pareja reproductiva o la cavidad para nidificar. Dentro de las estrategias conductuales, las estrategias indirectas incluyen todas aquellas que disminuyen las probabilidades de ser detectados por el depredador, como la selección del lugar y el tipo de nido, el acercamiento sigiloso, o el tamaño de las nidadas (Nice 1957, Martin 1995, Martin et al. 2000, Brightsmith 2005a, b, Caro 2005). Por otro lado, las conductas de defensa directas, suponen el enfrentamiento directo con la amenaza, como puede ser un depredador o un probable usurpador del nido o la pareja

(Caro 2005). La conducta antidepredatoria, la defensa del nido (de depredadores) y la conducta territorial constituyen tres tipos esenciales de conductas de defensa desplegadas durante la época reproductiva (Fig. 1).

La conducta antidepredatoria *per se* se refiere a un conjunto de características comportamentales que evitan la depredación. Entre ellas se pueden enumerar el alejarse del nido o aproximarse encubiertamente cuando se detectan depredadores cerca, la emisión de vocalizaciones que alertan acerca de la presencia de un depredador, los

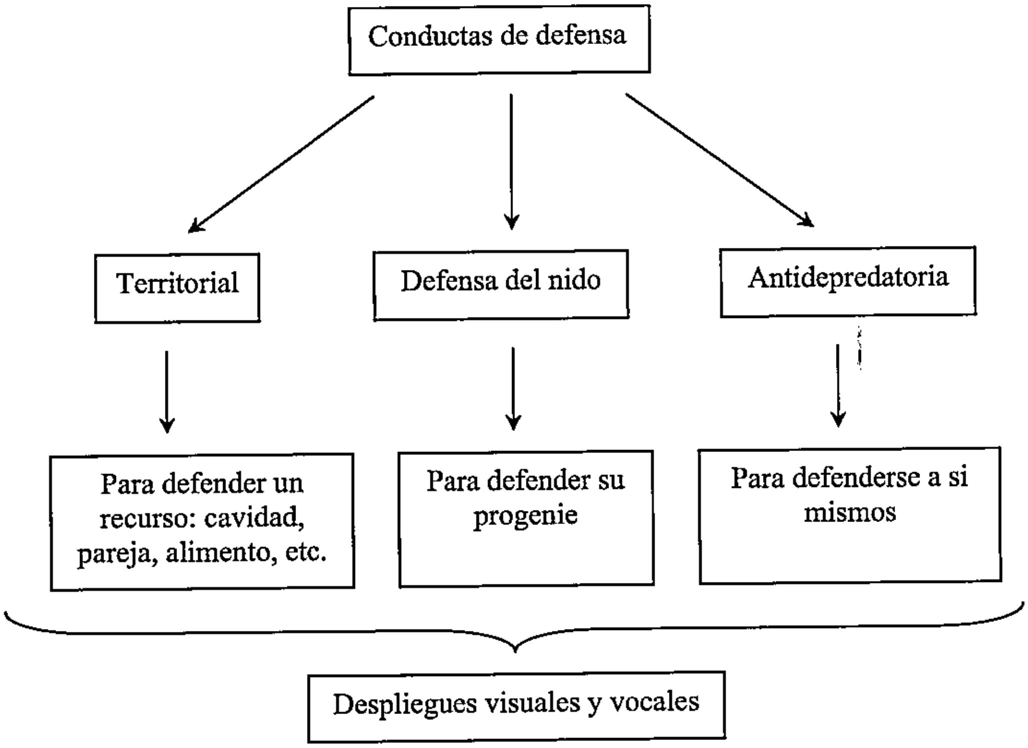


Fig. 1. Esquema simplificado de los tipos de conducta de defensa desplegados por las aves durante la estación reproductiva.

despliegues más o menos específicos como la conducta de "acoso" (i.e., mobbing behavior), entre otros (Caro 2005). Algunas conductas antidepredatorias tienen repercusiones sobre la sobrevivencia de la nidada, ya que si los padres están ausentes por un período largo de tiempo, los huevos pueden enfriarse y los polluelos aumentar el riesgo de inanición (Michl et al. 2000).

La defensa del nido constituye una forma de evitar o disminuir la depredación de huevos o polluelos a través de despliegues visuales y/o vocales, al mismo tiempo que aumenta la probabilidad de daño o muerte de los padres (Andersson et al. 1980, Montgomerie y Weatherhead 1988). La defensa del nido, entonces, conlleva costos en la sobrevivencia de los padres, y supone un gasto energético alto que podría disminuir los recursos destinados al cuidado parental y a la reproducción futura (Montgomerie y Weatherhead 1988). Por esta razón, se considera que la defensa del nido puede constituir una inversión de cuidado parental (Barash 1975, Andersson et al. 1980).

La defensa territorial frente a conespecíficos, incluye también despliegues vocales y visuales dirigidos a otros individuos con los cuales compiten por diversos recursos como cavidades, pareja, o alimento. En paseriformes los cantos son fundamentales en este tipo de interacción, donde son utilizados para delimitar territorios y repeler rivales (Searcy y Andersson 1986, Brumm y Todt 2004, Collins 2004). La conducta territorial supone una disminución en el tiempo destinado a la vigilancia y por lo tanto, un aumento en la probabilidad de ser depredado (Dunn et al. 2004). En especies cuya reproducción requiere recursos potencialmente limitantes como las cavidades naturales (Tomasevic y Estades 2006, Cornelius et al. 2008), la competencia por éstas puede ser un factor determinante de la conducta y del éxito reproductivo. Por otro lado, la competencia por pareja o el riesgo de apareamientos fuera de la pareja, puede influir en que uno o ambos sexos presenten una conducta de defensa territorial marcada, en presencia de individuos de la misma especie y sexo (Busch et al. 2004). La conducta de defensa territorial, generalmente es ejercida por los machos y va dirigida hacia otros machos de la misma especie (Schlinger 1987, Hau et al. 2000, Busch et al. 2004), siendo la conducta vocal una de las más estudiadas. Por ejemplo, la presencia de machos rivales puede influir en la amplitud del canto emitido por el macho del territorio defendido (Brumm y Todt 2004) y, a largo plazo, en el tamaño del repertorio de cantos que poseen los machos (Hughes et al. 1998, Busch et al. 2004, Beecher y Brenowitz 2005). Sin embargo, recientemente se ha comenzado a estudiar la territorialidad en las hembras, las cuales pueden incluso emitir vocalizaciones de territorialidad (Cooney y Cockburn 1995, Pärn et al. 2008), aunque suelen ser menos agresivas que los machos (Fedy y Stutchbury 2005), pero también respondiendo más fuertemente a individuos de su mismo sexo (Logue y Gammon 2004).

La comunicación vocal es un factor relevante dentro de todos los tipos de conductas de defensa de los paseriformes. Básicamente, las vocalizaciones pueden clasificarse como **cantos** (i.e., señales de estructura acústica compleja y producida generalmente por los machos durante la época reproductiva) y **llamadas** (i.e., sonidos breves y simples producidos por un requerimiento inmediato, tal como el contacto o la alarma) (Searcy y Andersson 1986, Kumar 2003, Beecher y Brenowitz 2005, Catchpole y Slater 2008). Como ya se ha señalado, los cantos son fundamentales durante la época reproductiva, en la defensa territorial y en la comunicación y atracción de la pareja

(Searcy y Andersson 1986, Collins 2004). Las llamadas, por su parte, pueden clasificarse en numerosos tipos según su funcionalidad: de contacto, de alarma, de "precaución", entre otros (Marler 2004). Las llamadas de alarma son utilizadas en situaciones que representan algún tipo de riesgo para el ave que los emite. Además, existen numerosos tipos de llamadas de alarma. Un ejemplo clásico en la literatura es la llamada de alarma de algunos páridos frente a un halcón, la cual se caracteriza por ser un sonido de escaso ancho de banda y con una frecuencia suficientemente alta como para que esté fuera del rango de audición del depredador. De esta manera la señal se transmite sólo a cortas distancias y puede ser detectada por otros páridos mientras el emisor disminuye los costos de emitir dicha señal (Klump et al. 1986). Otro ejemplo son las llamadas de alarma que forman parte del comportamiento de acoso, que consiste en el acercamiento de la presa a un depredador inactivo (Hartley 1950 citado en Altmann 1956). En este caso, las llamadas son fuertes y fácilmente localizables, ya que deberían ser capaces de reclutar más individuos-presa alrededor del depredador (Caro 2005). Este patrón comportamental es considerado una estrategia antidepredatoria que ocurre especialmente en aves y mamíferos (Altmann 1956).

Las llamadas de alarma en conjunto con el comportamiento desplegado frente a un depredador pueden incluir información adicional sobre la peligrosidad y/o identidad del depredador. Se ha registrado, por ejemplo, que a mayor cercanía del depredador, mayor es el número de elementos de la llamada y mayor la frecuencia mínima emitida (Leavesley y Magrath 2005). En algunas especies de aves y mamíferos se han observado respuestas depredador-específicas donde el tipo de canto (o la proporción de los mismos) varía según el depredador (Gottfried 1979, Gottfried et al. 1985), o según la procedencia del ataque (i.e., si es aéreo o terrestre) (Evans et al. 1993, Marler y Evans 1996, Fichtel et al. 2005). Experimentos de laboratorio han mostrado que *Gallus gallus* emite una llamada de alarma consistente en una única nota de baja amplitud ante un depredador aéreo. En cambio, si el depredador es un mamífero terrestre las llamadas son pulsátiles y más fuertes (Evans et al. 1993, Marler y Evans 1996, Marler 2004). En paseriformes, *Turdoides squamiceps* tiene llamadas de alarma específicas para depredadores aéreos y terrestres (Naguib et al. 1999), *Turdus migratorius* emite dos llamadas diferentes cuando enfrentan a dos depredadores distintos, que incluyen información acerca de la intensidad de la defensa del nido en el futuro inmediato (Gottfried et al. 1985) y *Dendroica petechia* posee llamadas de alarma específicas para la defensa del nido de aves parásitas de nidos (Gill y Sealy 2004). Por otro lado, estudios recientes han encontrado que las llamadas de alarma en paseriformes no siempre serían funcionalmente referenciales, sino que la tasa de repetición incluye información sobre el grado de peligro del nido (Leavesley y Magrath 2005, Welbergen y Davies 2008), sugiriendo que la selección natural habría "privilegiado" la señalización acerca de la urgencia del peligro por sobre la identidad del mismo (Gill y Sealy 2004). Por lo tanto, existiría una gran variabilidad dentro los paseriformes respecto de la información adicional que acompaña las vocalizaciones de alarma.

El ensamble de los depredadores, así como la intensidad de la competencia por recursos, no son constantes a lo largo del rango de distribución de las especies, lo cual resulta en cambios o ausencia de determinadas conductas antidepredatorias o territoriales (Baker 1994, Berger 1998, Stoks et al. 2003). Por ejemplo, en poblaciones insulares es común la ausencia de grandes carnívoros. Como consecuencia, muchas especies de aves han perdido la capacidad de reconocer a los depredadores, determinando una mayor vulnerabilidad cuando llegan depredadores exóticos o se reintroducen depredadores previamente extintos (Martinez-Morales y Cuaron 1999, Cuthbert y Hilton 2004). También se ha reportado que los cantos territoriales pueden perder complejidad en poblaciones insulares, al cambiar el ensamble de aves con el que previamente compartían el hábitat (Hamao y Ueda 2000). Más allá de las importantes implicancias en relación a la conservación de la biodiversidad, estudios sobre la variación geográfica de diferentes aspectos de la conducta pueden ayudar a comprender los cambios microevolutivos e incluso la especiación (Foster 1999). Debido a que la conducta de defensa juega un papel clave en el éxito reproductivo de los paseriformes, y que por lo tanto, podría tener efectos en la adecuación biológica (*fitness*), se espera que cuando la presión selectiva se relaja, dicho comportamiento pierda intensidad e incluso pueda llegar a desaparecer. Sin embargo, el tiempo requerido para estos cambios dependerá del costo de mantenimiento de dicha conducta (Andersson et al. 1980, Montgomerie y Weatherhead 1988, Dunn et al. 2004, Blumstein 2006), y de los mecanismos genéticos y/o fisiológicos que subyacen a estas estrategias (Hollén y Manser 2007). Las vocalizaciones que acompañan las conductas de defensa pueden incluir información sobre el tipo de amenaza y/o peligrosidad de la misma, por lo tanto, si se producen cambios en el "ensamble de amenazas", podrían producirse paralelamente cambios en las características de las vocalizaciones y en la conducta que acompaña la emisión de la vocalización.

Existe un gran número de estudios sobre variación geográfica de vocalizaciones en paseriformes oscinos (suborden Passeri). En este grupo se ha hipotetizado que la selección sexual asociada a la evolución cultural de las vocalizaciones (es decir, la formación de dialectos regionales) estimularían la divergencia reproductiva y eventualmente la especiación (Endler 1992, Boughman 2002, Slabbekoorn y Smith 2002a). La rápida formación de dialectos en los oscinos se relaciona con el proceso de aprendizaje por imitación de sus vocalizaciones, durante el cual pueden ocurrir errores de imitación, los cuales quedan plasmados en cantos diferentes (Beecher y Brenowitz 2005). Sin embargo, no sólo los procesos de formación de dialectos regionales promueven la diferenciación de las vocalizaciones, sino también aquellos que permiten maximizar la transmisión a través de hábitats estructuralmente diferentes (Morton 1975, Richards y Wiley 1980, Wiley 1991, Endler 1992). Esta idea ha sido acuñada con el nombre de hipótesis de adaptación acústica y se ha reportado que podría ser un importante factor de diferenciación vocal tanto en oscinos (véase por ejemplo, Dubois y Marten 1984, Tubaro y Segura 1994, Slabbekoorn y Smith 2002b) como en suboscinos (Suborden Tyranni) (Seddon 2005). Las modificaciones resultantes de estos cambios también pueden influir en los procesos de comunicación intra e intersexual.

Contrariamente a lo que sucede con los oscinos, los estudios sobre la evolución de las señales acústicas en paseriformes suboscinos son escasos (Kroodsma 1984, Kroodsma et al. 1987, Lovell y Lein 2004a, b, Seddon 2005). Sin embargo, cada especie de este suborden constituye un modelo ideal para analizar y comparar vocalizaciones y otras conductas asociadas, debido a que los resultados no están sesgados por evolución cultural ya que no existe aprendizaje de cantos (Seddon 2005). Por lo tanto, estudios en diferentes hábitats y/o a lo largo de la distribución geográfica de una especie focal de suboscino podría contribuir a comprender el valor adaptativo y el contexto ecológico de las vocalizaciones en este grupo de aves, así como a desarrollar información básica sobre su papel en la evolución de paseriformes no oscinos (Foster 1999, Seddon 2005) que eventualmente podría extrapolarse a aves sin aprendizaje vocal. El estudio simultáneo de la conducta de defensa, en la cual las vocalizaciones tienen un papel preponderante, ayudaría a clarificar la funcionalidad de cada tipo de vocalización y el papel que la conducta desempeña en la evolución de este grupo de aves. En general, los estudios sobre vocalizaciones de suboscinos están concentrados en dos familias, Thamnophilidae y Tyrannidae, y se focalizan en el posible reconocimiento individual producto de la variación entre individuos en una población (véase por ejemplo: Payne y Budde 1979, Morton y Derrickson 1996, Isler et al. 1998, Bard et al. 2002, Lovell y Lein 2004a, b, 2005, Wiley 2005).

Los suboscinos son el grupo dominante de la avifauna neotropical (Irestedt et al. 2001, Irestedt et al. 2002, Ricklefs 2002). El rayadito (*Aphrastura spinicauda*) es un suboscino perteneciente a la familia Furnariidae, endémico de los bosques templado – australes (Fig. 2). La familia Furnariidae es una de las más diversificadas en el hemisferio sur (Irestedt et al. 2001) con 240 especies en 59 géneros (Zyskowski y Prum 1999), de las cuales 33 especies se encuentran en Chile (Jaramillo 2003). Pese a su importancia en cuanto a número de especies, es una familia relativamente poco estudiada. El género *Aphrastura* incluye sólo otra especie, *A. masafuerae*, restringida a la isla oceánica de Masafuera, la cual se encuentra en peligro de extinción (Hahn y Römer 2001). El rayadito, en cambio, tiene una amplia distribución que, si bien se restringe a hábitats boscosos y/o de alta cobertura arbórea, se extiende desde el Parque Nacional Fray Jorge (30° S) hasta el Cabo de Hornos (56° S) (Johnson y Goodall 1967, Remsen 2003, Rozzi 2003). A lo largo de su distribución se han descrito tres subespecies en base a coloración del plumaje (Johnson y Goodall 1967). *Aphrastura s. fulva* (Angelini) habita únicamente en la isla Grande de Chiloé, *A. s. bullocki* (Chapman) se encuentra en la isla Mocha, mientras que *A. s. spinicauda* (J. F. Gmelin, 1789), se encuentra en la mayor parte de la distribución de la especie (Johnson y Goodall 1967).

Fig. 2. Rayadito (*Aphrastura spinicauda*) anillado en la isla Navarino. Fotografía Juan José Sanz.

Las diferencias fenotípicas en coloración del plumaje y las distancias relativamente cortas que separan a estas islas del continente (tanto Chiloé como isla

Mocha son islas continentales), sugieren que el rayadito posee una relativamente baja capacidad de dispersión, dada quizás por un uso especializado del bosque y/o por una baja capacidad de vuelo. El rayadito es un ave no migratoria, usuaria secundaria de cavidades, que suele formar bandadas mono o multiespecíficas en época no reproductiva (Vuilleumier 1967, Ippi y Trejo 2003). Su dieta es principalmente insectívora, aunque consume material vegetal ocasionalmente (Grigera 1982, Estades 2001).

El rayadito utiliza con cierta facilidad cajas anideras, lo que ha permitido estudios acerca de su biología reproductiva (Moreno et al. 2005). Es una especie que no presenta dimorfismo sexual, donde ambos sexos realizan cuidado parental de forma equitativa, aunque el macho es levemente más grande que la hembra (Moreno et al. 2007). En época reproductiva defiende activamente su territorio, acercándose al intruso, emitiendo fuertes y repetidas vocalizaciones (i.e., llamadas de alarma) durante el tiempo que dura la amenaza (S. Ippi obs. pers.). Durante este lapso, generalmente no entra al nido a alimentar a los pichones. La presencia de un depredador cerca del nido también produce una disminución de la tasa de visitas de casi el 50 % en *A. masafuerae* (Hahn et al. 2004). Además de la llamada de alarma, el rayadito posee otros tipos de llamadas (Vuilleumier 1967, Ippi y Trejo 2003), las cuales tampoco han sido descritas con parámetros acústicos. En esta tesis se reconocen cuatro tipos de vocalizaciones: llamada de alarma y llamada de contacto y dos tipos de trinos que se denominarán descriptivamente como trinos fuertes y trinos repetitivos, para evitar confusiones respecto de su funcionalidad, la cual no ha sido estudiada previamente.

El rayadito es una especie muy abundante, en relación a las otras especies del ensamble de bosque, en casi todo su rango de distribución, el cual incluye gran parte de las numerosas islas situadas a lo largo de Chile (Johnson y Goodall 1967, Rozzi et al. 1996a, b, Anderson y Rozzi 2000, Cornelius et al. 2000). Este amplio rango latitudinal implica que sus poblaciones están sometidas a una gran variación climática, dada por una disminución en las temperaturas promedio acompañada de un aumento en las precipitaciones y el viento, a medida que se avanza hacia el sur (Hajek y di Castri 1975). Más aún, la geografía particular de los bosques chilenos, que incluyen bosques relictos aislados y numerosas islas con distintos ensambles de depredadores y competidores, permite describir y poner a prueba hipótesis concernientes a la pérdida de la conducta antidepredatoria en ausencia de depredadores. Por lo tanto, las variables ecológicas que afectan el desarrollo de los individuos de estas poblaciones pueden determinar respuestas diferentes frente a determinadas situaciones en relación a las características de sus vocalizaciones y la conducta de defensa.

El objetivo de esta tesis fue evaluar la variación interpoblacional de la conducta de defensa en la época reproductiva de un suboscino (el rayadito) de amplio rango geográfico, y el tipo de vocalizaciones emitidas frente a distintas situaciones de defensa asi como su variación a lo largo de su distribución geográfica. Para llevar a cabo dicho objetivo, se estudiaron cinco poblaciones de rayadito, que incluyen las tres subespecies descritas por Johnson y Goodall (1967) y una isla donde no existen depredadores mamíferos nativos (véase Redford y Eisenberg 1992, Muñoz Pedreros y Yañez Valenzuela 2000). A la vez, estas poblaciones habitan en ambientes donde predominan distintos tipos de bosques (Armesto et al. 1996a, b, Arroyo et al. 1996), que pueden afectar diferencialmente la transmisión del sonido (Morton 1975, Richards y Wiley 1980, Wiley 1991), pudiendo generar diferencias acústicas interpoblacionales. La conducta de defensa se evaluó durante la época reproductiva en respuesta a la presencia de un rival conespecífico macho, un depredador aéreo (chuncho; *Glaucidium nanum*) y un mamífero depredador de nidos (monito del monte; *Dromiciops gliroides*). Las características descritas para el rayadito lo convierten en un sujeto de estudio apropiado para analizar preguntas en relación a la variación geográfica en relación a la conducta de defensa y, en particular, a las vocalizaciones. La información obtenida constituiría la línea de base que permitirá diseñar, *a posteriori*, estudios de reconocimiento entre individuos, de la función inter e intraespecífica de las llamadas de alarma, y postular hipótesis acerca de la evolución del canto, en aves sin capacidad de aprendizaje de cantos (Lovell y Lein 2004a, b, 2005, Seddon 2005), y de su papel en la divergencia de rasgos en poblaciones insulares, entre otros temas (Kroodsma et al. 1987). El análisis de las vocalizaciones y de la conducta de defensa en diferentes poblaciones puede brindar información acerca de la diferenciación interpoblacional en relación a pautas comportamentales, las cuales pueden "conducir" cambios microevolutivos en paseriformes (Endler 1992, Boughman 2002). Por lo tanto, específicamente, en este estudio se evaluó la conducta de defensa del nido, la conducta antidepredatoria y la conducta territorial del rayadito en tres poblaciones y la existencia de variación en las señales acústicas de *A. spinicauda* a nivel poblacional, a lo largo de su rango de distribución.

Las preguntas específicas que esta tesis intentó responder fueron:

1. Las poblaciones del rayadito alopátricas con un tipo de depredador ¿muestran conducta antidepredatoria frente a dicho depredador?
2. La conducta antidepredatoria del rayadito ¿varía entre las distintas poblaciones para un mismo depredador?
3. ¿Existen vocalizaciones específicas para cada situación de conducta de defensa?
4. ¿Varían los cantos y las llamadas del rayadito entre poblaciones aisladas que habitan ambientes boscosos diferentes?

Las hipótesis propuestas son:

<u>Hipótesis 1</u>: La presencia de un tipo de depredador que ha coexistido históricamente con la presa, favorece la ocurrencia de las conductas antidepredatorias en esta última.

Entonces,

a. En las poblaciones donde no existen depredadores de nido, el rayadito no mostrará una conducta de defensa del nido y por lo tanto, el comportamiento expresado diferirá entre las poblaciones estudiadas.
b. La conducta antidepredatoria del rayadito, expresada frente a un depredador específico, no será diferente entre todas las poblaciones simpátricas con dicho depredador (i.e., el chuncho).

<u>Hipótesis 2</u>: Las características estructurales del ambiente influyen en las cualidades de las señales acústicas del rayadito que favorecen la transmisión de dichos sonidos.

Entonces,

c. Las características acústicas de las vocalizaciones de los rayaditos de las poblaciones en estudio serán diferentes debido a que habitan ambientes donde predominan diferentes tipos de bosques.
d. En hábitats boscosos más cerrados y complejos las vocalizaciones tendrán frecuencias más bajas, y anchos de banda más angostos que en hábitats boscosos menos densos. Los sonidos altamente modulados, como los trinos, tendrán una menor tasa de notas por segundo en ambientes más cerrados.

Con el fin de estudiar las hipótesis y predicciones mencionadas, se enuncian los siguientes objetivos particulares:

1. Describir tres tipos conducta de defensa (i.e., defensa antidepredatoria, defensa del nido y defensa territorial) y las vocalizaciones utilizadas por el rayadito, durante el periodo reproductivo, y en la cercanía del nido.
2. Evaluar la conducta del rayadito frente a un depredador de nidos históricamente ausente en un área de estudio.
3. Describir la conducta de defensa territorial y las vocalizaciones utilizadas por el rayadito y compararla con la conducta antidepredatoria, durante la época reproductiva.
4. Describir los cantos y llamadas del rayadito en poblaciones diferentes.
5. Analizar la variación geográfica de las vocalizaciones del rayadito en relación a la hipótesis de adaptación acústica.

Cabe señalar que existe poca información relacionada con la participación de los distintos sexos en las conductas de defensa de suboscinos (Bard et al. 2002, Fedy y Stutchbury 2005). Al respecto, este estudio permitió describir la participación de ambos sexos en las conductas de defensa durante la época reproductiva del rayadito y las vocalizaciones asociadas. Por lo tanto, un último objetivo fue aportar información experimental sobre el comportamiento de machos y hembras de una especie de suboscino en conductas de defensa.

En cualquier parte donde nos encontremos, a toda hora del día o de la noche, ¡miembros de la familia! Parientes más o menos lejanos, pero con una ascendencia idéntica a la nuestra.

¿Cualquier gato se asoma a la ventana y se lame las nalgas?... ¡Los mismos ojos de tía Carolina! ¿El caballo de un carro resbala sobre el asfalto?... ¡Los dientes un poco amarillentos de mi abuelo José María!

¡Lindo programa el de encontrar parientes a cada paso! ¡El de ser un tío a quien lo toman por primo a cada instante!

Y lo peor, es que los vínculos de consanguinidad no se detienen en la escala zoológica. La certidumbre del origen común de las especies fortalece tanto nuestra memoria, que el límite de los reinos desaparece y nos sentimos tan cerca de los herbívoros como de los cristalizados o de los farináceos. Siete, setenta o setecientas generaciones terminan por parecernos lo mismo, y (aunque las apariencias sean distintas) nos damos cuenta de que tenemos tanto de camello, como de zanahoria.

Después de galopar nueve leguas de pampa, nos sentamos ante la humareda del puchero. Tres bocados...y el esófago se nos anuda. Hará un período geológico; este zapallo, ¿no sería hijo de nuestro papá? Los garbanzos tienen un gustito a paraíso, ¡pero si resultara que estamos devorando a nuestros propios hermanos!

A medida que nuestra existencia se confunde con la existencia de cuanto nos rodea, se intensifica más el terror de perjudicar a algún miembro de la familia. Poco a poco, la vida se transforma en un continuo sobresalto. Los remordimientos que nos corroen la conciencia, llegan a entorpecer las funciones más impostergables del cuerpo y del espíritu. Antes de mover un brazo, de estirar una pierna, pensamos en las consecuencias que ese gesto puede tener, para toda la parentela. Cada día que pasa nos es más difícil alimentarnos, nos es más difícil respirar, hasta que llega un momento en que no hay otra escapatoria que la de optar, y resignarnos a cometer todos los incestos, todos los asesinatos, todas las crueldades, o ser, simple y humildemente, una víctima de la familia.

Oliverio Girondo. Espantapájaros (Al alcance de todos). 1932.

Capítulo I:

Antipredator and territorial behavior of Rayadito (*Aphrastura spinicauda*): Interpopulation comparisons

Abstract

Due to the high impact of predators and competitors in the breeding success of birds, diverse behavioral strategies that drive to enhance the survivorship of each individual (antipredator behavior), their eggs or chicks (antipredator nest defense), or to maintain their territory (territorial defense) have been developed. Predators, predation pressure and intensity of resource competition are not constant throughout distribution range of species, resulting in changes or absence of antipredator and territorial behavior. This study focused on the geographic variation of three types of defense behaviors in Rayadito (*Aphrastura spinicauda*), a species that inhabits a wide latitudinal range in southern South America. Specifically, through experimental manipulation, I examined Rayadito responses to an avian adult predator, a mammalian nest predator (in populations where nest predators are present and where they are absent) and a conspecific male. There were no behavioral differences between the responses elicited by a control male and a Rayadito male, suggesting the existence of intra- as well as inter-specific territoriality, during the breeding season. Antipredator behavior was more intense than nest defense or "control" behavior while no differences in nest defense behavior were found among the three populations, in spite of the absence of nest

predators in one population. Mobbing behavior, including calls, was displayed during territorial and antipredator defense, although the avian predator elicited a more intense and longer response. Rayaditos have a high intra- and inter-specific territoriality, that could be useful along their geographical distribution, due to variable number of passerines and other small vertebrates that can compete for cavities and other resources. Results of this study suggest that indiscriminate inter-specific territoriality and mobbing behavior are a key component of defense behavior, and they would constitute fundamental characteristics that determine that rayaditos inhabit successfully a wide distribution range.

Introduction

Nest and adult predation and the loss of nests to rivals are the most relevant factors interfering the normal course of breeding in birds (Lack 1954, Martin 1995, Martin et al. 2000). Birds have evolved diverse behavioral strategies to counteract these threats. Parents allocate time and energy to vigilance, antipredator and territorial displays. Eventually, these displays may end up in physical attacks. However, participation in these behaviors diminishes the time available for behaviors important to reproductive success, such as nest construction, egg incubation and chick feeding. For example, the risk of predation may be increased during territorial defense, due to reduced vigilance (Dunn et al. 2004), and offspring defense may increase the probability of injury of parents (Andersson et al. 1980, Montgomerie and Weatherhead 1988). In addition, some antipredator behaviors have repercussions on the survivorship of nestlings, because if parents are absent for a time, eggs become cold, or chicks suffer a higher risk of starvation (Michl et al. 2000). Moreover, male-male competition and aggressiveness toward competitors can reduce feeding rate of the incubating females, decreasing breeding success (Duckworth 2006). Thus, three types of "defense behaviors" are distinguishable: adult antipredator defense, nest defense, and territorial defense. These three types of defense behavior could be linked by a set of individual decisions in response to different threats during the nesting stage or by an underlying individual personality (Sih et al. 2004) such as have been mentioned for some taxa (Huntingford 1976, Knight and Temple 1988, Quinn and Cresswell 2005). These situations would imply that each defense behavior would not be independent from another, and these could have important consequences on the breeding success.

Antipredator behaviors comprise a suite of behavioral characters that are used in the avoidance of predation (Caro 2005). During the breeding season, adult antipredator behaviors can include nesting site selection, silent approaches to the nest, a cessation of nestlings feeding, alarm calls, and mobbing, among others. The kind or species of predator can elicit different types of antipredator responses (Evans et al. 1993), and individual variation can exist within the same prey species (Huntingford 1976). On the other hand, antipredator nest defense contributes to reduce or avoid predation on eggs and chicks, by means of displays and defensive attacks by parents. However, this also simultaneously increases the probability of injury to themselves (Montgomerie and Weatherhead 1988). Thus, because this behavior involves survival costs and also a decrease in other aspects of parental care and future reproduction (Montgomerie and Weatherhead 1988), antipredator nest defense represents a form of parental investment (Barash 1975, Andersson et al. 1980). The type of nest predator can also elicit different behaviors and associated vocalizations (Gottfried 1979, Knight and Temple 1988). For example, Knight and Temple (1988) conducted an experiment with the Red-winged Blackbird (*Agelaius phoeniceus*) with two different nest predators (a crow and a raccoon), one adult predator (a hawk) and a control. In this experiment, the hawk was attacked the most and the raccoon the least, with differences among the proportions of the various call types to the different predator models. Furthermore, they found that male and female Blackbirds were consistent in their intensity of nest defense across the different predators.

Territorial behavior involves a variety of displays and songs against individuals of the same or different species that compete for diverse resources, such as cavities, food or mates. In passerines, an important function of vocalizations is in territoriality and repelling rivals (Searcy and Andersson 1986, Brumm and Todt 2004, Collins 2004). While in oscine passerines (Suborder Passeri) the male is generally the singer, in suboscine species (Suborder Tyranni) both sexes usually sing (Catchpole and Slater 2008). In some groups of passerine birds, such as tropical forest birds, both male and female defend their territories (Cooney and Cockburn 1995), even though males are commonly more aggressive than females (Fedy and Stutchbury 2005).

Behavior, like other phenotypic characteristics, often exhibit geographic variation (Foster 1999). Predators, predation pressure and intensity of resource competition are not constant along distribution range of species, resulting in changes of antipredator (Berger 1998, Stoks et al. 2003) and territorial behavior (Baker 1994). For example, in insular populations where large carnivores are commonly absent, birds can lose the ability to recognize predators. This can leave the populations highly vulnerable when exotic predators arrive or when extinct predator are reintroduced (Martinez-Morales and Cuaron 1999, Cuthbert and Hilton 2004). Beyond the conservation implications, studies about geographic variation of different aspects of behavior can help us understand behavioral microevolutionary change and, ultimately, speciation (Foster 1999). Because defense behavior plays a key role in breeding success, and those behaviors ultimately have fitness costs, I predict that when selection pressure is relaxed, behavior can lose its intensity and, finally, it may disappear. Time required for this process will depend of costs (Blumstein 2006) and the mechanism that underline such behavior (Hollén and Manser 2007).

The Thorn-tailed Rayadito or Rayadito (*Aphrastura spinicauda;* Furnariidae) is a suboscine passerine, endemic to the temperate forests of Chile and Argentina that occurs from Fray Jorge National Park (30°S) in central Chile to Sub-Antartic forests of Cape Horn (56°S) (Johnson and Goodall 1967, Remsen 2003, Rozzi 2003). The Rayadito is a small insectivorous non-migratory bird, that nests in tree cavities and forages in single- or mixed-species flocks in winter (Vuilleumier 1967, Grigera 1982, Ippi and Trejo 2003). Males and females have no difference in parental care (Moreno et al. 2007) and both parents defend their territory with loud and repetitive calls and trills (S. Ippi pers. obs.).

The wide latitudinal range distribution of the Rayadito makes it an excellent subject to study interpopulation differences in defense behavior in different and distant types of forested habitats and its relationships among the strategies to confront different threats, such as adult predators, nests predators or conspecific rivals. Moreover, the geography of temperate austral forests in Chile allows testing defense behaviors in populations with different histories of predator presence, to ascertain how their behavior has changed across populations and how the species respond to novel predators. I tested these ideas in three Chilean populations: Navarino Island (Austral Chile), where Rayaditos have no native mammalian predators, and in Chiloé Island (Southern Chile) and Cerro Manquehue (Central Chile), two populations where rayaditos live sympatrically with diverse mammalian predators, including some species inhabiting both populations.

This study focused on the three different defense behaviors mentioned earlier and their possible geographic variation. Specifically, through experimental manipulation, I examined whether Rayaditos 1) respond differently to an avian adult predator *versus* a mammalian nest predator; 2) express nest defense behavior in populations where nest predators are absent; 3) express territorial defense during egg laying stage; 4) express variation in the three types of defense behavior across the three populations; and 5) express a relationship among the different components of defense behavior. Additionally, I tested if male and female defense behaviors are distinct and if different vocalization were used with different stimuli.

Methods

Study area

Field work was conducted in three populations, in the austral spring (September-January), in Chiloé Island (2006 and 2007), Navarino Island and Manquehue (2007). Since 2002, 600 nest boxes have been installed in these populations (300 in Chiloé, 200 in Navarino and 100 in Cerro Manquehue) (see Moreno et al. 2005), for nest boxes details).

Navarino Island (54°S and 67°W) Navarino Island is located 5 km south of Isla Grande de Tierra del Fuego, in the Cape Horn Biosphere Reserve. Vocalizations were recorded at the Omora Etnobothanical Park, located 3 km west from Puerto Williams, and predator' experiments were conducted in the adjacent and similar but more disturbed forest, 1-2 km from de park. Both locations are dominated by the Magellanic Sub-Antartic forests that include 3 species of *Nothofagus* (*N. pumilio, N. antarctica* and *N. betuloides*) and scarce shrubs of *Berberis spp* (Anderson and Rozzi 2000). There is some degree of anthropic disturbance including pasture for cattle and horses. Precipitation in the area reaches approximately 450 mm per year, with snow in winter, mean relative humidity is 84 % and the mean annual temperate is 6°C (Hajek and di Castri 1975).

The avian forest assemblage includes approximately 29 species, 8 of which are raptor species and 18 are passerines (Ippi et al. 2009; Appendix I). No detailed counts of raptors have been conducted in this place at present. Additionally, no amphibian or reptilian species have been described at this latitude.

Chiloé Island (41°S and 73°W) Chiloé is an island located 2–5 km from the mainland. Nest boxes were placed in two large forest blocks, Senda Darwin Biological Station and Fundo "Los Cisnes", at the northern tip of the island. Vocalizations were recorded in the same study area. Both study sites include large fragments of regenerating evergreen forests of *Drimis winteri*, *Nothofagus nitida*, and several myrtaceous species (Aravena et al. 2002), surrounded by an agricultural landscape (Willson and Armesto 1996). The understory included dense *Chusquea* spp. (bamboo) thickets and tree saplings. Precipitation reaches 2097 mm per year and the mean annual temperature is 10.0°C (Carmona et al. in prep.). The mean relative humidity is 82 % (data from Castro, Chiloé; Hajek and di Castri 1975).

Forest bird assemblage includes 38 species of which 22 are passerine and 13 are raptor species, excluding aquatic and semi-aquatic species (Rozzi et al. 1996a; Appendix I).

<u>Cerro Manquehue</u> (33°S and 70°W) Cerro Manquehue is located at the northeastern of the Santiago city close to the north coast of the Mapocho river. Nest boxes were located at *Granja Educativa Manquehue* at the west slope of the mountain. Fragments of sclerophyllous forests at Cerro Manquehue are remnants of a large extension of forests dominated by *Cryptocarya alba* and scarce understory. Recreational and educational activities are periodically conducted inside the farm. The climate is Mediterranean with a mean annual precipitation of 356 mm, a mean relative humidity of 72 % and mean temperature of 13.9°C (Hajek and di Castri 1975).

No detailed census exists in this forest, but some reports indicate that a total of 32 species of birds could be found in the area, with 14 passerine birds, and 12 birds of prey (Chicharro et al. 2007, Armesto et al. 2008; Appendix I).

General Protocol

Nest boxes were monitored weekly starting in September at Cerro Manquehue and in October in Navarino and Chiloé Islands. When I detected nesting material in nest boxes, I increased the frequency of nest visitation in order to detect the date of first egg laying. Adults captures (one or both adults at each nest) occurred on the date of the first egg. I captured Rayaditos with mist nets and playback from the commercial compact disc *Voces de Aves Chilenas* (Unión de Ornitólogos de Chile), and banded each animal with a unique combination of colored rings and a numbered metal band (National Band and Tag, Co., Newport, KY, model 1242–3) under the authority of *Servicio Agrícola y Ganadero* (Chile Agricultural and Livestock Service). I took a small sample of blood by brachial venipuncture and stored samples on FTA® cards for DNA preservation (Gutiérrez-Corchero et al. 2002) to allow genetic sex determination analysis, because sexes are similar in color and morphology, and therefore, difficult to distinguish them in the field (see Moreno et al. 2007). Rayaditos were released immediately after they were sampled, and the total time of manipulation never exceeded 3–4 minutes. Breeding cycles were apparently not disturbed by this first capture, except in the two cases where adult pairs abandoned the nest, although one pair of these successfully re-nested in a neighboring nest box shortly afterwards.

All trials were conducted between 6:50 and 13:00 h. Models were mounted on top of each nest box at Navarino and Manquehue. Because nest boxes in Chiloé experienced a very high predation rate by the marsupial Monito del monte (*Dromiciops gliroides*), I installed a metal bell-like structure above the nest boxes to increase the difficulty for mammalian predators. Therefore, I placed the model predators on a telescopic pole at the same distance from the nest box in this population only (i.e. 0.2 m from the entrance, approximately). All experiments were recorded using video cameras (Panasonic NV-GS 320) coupled with personal observations of activities recorded with a digital audio recorder (Olympus VN-960PC). To prevent damage to the models, all experiments were stopped when physical aggressions by focal animals to the model exceeded five pecks.

During the egg laying period, Rayaditos do not visit the nest frequently, thus playback of repetitive trills were used to attract them to the nest boxes. In contrast, Rayaditos visit their nests very frequently when chicks are 4–6 days old (10–12 times/hour with 3 days old chicks, see Moreno et al. 2007), making more difficult the installation of predator models and video camera without disturbing their normal behavior. Therefore, although latency (i.e., time taken before the first response by the focal bird) is a commonly used variable to measure caution in antipredator and territorial experiments (see for example, Dunn et al. 2004, Fedy and Stutchbury 2005, Stenhouse et al. 2005, among others) I excluded this variable from the analyses and waited 2 minutes after installation of stimuli, before starting behavioral recordings. Nevertheless, some Rayaditos responded aggressively to the stimulus before 2 minutes, with more than five pecks in a few seconds; in these cases, I included these trials in the analyses.

Territorial and antipredator experiments were controlled with a male of Rufous-collared Sparrow or Chincol (*Zonotrichia capensis*). The Chincol (20–23 g) is an open-cup nesting passerine, principally granivorous (Grigera 1976, López-Calleja 1995, Mezquida 2003, Willson et al. 2005). Because, to our knowledge, Chincols do not represent a threat nor a strong competitor of any kind, I considered the reaction of the subject to this stimuli to represent a baseline aggressive response (other studies have also used a similar non-interacting species as control stimuli; see e.g., Dunn et al. 2004, Stenhouse et al. 2005, Duckworth 2006).

Territoriality experiments

I measured aggressive behavior toward Rayadito males (hereafter referred to as territorial defense behavior) conducting trials with taxidermic mounts of a Rayadito male (treatment) and a Chincol male (control). Experiments were conducted on successive days, except in case of rain, strong wind or snow, starting at day 2 after laying the first egg. Because females are fertile during the laying stage, male aggression toward conspecific males, should be maximized due to mate guarding (Duckworth 2006). The total time of experimentation was 12 minutes, with the first 2 minutes without observations to avoiding human interference in behavior of birds, the next 5 minutes of playback of repetitive trill of one Rayadito, and the last 5 minutes of silence. Mounts were presented at random.

Rayaditos have at least four different vocalizations: alarm mobbing calls, contact calls, loud trills and repetitive trills (for more details see Chapter 2). Through previous field observations, I suspected that repetitive trills have a territorial and/or mate attracting function, because Rayaditos sing this song-type more frequently in the late winter season and during the breeding season. Furthermore, it is relatively common that repetitive trills from one individual cause a similar response from another individual, a behavior which can be interpreted as a sex duets or male-male challenges. In suboscine birds sex duets of songs are common (del Hoyo et al. 2003), but no information exist about this subject in Rayaditos. I selected this type of vocalization to conduct territorial experiments in order to quantify about male and female vocal responses. Playbacks for these experiments were obtained in each population with a digital recorder (Sony PCM-M1) and a Sennheiser ME 66 microphone, with a sampling rate of 48 kHz. Repetitive trills from three different individuals from each population were edited with Cool Edit Pro 2.0, extending the playback period for five minutes and deleting noise and other low frequencies. These songs were selected randomly in each trial. Repetition rate of trills varied between 4.2 trills/min and 22.0 trills/min (17.1 trills/min on average), which was in the common range of this type of song (see chapter 2). Both males and females sing repetitive trills and, due to difficulties in field sex determination, I could unfortunately, not assure that playbacks were always of male Rayadito trills. This potential inconsistency may influence the response of each sex during experiment. Playbacks of three Chincols song were obtained from each population and edited in a similar way, except for Chiloé, where I used only one song obtained for a commercial compact disc *Voces de Aves Chilenas* (Unión de Ornitólogos de Chile).

Antipredator experiments

To document antipredator behavior toward an adult- and a nest-predators, I conducted experiments with stuffed mounts of (i) an avian predator, the Austral Pygmy Owl or Chuncho (*Glaucidium nanum*; 70–80 g), a common diurnal predator of juvenile and adults birds (hereafter referred to as antipredator defense behavior), (ii) a mammalian nocturnal and/or crepuscular nest predator, the Monito del Monte (*Dromiciops gliroides*; 20–40 g), a predator of eggs and chicks (hereafter referred to as nest defense behavior), and (iii) a control, the Chincol. The Chuncho and the Chincol are present in the all three study areas, while the Monito del monte is only found at the Chiloé site, although in Cerro Manquehue there is another marsupial predator, the Yaca (*Thylamys elegans*) which is very similar to the Monito in morphology, size and diet (Redford and Eisenberg 1992, Palma 1997, Muñoz Pedreros and Yañez Valenzuela 2000). I assumed that birds would react in the same way in the face to the Monito and the Yaca, due to an integrated predator recognition system (Curio 1973 in Blumstein 2006). Trials were conducted when chicks were 4 days old. Mounts were presented in successive days (weather permitting) and the order of control and each treatment was chosen randomly. Trials consisted of 2 minutes of habituation (to avoid the Rayaditos' response to previous human disturbance) and 10 minutes of behavioral observations and records of vocalizations (no playbacks were used in this experiment).

Data analyses

From the recordings of behaviors, I used the software JWatcher 1.0 (Blumstein et al. 2000) to extract the data and produce the ethograms (sequence of behaviors during the 10 minutes recordings). Dependent variables measured were: number of times the focal individual pecked the mount, average distance to the mount (m), minimum distance (m), proportion of time spent within 2 m around the mount, and proportion of time performing mobbing alarm calls. In the territorial experiments, variables included proportion of time performing repetitive trills and number of loud trills during the experimental period. In the antipredator experiments, I also measured the proportion of time inside the nest and proportion of time spent searching for food or eating. Because some trials were stopped before the 10 minutes, I standardized all the measurements to the total experimentation time of each trial. I included all the experiments in the analyses, including those which one or both parents have been absent because I considered that the absence is another aspect of defense behavior.

Because trials were conducted in two consecutive years (2006 and 2007) in Chiloé, I excluded from the analyses those nest boxes with Rayaditos observed more than once. Therefore, each male and female was tested only once and observations were independent.

Principal component analysis (PCA) was performed on the data set of all trials, and three principal components (PC) were extracted. There are no distributional assumptions associated with the descriptive use of PCA (Quinn and Keough 2002), and therefore I used this analysis to reduce the number of variables. Because normality was not obtained for scores of these PC (Shapiro Wilks test; $P < 0.05$), I used non parametric tests. Differences between males and females were analyzed with non parametric Wilcoxon signed ranks test and a Mann-Whitney U tests were performed on the 2006 and 2007 data from Chiloé (Siegel and Castellan 1988). When no difference existed between males and females, I pooled all data for comparisons. Differences in behavior among the three populations were analyzed with a Kruskal Wallis test and differences among the models were analyzed with a Wilcoxon signed rank test (2 stimuli) and a Friedman Anova by ranks (3 stimuli) (Siegel and Castellan 1988). Bivariate non parametric correlations were also conducted between pairs of different behaviors and Spearman rho coefficients were calculated, in order to know the nature of the relationship between them. All statistical analyses were conducted with SPSS 13.0 for Windows.

Results

Territorial experiments were conducted in Chiloé (nine experiments in 2006 and 15 in 2007), Manquehue (15 in 2007) and Navarino (10 in 2007). Thirty one anti-predator experiments were conducted in Chiloé (13 in 2006 and 18 in 2007, respectively), 13 at Manquehue and 12 in Navarino, both in 2007. However, in Chiloé some Rayaditos were tested in both years. I therefore excluded these nests from the analyses to test only the first time that experiments were conducted. Therefore, in Chiloé 21 nests accounted for territorial experiments (nine in 2006 and 12 in 2007) and 26 for anti-predator experiments (10 in 2006 and 16 in 2007).

Territorial defense behavior during laying

In all three populations, both females and males generally responded to the Rayadito and Chincol models (Table 1), although females never (except in one case) responded without the presence of their mates. However, this fact does not mean that the first response always was produced by the male; males responded first in 30 trials, females in 23 cases, and in 3 experiments both parents responded simultaneously (N = 56 trials with responses by both parents, pooling Chincol and Rayadito together). In summary, stimuli did not elicit any response for the breeding pair in almost 14 % of the total trials with Rayadito and in 21 % of the total trials with Chincol.

The percentage of individuals that pecked the model was low; 9.9 % of the females and 27.3 % of the males pecked the Chincol (N = 44) while the 14.0 % of females and 32.6 % of the males pecked the Rayadito model (N = 43). Loud and repetitive trills were recorded in low proportion and repetitive trills were not recorded in Navarino, excepting for males responding to a male conspecific intruder. At Manquehue, repetitive trills were used by males responding to Rayadito and females responding to Chincol. Rayaditos did not enter into the nest boxes during trials and they fed or searched food in a very low proportion (See the appendix II for the mean values of the variables).

Table 1. Presence/absence of one or two parents during territorial experiments in each population, during the breeding season.

Population	Experiment (model)	Both parents present (%)	Only female present (%)	Only male present (%)	No parent present (%)	Total nests
Navarino	Rayadito	70.0	0.0	20.0	10.0	10
	Chincol	80.0	0.0	20.0	0.0	10
Chiloé	Rayadito	71.4	4.8	9.5	14.3	21
	Chincol	57.1	0.0	28.6	14.3	21
Manquehue	Rayadito	76.9	0.0	7.7	15.4	13
	Chincol	38.5	0.0	15.4	46.2	13
Total	Rayadito	72.7	2.3	11.4	13.6	44
	Chincol	56.8	0.0	22.7	20.5	44

Analyses of territorial defense behavior

PCA was conducted on seven variables that resulted in three PC that explained 83 % of the variance (Table 2). All three PC were correlated positively with aggressive and territorial behavior (Table 2). Although scores of PCA were always higher in males, only PC1 was significantly different between males and females after sequential Bonferroni corrections (Wilcoxon signed ranks test; PC1: $Z = -4.257$; $p < 0.001$; PC2: $Z = -1.390$; $p = 0.165$; PC3: $Z = -1.208$; $p = 0.227$; $N = 87$). However, since PC1 explained the highest percentage of variance, the following analyses were performed separately.

Table 2. Factor loadings of the first three principal components for the seven variables of territorial behavior. Factor loadings values correspond to Varimax with Kaiser normalization rotation method.

	PC1	PC2	PC3
Eigenvalues	3.42	1.28	1.15
% of variance	48.71	18.27	15.94
Cumulative % of variance	48.71	66.98	82.92
Factor loadings			
Average distance	–0.929	–0.187	–0.149
Minimum distance	–0.819	–0.111	–0.222
Time spent around 2 m	0.834	0.307	–0.103
Rate of pecks	0.089	0.886	–0.095
Proportion of time alarming	0.849	0.025	–0.265
Rate of loud trills	0.238	0.863	0.110
Proportion time of repetitive trills	0.010	–0.004	0.971

There were no differences between year 2006 and 2007 from Chiloé after sequential Bonferroni corrections (Mann-Whitney U test; Females, PC1: U = 164; p = 0.180; PC2: U = 165; p = 0.188; PC3: U = 169; p = 0.225; Males, PC1: U = 148; p = 0.083; PC2: U = 201; p = 0.702; PC3: U = 132; p = 0.032; N = 42), and therefore, I pooled data for both years.

There were no differences in male and females behavioral responses toward both models among the three populations (Table 3) excepting for PC2, when faced with the Chincol model. Males pecked less and emitted less loud trills in Chiloé than Navarino and Manquehue, and females pecked less and emitted less loud trills in Chiloé and

Table 3. Kruskal Wallis tests assessing if the three populations of Navarino, Chiloé and Manquehue differ for each PC variable, in territorial experiments, during laying stage. * = significant test after sequential Bonferroni corrections.

		Female PC1	Female PC2	Female PC3	Male PC1	Male PC2	Male PC3
Both models	χ^2	2.51	3.42	6.84	9.18	11.71	3.81
	p	0.28	0.18	0.03	0.01	0.003 *	0.15
	N	87	87	87	87	87	87
Rayadito	χ^2	0.64	0.47	5.17	2.27	6.26	0.54
	p	0.73	0.79	0.07	0.32	0.04	0.76
	N	43	43	43	43	43	43
Chincol	χ^2	4.88	12.05	7.99	7.93	12.31	3.96
	p	0.09	0.002 *	0.02	0.02	0.002 *	0.14
	N	44	44	44	44	44	44

Navarino, compared to Manquehue (Fig. 1a-c). Overall, Chincol and Rayadito models were attacked more in Manquehue, for males and females, although I only detected a significant difference for trials using Chincol mounts (Table 3 and Fig. 1b).

Because differences among the three populations were minimal (only PC2 for Chincol model), I pooled the data from the three populations to analyze behavioral response when Rayaditos were confronted with Rayadito and Chincol male models. Rayaditos, males and females, behaved similarly when facing Rayadito and Chincol males (Table 4 and Fig. 1a-c). However, although differences were not significant, male PC2 responses (correlated with number of pecks and number of loud trills), was higher toward to Rayadito mounts compared to Chincols, but this was not always the case in females PC2 responses (Fig. 1b).

Table 4. Wilcoxon signed rank tests assessing if the responses to both estimuli (Chincol and Rayadito males) differ for each PC variable, in all three pooled populations. * = significant test after sequential Bonferroni corrections.

	Female PC1	Female PC2	Female PC3	Male PC1	Male PC2	Male PC3
Wilcoxon Z	−2.76	−0.73	−1.12	−1.08	0.46	−0.16
p	0.006*	0.464	0.261	0.279	0.648	0.876
N	42	42	42	42	42	42

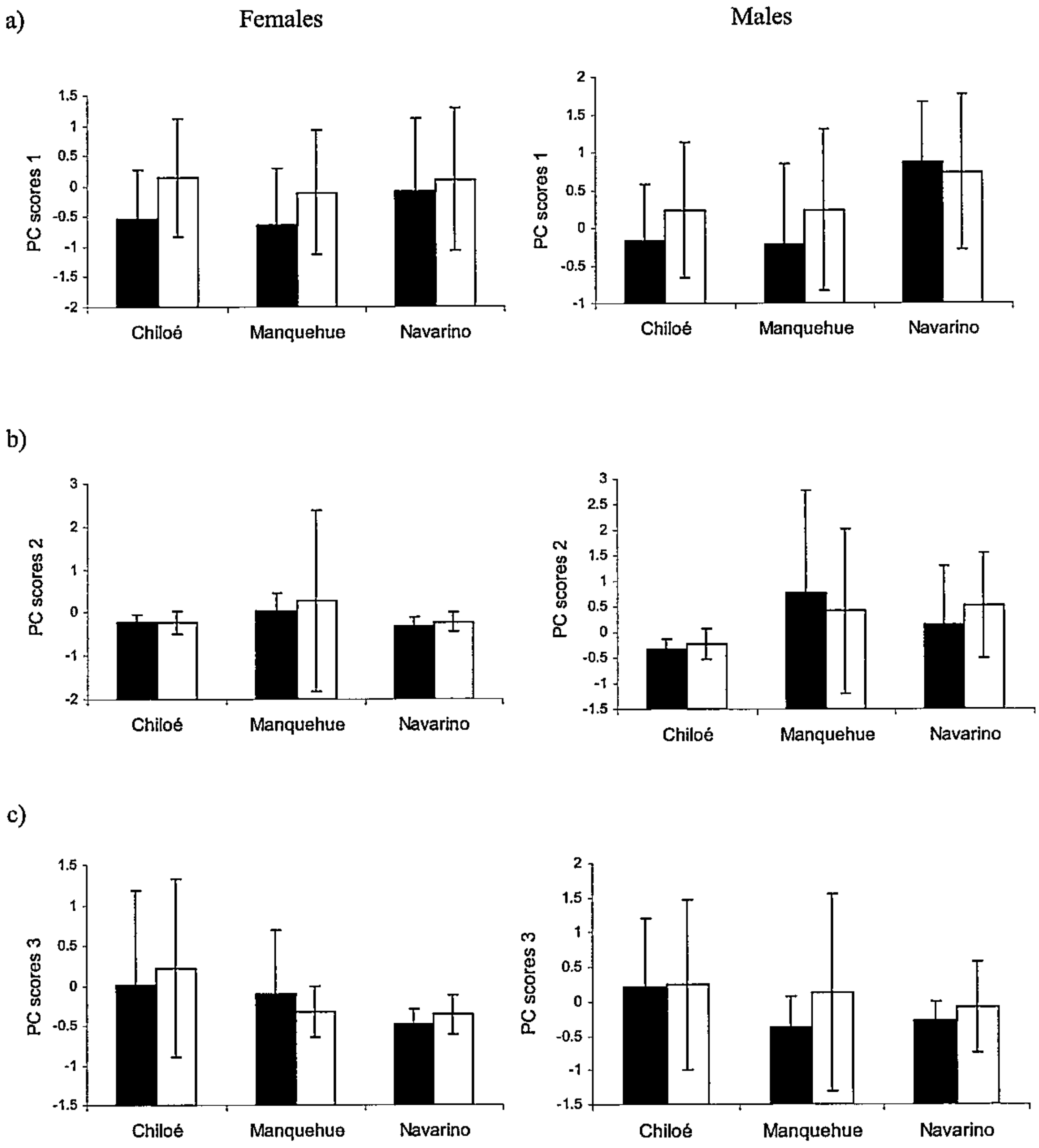


Fig. 1. Principal component scores (a=PC1; b = PC2, c=PC3) for territorial behavior of Rayaditos when facing a Rayadito (open columns) and a Chincol male models (black columns) in Navarino, Chiloé and Manquehue. Data are means ± SD.

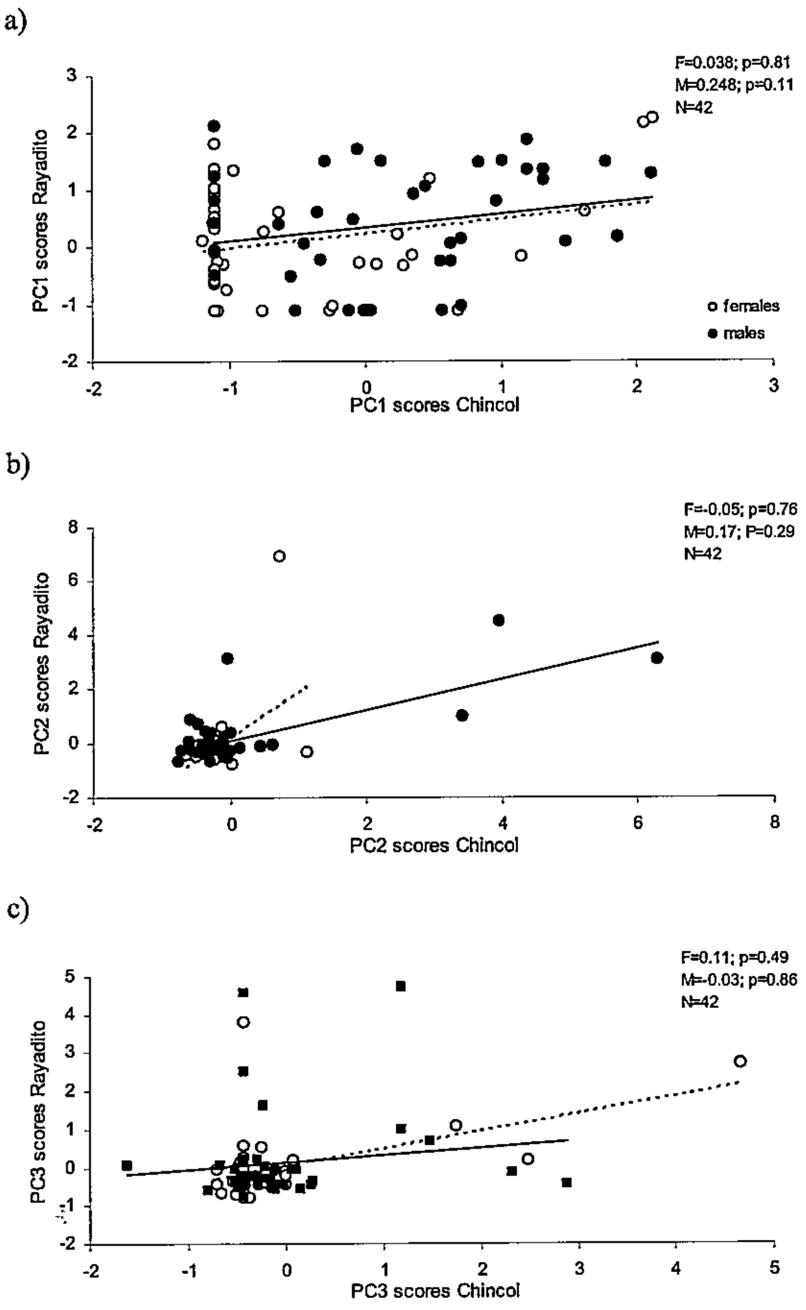


Fig. 2. Correlations between PC scores obtained for behavior of male and female Rayaditos facing the Rayadito and the Chincol models (a=PC1; b = PC2, c=PC3). Each data point represents a different individual from the three studied populations (Navarino, Chiloé and Manquehue). F and M indicate the Spearman's rho correlation coeficient for females and males, respectively. Continuous (male) and broken (females) lines correspond to correlation functions.

Relationships between territorial defense behaviors

In order to assess the relationship between territorial defense toward a conspecific male and a different species of passerine, I conducted non-parametric correlations between each PC for Chincol and Rayadito responses. No relationship was found between behaviors when facing both stimuli for any PC, nor for males or females pooling data from the three populations (Fig. 2). Because no correlation was significant analizing populations separately, after sequential Bonferroni corrections, statistics are no shown.

Antipredator and nest defense behaviors during nestling stage

Males and females of Rayaditos responded in almost all the antipredator trials conducted during nestling stage. Generally, both parents were present during the experiments in all three populations (Table 5).

In the three populations, Rayaditos entered to the nest boxes in presence of the Monito, but only in Chiloé when were in presence of the Chincol. In Navarino, Rayaditos did not search for food nor eat when stimuli were present, in contrast to the other two populations where they fed in the presence of the Monito and Chincol (See the appendix III for the mean values of the variables).

Table 5. Presence/absence of one or two parents during antipredator behavior experiments in each population, during the breeding season.

Population	Experiment (model)	Both parents present (%)	Only female present (%)	Only male present (%)	No parent present (%)	Total nests
	Chuncho	90.9	9.1	0.0	0.0	11
Navarino	Monito del monte	81.8	18.2	0.0	0.0	11
	Chincol	100.0	0.0	0.0	0.0	10
	Chuncho	88.5	3.8	3.8	3.8	26
Chiloé	Monito del monte	96.2	3.8	0.0	0.0	26
	Chincol	92.3	0.0	7.7	0.0	26
	Chuncho	90.9	9.1	0.0	0.0	11
Manquehue	Monito del monte	81.8	9.1	9.1	0.0	11
	Chincol	66.7	8.3	16.7	8.3	12
	Chuncho	89.6	6.3	2.1	2.1	48
Total	Monito del monte	89.6	8.3	2.1	0.0	48
	Chincol	87.5	2.1	8.3	2.1	48

Analyses of antipredator and nest defense behaviors

PCA were performed on six variables (Table 6). I obtained three PC that explained 85 % of the total variance (Table 6). The first PC was interpreted as *submissive* behavior, because higher PC1 values corresponded to less aggressive responses; the second PC was correlated with the time spent inside the nest. Finally, the third PC corresponds to *foraging* behavior, because their variance is explained by the time that Rayaditos spent eating or looking for food, during the experiments. All the following analyses were conducted with the three new variables.

Because no differences between males and females were found (Wilcoxon signed rank test; PC1: $z = -0.924$; $p = 0.356$; PC2: $z = -0.539$; $p = 0.590$; PC3: $z = -0.148$; $p =$

Table 6. Factor loadings on the first three principal components for the six variables of antipredator behavior. Factor loadings values correspond to Varimax with Kaiser normalization rotation method.

	PC1	PC2	PC3
Eigenvalues	2.81	1.23	1.05
% of variance	46.86	20.50	17.51
Cumulative % of variance	46.86	67.36	84.87
Factor loadings			
Average distance	0.942	0.023	–0.040
Minimum distance	0.767	–0.128	–0.147
Time spent around 2 m	–0.891	–0.023	–0.185
Proportion of time alarming	–0.691	–0.583	–0.200
Proportion of time inside the nest	–0.107	0.954	–0.079
Proportion of time searching food/eat	0.001	–0.034	0.981

0.883; N = 144), I pooled the data from both sexes in the following analyses. Moreover, no differences existed between antipredator experiments from year 2006 and 2007 in Chiloé for the three PC (Mann-Whitney U test; PC1: U = 303.00; p = 0.749; PC2: U = 297.00; p = 0.665; PC3: U = 270; p = 0.347; N = 52), therefore I analyzed both years together.

Behavioral responses to Chuncho expressed by PC1 and PC2 were different in the three populations (Table 7). Figure 2a shows that PC1 (submissive PC) is lowest in Navarino. Nevertheless, and contrary to the expectations, there were no significant differences among Rayaditos' behavior when confronted with the Monito del monte (antipredator nest defense) among populations for any PC (Table 7). Responses to Chincol were more complex, because two PC were not different among populations

(PC1 and PC3), but for PC2, there were very significant difference among populations (Table 7).

Behavioral responses to different type of predators and to the control were significantly different after sequential Bonferroni correction when analyzing all regions together (Table 8) and, also, in each region separately. In Chiloé and Manquehue, PC1 represented the same pattern, being highest for the Chincol, intermediate for the Monito and smallest for Chuncho while PC2 and PC3 were smallest for Chuncho and higher for Monito (Fig. 3). In Navarino, the situation was slightly different, because, PC1 was highest for the Monito, and lowest for the Chuncho. In a subsequent analysis, excluding Chuncho, I failed to detect any difference between the Monito and the Chincol in all three PCs in each population, separately (Table 9), even though a tendency for more pecks to Chincol in Manquehue was observed.

Table 7. Kruskal Wallis tests assessing if the three populations of Navarino, Chiloé and Manquehue differ for each PC variable in the antipredatory experiments, during nestling stage. * = significant test after sequential Bonferroni corrections.

		PC1	PC2	PC3
Chuncho	Kruskal-Wallis χ^2	14.56	16.88	9.11
	p	0.001 *	< 0.001 *	0.011
	N	98	98	98
Monito del monte	Kruskal-Wallis χ^2	0.87	3.17	6.42
	p	0.65	0.20	0.04
	N	98	98	98
Chincol	Kruskal-Wallis χ^2	6.45	17.10	4.91
	p	0.04	< 0.001 *	0.086
	N	98	98	98

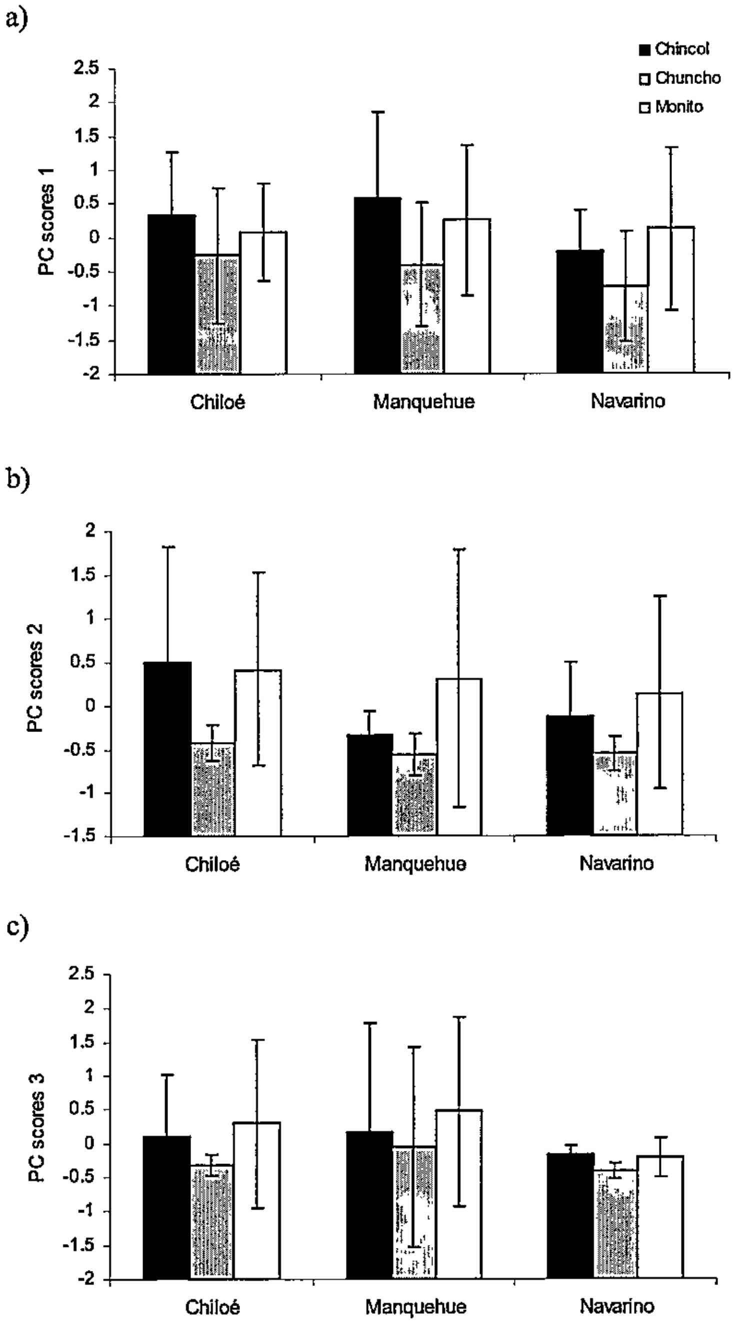


Fig. 3. Principal component scores (a=PC1; b = PC2, c=PC3) for antipredator behavior of Rayaditos in Navarino, Chiloé and Manquehue. Data are means ± SD.

Table 8. Statistics for non-parametric Friedman anova by ranks tests assessing if the responses to two predators (Monito and Chuncho) and a control (Chincol), differ for each PC variable, in each population, during nestling stage. * = significant tests after sequential Bonferroni corrections.

		PC1	PC2	PC3
All three populations	Friedman χ^2	34.85	68.12	46.91
	p	<0.001*	<0.001*	<0.001*
	N	94	94	94
Manquehue	Friedman χ^2	14.61	17.95	5.49
	p	0.001*	<0.001*	0.064
	N	20	20	20
Chiloé	Friedman χ^2	12.50	51.04	29.54
	p	0.002*	<0.001*	<0.001*
	N	52	52	52
Navarino	Friedman χ^2	10.92	7.88	17.03
	p	0.004*	0.02*	<0.001*
	N	22	22	22

Table 9. Statistics for Wilcoxon signed rank test between of Rayaditos responses when facing to Monito del monte and Chincol in each population, during nestling stage. No test was significant after sequential Bonferroni correction.

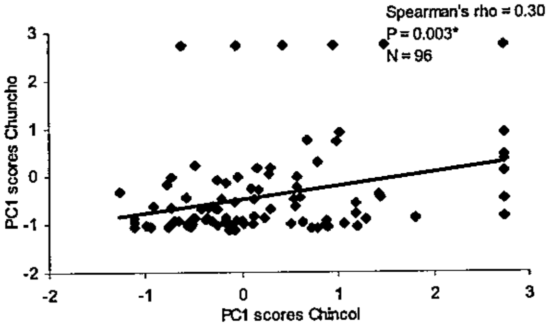
		PC1	PC2	PC3
Manquehue	Wilcoxon Z	–0.93	–2.13	-1.68
	p	0.351	0.033	0.093
	N	20	20	20
Chiloé	Wilcoxon Z	–1.08	–0.45	–0.32
	p	0.278	0.649	0.750
	N	52	52	52
Navarino	Wilcoxon Z	–0.79	–0.57	–0.63
	p	0.426	0.570	0.527
	N	22	22	22

Relationships between antipredator and nest defense behavior

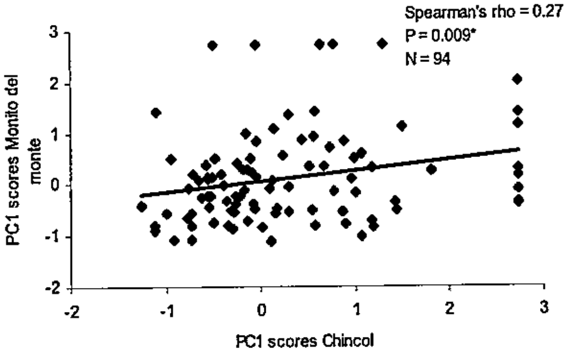
In order to assess the existence of relationships among antipredator nest defense behavior (Monito), antipredator behavior (Chuncho) and control behavior (Chincol), I performed non-parametric bivariate correlations with the three PCs. In general, associations were weak (range of Spearman rho = –0.11 – 0.33), and significant correlations were positive. Correlations between the first PC in response to each stimulus were significant, even after Bonferroni corrections, with the exception of the relation between responses to the Monito del monte and the Chuncho (Fig. 4). Correlations for PC2 (time inside the nest component) were only significant for the relation between the response to the Chuncho and the Chincol. No significant correlations for PC3 were detected (Fig. 3). Data for the analyses of populations separately are not shown, because there were no significant relationships in Manquehue and Navarino Island and, in Chiloé only PC2 were correlated between responses to the Monito and the Chincol, after sequential Bonferroni corrections.

The first PC in territorial experiments and antipredator/nest defense experiments explain mainly the variation in distance and alarm calls. Thus, it can be interpreted as an aggressive component variable (although in the case of antipredator experiments, PC1 was interpreted as submissive behavior because the sign was inverse). In order to assess the relationship between aggressiveness in territorial defense, nest defense and antipredator defense, I conducted non parametric correlations between pairs of these behaviors (Table 10). No relationship between pairs of behaviors was found, for males and females. Because no correlation was significant analizing populations separately, after sequential Bonferroni corrections, statistics are not shown.

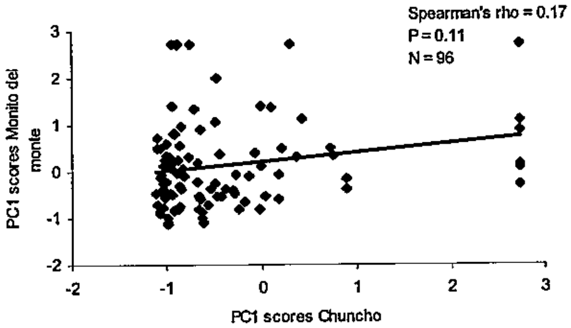
a)


Spearman's rho = 0.30
P = 0.003*
N = 96
PC1 scores Chuncho
PC1 scores Chincol
3
2
1
0
-1
-2
-2
-1
0
1
2
3

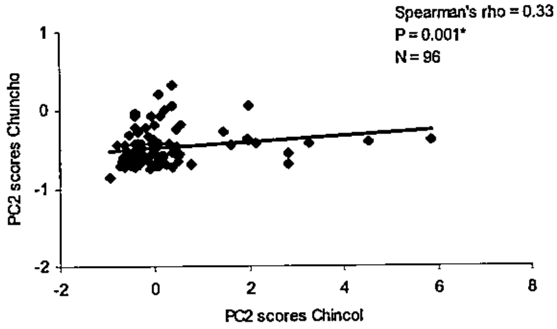
b)


Spearman's rho = 0.27
P = 0.009*
N = 94
PC1 scores Monito del monte
PC1 scores Chincol
3
2
1
0
-1
-2
-2
-1
0
1
2
3

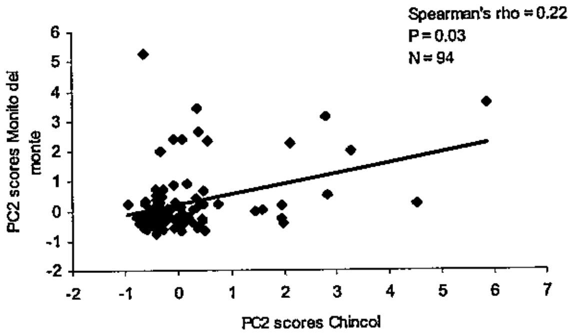
c)


Spearman's rho = 0.17
P = 0.11
N = 96
PC1 scores Monito del monte
PC1 scores Chuncho
3
2
1
0
-1
-2
-2
-1
0
1
2
3

d)


Spearman's rho = 0.33
P = 0.001*
N = 96
PC2 scores Chuncho
PC2 scores Chincol
1
0
-1
-2
-2
0
2
4
6
8

e)


Spearman's rho = 0.22
P = 0.03
N = 94
PC2 scores Monito del monte
PC2 scores Chincol
6
5
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-2
-1
0
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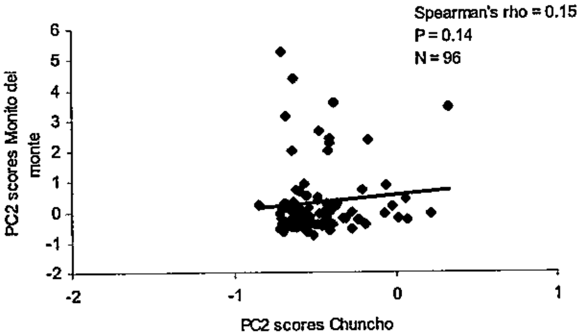
7

f)


Spearman's rho = 0.15
P = 0.14
N = 96
PC2 scores Monito del monte
PC2 scores Chuncho
6
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4
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-2
-2
-1
0
1

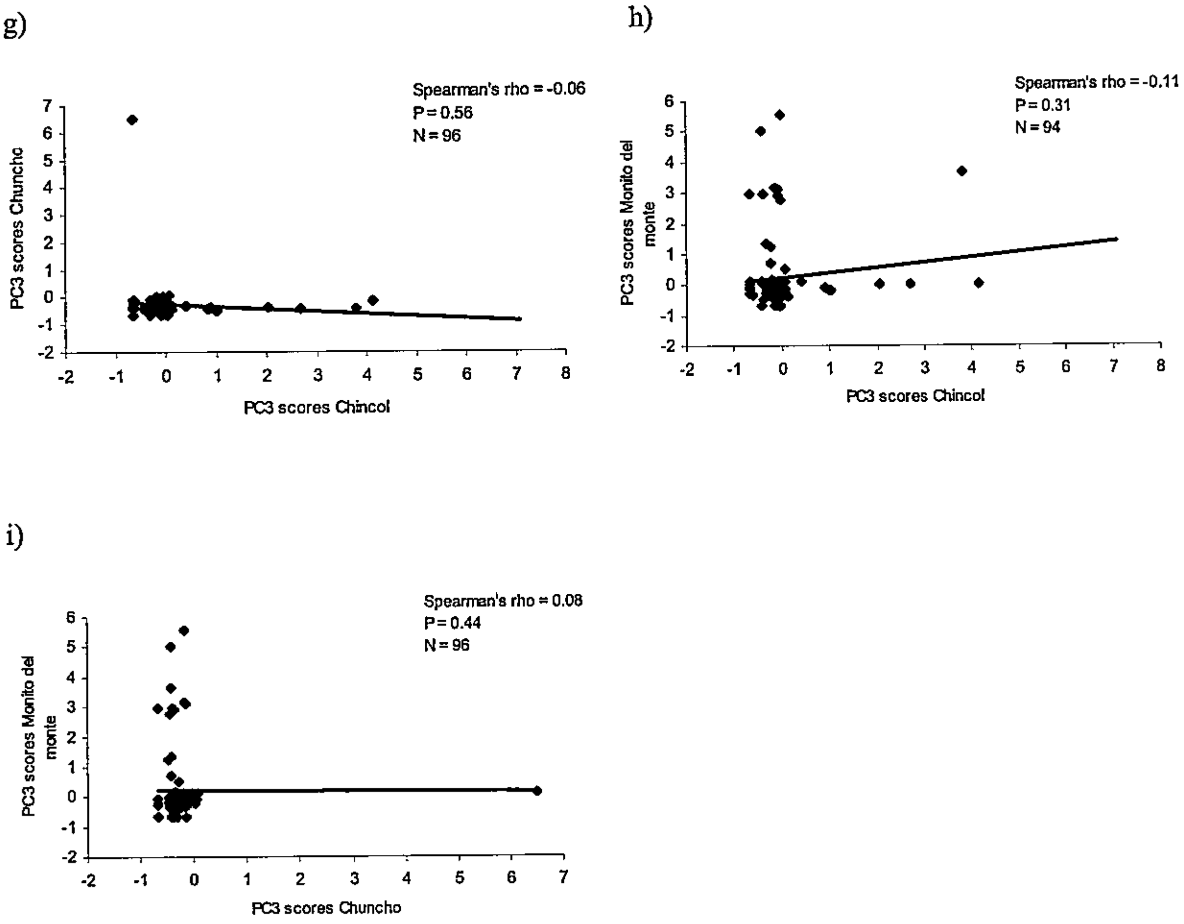

Fig. 4. Correlations between PC scores obtained for behavior of Rayaditos facing the three stimuli (Chuncho, Monito del monte and Chincol). Each data point represents a different individual. The three populations were analyzed all together. * = significant test after sequential Bonferroni corrections.

Table 10. Non-parametric correlations on the first PC extracted from behaviors during territorial experiments (Chincol 1 and Rayadito), antipredator (Chuncho) and nest defense (Monito del monte) experiments, including control (Chincol 2) in all three populations. No significant tests were found after sequential Bonferroni corrections.

		Spearman's rho	p	N
Females	Chincol 1 - Chincol 2	–0.147	0.41	33
	Chincol 1 - Chuncho	–0.132	0.47	32
	Chincol 1 - Monito del monte	–0.103	0.58	32
	Rayadito - Chincol 2	0.118	0.51	33
	Rayadito - Chuncho	0.157	0.39	32
	Rayadito - Monito del monte	–0.193	0.29	32
Males	Chincol 1 - Chincol 2	–0.234	0.18	34
	Chincol 1 - Chuncho	–0.360	0.04	33
	Chincol 1 - Monito del monte	–0.408	0.02	33
	Rayadito - Chincol 2	0.038	0.83	34
	Rayadito - Chuncho	–0.133	0.46	33
	Rayadito - Monito del monte	–0.360	0.04	33

Discussion

General description of behavior

1) Territorial defense during laying

Territorial behavior of male and female Rayaditos was similar, although time spent close to the intruder and time spent alarming were higher for males. This result is in accordance with other studies where males responded more vigorously than females (Bard et al. 2002), especially in response to male intruders (Fedy and Stutchbury 2005). However, both males and females emitted mobbing alarm calls, loud trills and repetitive trills during territorial experiments. The most common vocalizations during these situations were mobbing alarm calls (see chapter 2 for a description) in spite of the fact that a repetitive trill was used as playback. The proportion of time in mobbing calls ranged from 8 % of the experimental time (in Manquehue with Chincol) to 28 % (on Navarino with Chincol) in females, and 20 % (in Chiloé with Chincol) to 36 % (on Navarino with Chincol) in males. Calls are uncommon in male-male interactions in oscines, where elaborated songs are generally more used (Collins 2004, Catchpole and Slater 2008). This is also the case for suboscines (Bard et al. 2002), who sing simpler songs. Moreover, in some territorial interactions I observed that Rayaditos emitted loudly trills.

Interestingly, no differences in behavioral responses between stimuli of the Rayadito and the Chincol were detected in any population, except for the females, whom emitted more mobbing calls and spent more time close to the Rayadito male compared to the Chincol male, although they attacked similarly both types of intruders. Given that to my knowledge, Chincols did not represent any threat to Rayaditos, emitting alarm calls and attacking responses under their presence were surprising. However, Chincols have an omnivorous diet, including a small percentage of insects (Grigera 1976, López-Calleja 1995, Novoa et al. 1996, Sabat et al. 1998), and thus, there is some probability of food competition between both species. Alarm mobbing calls were used against both stimuli, although generally, time spent alarming did not totalize more than 50 % of the total duration of each experiment (see appendix II). Physical direct attacks were uncommon, but when they did occurr, pecks were directed toward both types of stimuli, and it was performed by males as well as by females.

The territorial behavior of Rayaditos suggests two important points: 1) The existence of inter-specific territoriality, if Rayaditos distinguish Chincol as another species during the breeding season, and 2) Mobbing behavior (and mobbing alarm calls) as a component of territorial defense. The first point, inter-specific territoriality, has been interpreted as a result of ecological interactions encompassing resource competition and/or erroneous species recognition (Murray 1971, Tynkkynen et al. 2006). However, Rayaditos and Chincols are very different in coloration and morphology, and, additionally, feeding and nesting resources are, also, different (Grigera 1982, López-Calleja 1995). Thus, both possibilities seem to be inappropriate to explain observed behavior. On the other hand, a high intra-specific territorial response seems to have been selected in Rayaditos in order to protect their nests, because cavities are scarce and valuable resources in their habitat (Tomasevic and Estades 2006, Cornelius et al. 2008), especially in human disturbed landscapes (Cornelius 2008). In such a case, inter-specific territoriality could be a by-product of highly selected intra-specific territoriality occasionally resulting in costly situations (Murray 1981). However, because competition for cavities, and possibly other resources such as insects, can occur also with other species (e.g., with the Southern house Wren or Chercán, *Troglodytes musculus*) a high intra- and inter-specific territoriality in Rayaditos could be advantageous, and particularly useful along the wide geographical distribution of Rayaditos, due to the variable number of different passerine species and other small vertebrates that can compete for cavities and other resources. Therefore, although the lack of recognition or discrimination of proper inter-specific competitors would not be cost free, inter-specific territoriality could be favored in the colonization of new habitats.

The second point, the mobbing behavior in territorial or no-predator defense situations, has been reported only in cooperative breeders, including injury or death of small heterospecific birds (Dow 1977, Arnold 2000). Arnold (2000) suggested that mobbing behavior is a display of social status or individual quality, used in order to show off to future mates. However, territorial mobbing of Rayaditos was displayed during the laying stages, that is, when adults were already paired. During trials no others Rayaditos approached the nest and, sometimes, only one member of the pair mobbed the intruder. Rayaditos that mob or attack conspecific or heterospecific males could be communicating their individual quality in order to make the intruder abandon their territory and not to come back in the future (Caro 2005).

Territorial behavior has generally been described for males. Recently, studies of territorial behavior in females have shown that they also defend their territories with songs and other displays, a behavior mainly observed in Neotropical birds (Cooney and Cockburn 1995). Nevertheless, females usually react more aggressively with female rivals (Morton and Derrickson 1996, Pärn et al. 2008). Rayadito females, however, attacked and/or mobbed males, probably because they can represent a threat to her nest and eggs and probably they do not represent an option for extra-pair copulations. Although genetic studies about extra-pair copulations in Rayaditos have not been conducted yet, I suspect that these are very rare in this species because both parents share high levels of cooperative parental care, including nest construction, egg incubation, and high levels of nestling provisioning (Moreno et al. 2007). Females would gain more benefits defending the nest from foreign males, rather than allowing them inside their territory because male mates could diminish parental care effort if infidelity is suspected (Neff and Gross 2001).

2) Antipredator and nest defense behavior during nestling stage

Antipredator and nest defense behavior of Rayadito were not different between males and females when nestlings were 4–6 days old. Antipredator behavior involved more intense displays than nest defense and control-Chincol behavior. That is, the Chuncho elicited a stronger mobbing response from both parents, who spent a large proportion of time closer to the model, alarming, spreading the wings, and continuously changing perches. Moreover, in 98 % of cases, Rayaditos did not enter in the nest when the Chuncho was present, and only one Rayadito male pecked this predator, in Navarino. By contrast, there were no differences in behavior against Monito del monte and Chincol, although Chincol was attacked more times than Monito (see appendix III).

During the non-breeding season, mobbing is performed by Rayaditos in flocks or with other species such as *Phrygilus patagonicus*, *Carduelis barbatus*, *Sephanoides sephaniodes*, and *Pygarrhichas albogularis*. Therefore, Chuncho experiments resemble a situation that is common in the wild, because owls generally perch for a time and, when they are discovered, elicit a mobbing behavior, generally led by Rayaditos. The same behavior was observed when they detect Rufous-legged Owls (*Strix rufipes*) (S. Ippi pers. obs.). However, during defense near the nest in the breeding season, only Rayaditos from the nest approached to the model. On the other hand, marsupials such as Monitos and Yacas have mostly crepuscular and nocturnal behavior (Redford and Eisenberg 1992, Muñoz Pedreros and Yañez Valenzuela 2000, Jiménez 2005), and when active, they never stay quiet in a place for period of several minutes. Therefore, a mounted Monito used as stimulus possible was not a proper on that can elicit a real nest defense behavior. It is also possible that Rayaditos do not recognize Monitos as a threat, because they are active mainly at night. Experiments with live mammalian predator would be necessary to address this question, because some evidence suggests that other coexisting bird species behave differently when they are exposed to a stuffed Monito and to a real one (S. Ippi, pers. obs. and J.L. Celis, pers. comm.). Rayaditos could use another strategy to counteract predation by Monitos, such as cavity selection in trunks with low epiphyte cover (Cornelius 2008) or to remember results of previous breeding attempts. In fact, before the year 2006, when there were no antipredatory structures in Chiloé nest boxes, unsuccessful Rayaditos did not use nest boxes in the next year (J. Moreno pers. comm. and C. Cornelius pers. comm.), suggesting the possibility that experience plays an important role in preventing nest predation (Bellrose et al. 1964, Hoover 2003). Furthermore, Monitos used nest boxes during winter to hibernate even with the mentioned nest-box protection. Although those Monitos were removed during July-August each year, no Rayaditos used those nest boxes the following breeding season. From 43 breeding attempts monitored during 2006 and 2007 in nest boxes, only one attempt occurred in a nest box previously used by Monitos (J.L. Celis and S. Ippi unpub. data).

Rayaditos from Navarino were bolder when faced to Chunchos than Rayaditos from Manquehue or Chiloé. They spent more time alarming around the nest and the average distance and closest distance to the nest were lower (Table 7). A higher predation risk perception could cause this unexpected behavior, possibly because

Chuncho are more abundant or because diversity of preys is lower in Navarino (see Appendix I and Rozzi et al. 1996a, Chicharro et al. 2007, Armesto et al. 2008, Ippi et al. 2009). However, and contrary to expectations, the lack of differences in nest defense among the three populations suggests that the possible relaxed selection occurring in Navarino is not enough for a change or loss of this behavior. Avifauna inhabiting Navarino and adjacent islands would have evolved in absence of native carnivorous mammals at least since the last re-colonization of forests (10 000–5 000 years BP), after the last glacial events (Heusser 1998, Coronato et al. 1999, Rabassa et al. 2000, Rozzi and Sherriffs 2003). Although, a long time is required for a change in innate antipredator behavior (Hollén and Manser 2007), loss of antipredator behavior has been reported for mammals that have been isolated from all predators for a period of 9500 years (Blumstein and Daniel 2002) or only 130 years (Blumstein et al. 2004). Therefore, the absence of only one or some predator species would not be enough to generate a loss or a change in antipredator or nest defense behavior (Blumstein and Daniel 2002, Blumstein 2006). The last idea is know as the "multi-predator hypothesis", and predicts that the presence of a single predator may be sufficient to explain evolutionary persistence of antipredator behavior (Blumstein et al. 2004, Blumstein 2006, Blumstein et al. 2006). This phenomenon would occur because there is a genetic basis, such as pleiotropy, or because maintenance of all these behaviors are not costly (Blumstein 2006). Thus, Rayaditos and other species inhabiting Navarino Island could maintain some or all antipredator and nest defense behavior, if aerial predators persist.

Defense behavior

Defense behavior was widely defined in this study as the suite of behaviors that enhance the survivorship of each individual (antipredator behavior), its eggs or chicks (nest defense), or the maintenance of its territory (territorial defense), because all these behaviors enhance fitness and/or breeding success. A common behavioral response was found in each experiment, that is, the mobbing behavior. Mobbing behavior in Rayaditos includes alarm calls (loudly and repetitive vocalizations), approaches to the stimulus, fast and continuous movements among perches, and wing spreading. Mobbing behavior is a common antipredator strategy in mammals and birds (Curio et al. 1978, Caro 2005) and it has been originally defined as "a demonstration made by a bird against a potential or supposed enemy belonging to another and more powerful species; it is initiated by the member of the weaker species, and is not a reaction to an attack upon the person, mate, nest, eggs or young" (Hartley 1950, cited in Altmann 1956). Although, more experimental evidence would be required to ensure that mobbing is used in territorial as well as in antipredator defense, my results suggest that this behavior is a core component of defense behavior in Rayaditos. Mobbing behavior can be costly, especially if no other individuals or species approach the mobbing birds (Krama and Krams 2005). Furthermore, loud mobbing alarm calls, also could attract other threats, increasing the inherent risk of mobbing behavior. Although several hypotheses have been proposed to explain mobbing, one of the most widely accepted is the move-on hypothesis that states that a predator should leave an area sooner the more intensely and/or longer it is bothered. This hypothesis implies the following aspects: 1) mobbing should deter the predator from hunting, and 2) it should increase the probability that the predator will not return to the area (Caro 2005). However, although some support for the first component of the hypothesis have been reported (Pettifor 1990, Caro 2005), unfortunately there is little information about the second component (Caro 2005), and in general, concerning the predators behavior when confronted with antipredator behavior (Caro 1989). Under the move-on hypothesis, Rayaditos would be protecting themselves and their nestlings, although mobbing extended for a long time, to ensure that the Chunchos leave and do not return when the nestlings fledge and are highly susceptible to predation. Thus, mobbing behavior when faced with the Chuncho could simultaneously be an antipredator and a nest defense strategy (Caro 2005). Also, because chicks stop begging upon hearing their parents alarming (S. Ippi pers. obs.), nest defense would operate at two levels: 1) avoiding the Chuncho returning to the same place in the future, and 2) diminishing localization of the nest when a threat is nearby (Knight and Temple 1988, Caro 2005). Mobbing alarm call, in this case, would also be a warning call (Caro 2005), functioning as a vocalization with two or even more functions (Marler 2004; see chapter 2). Furthermore, because mobbing behavior is a costly signal, it could also represent a honest signal about the high quality of emitter (Zahavi 1975), contributing to dissuade predators (or any other threat) to attack, now or in the future. In some colonial breeding birds, mobbing behavior works as a strategy to show the high individual quality to conspecifics or future mates (Arnold 2000, Maklakov 2002). The benefits of mobbing during territorial defense would be similar to antipredator and nest defense, avoiding that competitors will stay and/or return to the territory, and/or signalling individual quality or status. Therefore, mobbing behavior would be a relatively simple strategy, and it can efficiently accomplish a wide variety of benefits to the life of Rayaditos. Due to the wide geographic distribution of Rayaditos, mobbing would be a cheap and functional strategy to counteract great and variable threats along that distribution.

These results can be of importance to conservation. Recently, in 2001, the presence of mink (*Mustela vison*) was detected in Navarino. The mink is an exotic and invasive carnivore that could negatively affect reproduction of birds, mainly those that nest at low distance from the ground (Rozzi and Sherriffs 2003). Rayaditos and other species like the Chercans, that nest in cavities at lower heights in Navarino than in Chiloé (S. Ippi pers. obs.) would be affected by this new invasive predator. However, because antipredator nest defense regarding visual and audio displays have not changed in Navarino Island (and possibly neither in other predator-free islands), the impact of this new predator would be lower to what it was expected.

Relationship among defense behaviors

The variability in behavior could be influenced by individual choice, by mate behavior, internal factors including hormones, external factors such as scarcity of resources and/or previous experience (Wingfield and Silverin 1986, Dolnik 1993, Wright and Shanks 1993, Hau et al. 2000, Wingfield and Hunt 2002, Wingfield 2003, Schwartz et al. 2007, Thaker et al. 2009). The tendency of individuals to behave in a consistent way across different contexts, is known as behavioral syndromes (Bell 2007), and describes correlations between two or more types of behaviors.

In order to assess if there were some relationship between inter- and intra-specific territoriality I conducted bivariate correlations between each PC scores. However, correlation analyses showed that those Rayaditos that were more aggressive with conspecific individuals were not necessarily more aggressive with Chincol (and *viceversa*) in a period of time as short as one day. To the contrary, each behavioral decision seems to be independent from the following or previous decision, and, hence, it is probable that each choice will be related with the current physiological as well as ecological conditions (Hau et al. 2000, Wingfield 2003). For example, if one day is sunny and birds fed enough they will have energy for aggressive displays, but if the next day is rainy and windy, behavior could be less aggressive or individuals could not respond at all to the presence of a territorial threat. These situations would be very common in Chilean temperate forests due to climatic characteristics, principally in Chiloé and Navarino Islands. Moreover, some Rayaditos were not aggressive at all, and thus I suggest that in this species, territorial behavior would be a very flexible trait. Therefore, each Rayadito could be able to assess the situation and modulate optimally its response accordingly (Andersson et al. 1980). Birds can assess predation risk and adjust reproductive strategies, such as egg size or nest place selection (Forstmeier and Weiss 2004, Fontaine and Martin 2006). However, responses on the basis of experience can incur costs such as making mistakes or the energetic cost of processing information (Odling-Smee and Braithwaite 2003, Vásquez et al. 2006). Therefore, some habitat and/or community cues such as density of competitors or scarcity of resources could be assessed by Rayaditos and affect their intra- as well as their inter-specific responses independently.

The relationship between behavior of Rayaditos confronting Chuncho and Chincol was positive. That is, those Rayaditos that alarm for longer time and approach more closely to the predator, were also those bolder in response to the Chincol. The same correlation was found in the behavioral response to Monito del monte and Chincol (Fig. 4). Therefore, these results indicate that Rayaditos have a kind of behavioral syndrome, although surprisingly there was no relation between intra- and inter-specific territoriality. However, during laying stages, defense behavior could be reduced due to a high probability to re-nesting if the current attempt fails, because the breeding season is starting. For that reason, the current physiological and environmental conditions would influence independently the intra- and inter-specific aggressiveness. By contrast, when hatching has occurred, reproductive investment is higher and the possibility of re-nesting has diminished. This situation would be particularly stressful for Rayaditos because they lay eggs in alternate days and have a long incubation period (Moreno et al. 2005, Moreno et al. 2007). Therefore, defense behavior during this stage would be more associated to the current and future reproductive effort.

To conclude, high levels of aggressive behavior toward a wide selection of stimulus in Rayaditos (in this study: Rayadito male, Chincol male in two stages of breeding event, and Chuncho) would suggest that proximate causes that maintain this behavior allow them to survive in different habitats in a wide latitudinal range and in very different assemblages of threats. Although defense strategies might be coupled with other strategies such as nest site selection or previous breeding experience, my results suggest that indiscriminate inter-specific territoriality and mobbing behavior are a key component of defense behavior, and they would constitute fundamental characteristics that determine that rayaditos inhabit successfully a wide latitudinal range (Rozzi et al. 1996a, b, Anderson and Rozzi 2000, Cornelius et al. 2000).

Somewhere, always, the sun is rising, and somewhere, always, the birds are singing. As spring and summer move between northern and southern hemispheres, so, too, does this singing planet pour forth, like a giant player piano, in the north, then the south, and back again, as it has now for the 150 million years since the first birds appeared.

D. Kroodsma (2004)

Capítulo II

Geographic and behavioral variation of vocalizations of a suboscine bird: the Thorn-tailed Rayadito (*Aphrastura spinicauda*)

Abstract

Vocal communication is a key character in the natural history of passeriformes, with an important role in mating, agonistic encounters and predator alarming. Diversification of songs and calls could be related with acoustic adaptations in order to improve sound transmission in different environments (acoustical adaptation hypothesis, AAH). Such diversification also is related with species recognition, which can influence divergence in allopatric populations. Geographic variation in vocalizations have been poorly studied in suboscines (suborder Tyranni), although suboscines birds are a good model where to analize and compare acoustic signals from different populations, because results have no bias for learning and, as a consequence, for cultural evolution. The principal aims of the present study were to compare vocalizations of different distant populations of Rayadito (*Aphrastura spinicauda*) and to test experimentally whether the alarm vocalizations are different when faced to an avian adult predator and a mammalian nest predator. Three types of vocalizations of Rayaditos were recorded in five populations, including the three current accepted subspecies. Comparisons of each type of vocalization among five populations showed that some variation exist, mainly in repetitive trill, marginally in mobbing/alarm calls and no differences were found among loud trills. Repetitive trill

variations among populations, were no explained clearly by subspecies classification or AAH. Therefore, geographic differentiation in vocalizations suggests that certain degree of differential ecological pressures between populations do exist, although a strong inter-population differentiation does not occur because of a high gene flow. Mobbing alarm calls would be an important component of nest defense and antipredator behavior and, although they are no functionally referential, time spent vocalizing could indicate the degree of threat.

Introduction

Birds acoustic signals are essential in reproductive events (e.g., mating and territorial defense) (Searcy and Andersson 1986, Catchpole 1987, Collins 2004), as well as in communication (e.g., alarm calls) (Marler 1955), and their diversification can be an important factor in the radiation of species, particularly in passerines (Nottebohm 1972, Podos et al. 2004a). Song diversification can be a response to different associated factors, such as morphological adaptation, acoustic adaptations and species recognition (Seddon 2005), which can influence speciation (Endler 1992, Podos et al. 2004a). This is particularly important in isolated populations because studies have reported the loss of functionality of territorial songs (Baker 1994) or the simplification of songs in isolated populations (Hamao and Ueda 2000). For example, isolated bird populations can loss the ability to recognize predators (Griffin et al. 2000) and, as a consequence, modify or loss alarm calls. Nevertheless, it is important to note that the majority of vocal recording studies have been conducted in songbirds or oscine passerines (Suborder Passeri), which are able to learn songs (Bolhuis and Eda-Fujiwara 2003, Beecher and Brenowitz 2005).

Studies in some species of Tyrannidae, suggest that suboscine passerines (Suborder Tyranni) have no ability to learn songs (Kroodsma 1984, Kroodsma and Konishi 1991). Therefore, authors generally accept that suboscine songs are innate and that suboscine birds have a poor vocal richness in comparison with oscine birds.

Birds vocalizations can be divided in songs (defined as a signal that tends to be long and complex, generally produced by males, during the breeding season) and calls (shorter, simpler and produced by both sexes throughout the year) (Catchpole and Slater 2008). Because songs have been defined for oscine birds, some authors refer to "songs" in suboscine as loudsongs (Seddon 2005). There are many types of calls (e.g., contact, flight, food, agonistic and alarm calls, among others) and there are many types of alarm calls like aerial (hawk) alarm call, mobbing calls, and distress calls, among others (Marler 2004). An antipredator hawk alarm call, for example, is a narrowband pure tone, pitched high enough so that it does not travel far and in a range where hawks cannot hear adequately (Klump et al. 1986). Such call serves to communicate alarm to companions while at the same time minimizing risk to the caller (Marler 2004). Mobbing calls, on the other hand, are typically loud, harsh, or ringing in tone, given in long, repetitive sequences (Marler 1955). Although different degrees of specificity in alarm calls among mammals are largely documented (Seyfarth et al. 1980, Blumstein and Armitage 1997, Zuberbühler 2001, Fichtel et al. 2005) a relatively scarce knowledge exists about predator-specific calls in birds. However, some experiments have demonstrated that some avian species, like domestic fowls, Arabian babblers (*Turdoides squamiceps*), and Pale-winged trumpeters (*Psophia leucoptera*) could have aerial and ground alarm calls to different predators or threats (Marler 1955, Collias and Collias 1967, Evans et al.

1993, Naguib et al. 1999, Seddon et al. 2002), and American robins (*Turdus migratorius*) emit two different calls when facing two types of nest predators, including in their vocalizations information about the intensity of future nest defense (Gottfried et al. 1985). Recent studies about specific calls in passerine species found that alarm calls are not functionally referential, but repetition rate involves information about the degree of nest danger (Leavesley and Magrath 2005, Welbergen and Davies 2008; but see Gill and Sealy 2004). However, although the most common question in the literature is whether different calls have functional specificity, it is important to note that "alarm call with multiple functions are probably more widespread than we think" as stated by Marler (2004), and graded signals seems a reliable option (Leavesley and Magrath 2005, Welbergen and Davies 2008).

Bird sounds can be adjusted to the acoustics of natural environments in order to improve sound transmission according to different habitats, minimizing reverberation and frequency dependent attenuation (Wiley 1991). For instance, pure tonal notes are better transmitted in understory meanwhile highly modulated sounds or trills are better transmitted in open habitats, and lower pitched sounds in forested habitats (Morton 1975, Brown and Handford 1996, Seddon 2005). Frogs and birds that inhabit nearby to waterfalls have lower wide band of frequencies (Dubois and Marten 1984) and Little greenbuls (*Andropadus virens*) sing with lower frequencies in rainforest than in ecotone areas (Slabbekoorn and Smith 2002b). Morton (1975) proposed that "habitat acoustics produce selective forces favoring certain features of sound signals: pure tonelike sounds within a relatively narrow frequency range in forest birds living near the ground, and highly modulated or trilled sounds in open habitat species". As a result, acoustic parameters of long-range signals of the same species from different populations inhabiting different environments could be different. This hypothesis have been called acoustic adaptation hypothesis (AAH) and there are some examples analyzing its predictions (Morton 1975, Rothstein and Fleischer 1987, Tubaro and Segura 1994, Brown and Handford 1996).

Vocalizations, like others signals communication, have a main role in sexual selection and thus, play a role in the divergence between allopatric populations or in the reinforcement of the reproductive isolation (Endler 1992, Boughman 2002). Signals transmission depends on the environmental conditions and they will change accordingly with habitat changes (Morton 1975, Wiley 1991, Endler 1992) influencing the communication process between sexes and, eventually other conspecific birds. In songbirds, sexual selection and cultural evolution (due to learning abilities), stimulate the diversification of songs and species, while mechanisms of vocal production would constrain it (Podos et al. 2004a). However, the current knowledge about evolution of acoustic signals in non-oscine passerine birds are scarce (Kroodsma 1984, Kroodsma et al. 1987, Lovell and Lein 2004a, b, Seddon 2005), in spite that suboscines birds are a proper model where to study and compare acoustic signals from different populations. This is because, potential inter-population differences in songs of a non-learning species will not be attributable to learning bias, thus strongly suggesting genetic differentiation and local adaptation between populations (see Seddon et al. 2002). Such as a result would also contribute to elucidate the direction of evolution of that signals in response to different selective pressures. Therefore, studies in different habitats and/or along the geographic distribution of a focal suboscine species could contribute to understand the adaptive value and the ecological context of vocalizations in this avian group, and to gain insight about their role on the evolution of non-oscine avian species (Foster 1999, Seddon 2005). To my knowledge no previous studies about long range geographic variation in acoustic signals have been conducted on suboscines. In general, studies about suboscine vocalizations are concentrated in Thamnophilidae and Tyrannidae families and in individual song variation or recognition within a single population (see for example; Payne and Budde 1979, Morton and Derrickson 1996, Isler et al. 1998, Bard et al. 2002, Lovell and Lein 2004a, b, 2005, Wiley 2005).

Suboscine passerines make up approximately 20 % of the order Passeriformes and they are dominant in the Neotropical region (Irestedt et al. 2001, Irestedt et al. 2002, Ricklefs 2002). Furnariidae is one of the most diverse families, distributed in Central and South America (Irestedt et al. 2001) accounting 240 species in 59 genus (Zyskowski and Prum 1999), with 33 species inhabiting in Chile (Jaramillo 2003). The Thorn-tailed Rayadito or Rayadito (*Aphrastura spinicauda*) is an endemic Furnariidae inhabiting temperate austral forests of Chile and Argentina, distributed from Fray Jorge National Park (30°S) to the subantartic forest in Cape Horn Region (56°S) (Johnson and Goodall 1967, Rozzi 2003). Three different subspecies have been described: *A. s. spinicauda* (J. F. Gmelin, 1789), the most widespread form inhabiting the mainland in Chile and Argentina and some islands along the Chilean coast, while *A. s. bullocki* (Chapman) is found only in Mocha Island, and *A. s. fulva* (Angelini) only in Chiloé, according to Johnson and Goodall (1967; see also Remsen 2003). The Rayadito is a small insectivorous non-migratory bird that nests in tree cavities and forages in single or mixed flocks during the non-breeding season (Vuilleumier 1967, Grigera 1982, Ippi and Trejo

2003). Rayaditos have, at least, four different types of vocalizations: a conspicuous and loudly alarm mobbing call, a contact call, a strong and loudly trill call and a probable territorial trilled song (S. Ippi pers. obs.). In order to learn about the possible function of different calls and songs, experiments that show "production specificity" should be performed (Macedonia and Evans 1993). Therefore, at present time, I can only speculate about vocalization functions in the Rayadito, given the scarcity of available information. In order to avoid potential confusions I will use descriptive names for the trills: loud trill and repetitive trill. Contact and mobbing alarm calls will be named from records of previous observations and information obtained from the literature (Vuilleumier 1967, Ippi and Trejo 2003).

The wide geographic distribution of Rayadito makes it a proper subject to study variation of vocalizations in different and isolated populations. Moreover, the presence of Rayaditos on islands with no nest predators allows to analyze variation in vocalizations and behavior in those situations and, because Rayaditos live in different forested habitats, their vocalizations should be different in order to maximize transmission across a diversity of conditions, particularly if Rayaditos follow the AAH.

The principal aims of the present study were to compare vocalizations of different populations of Rayaditos and to test experimentally whether the vocalizations are different when faced to two different predators. Because there are no published recordings of the species' vocalizations, the first step was to describe their songs and calls. I recorded three types of vocalizations in five different populations: Navarino island, in the Cape Horn Region, Chiloé island, Mocha island, Cerro Manquehue, and relict forest of Santa Inés. Forests in all these sites are included in the Southern

Temperate Forest (30°S–56°C), but there are some organizational and structural differences among them (see below and Armesto et al. 1996b). I also recorded vocal responses of Rayaditos to different predators in two populations using three taxidermic mounts: (i) an avian adult's predator, the Austral Pygmy Owl or Chuncho (*Glaucidium nanum*); (ii) a mammalian nest's predator, Monito del monte (*Dromiciops gliroides*); and (iii) a harmless coexisting species of passerine used as a control, the Rufous collared sparrow or Chincol (*Zonotrichia capensis*). Finally, because habitats are very different along to geographic distribution of Rayaditos and because songs and/or long range calls need to maximize transmission, my hypothesis is that the vocalizations will be different among the regions, assuming significant habitat differences. Forests of Chiloé, Mocha, and Santa Inés are more complex and dense than Manquehue or Navarino. Although acoustic signals of Rayadito are not purely tonal, as predicted by the AAH (Morton 1975), my predictions are that bandwidth of trills will be narrower, with lower frequencies and less number of notes per trill in Chiloé, Mocha and Santa Inés compared to Navarino and Manquehue. Additionally, if forest characteristics affect acoustic signals transmission, some differences in bioacoustic parameters can occur between songs in the breeding and the non-breeding season, in deciduous forests but no in evergreen forests.

Methods

Study area

Recording of vocalizations of Rayaditos were made in the austral spring (September-January) in 2006 and 2007 in five different study sites, encompassing over 2400 km from south to north.

Navarino Island (54°S and 67°W) Navarino Island is located 1.3–4 km south of Isla de Tierra del Fuego, in the Cape Horn Biosphere Reserve. Vocalizations were recorded at the Omora Etnobothanical Park and antipredatory experiments were conducted in the adjacent areas, up to 1–2 km away, where the forest was similar to the park or somewhat more disturbed. In both places prevail the Magellanic subantartic forests that include three species of *Nothofagus* and some *Berberis spp* shrubs (Anderson and Rozzi 2000). Some degree of anthropic disturb exists and cattle and horses pasture frequently. Precipitation in the area reaches approximately 450 mm per year, relative humidity is 84 % and the mean annual temperate is 6°C (Hajek and di Castri 1975). Mean temperature in the non-breeding season (April-September) is 3.4°C, relative humidity is 85.3 % and total precipitation reaches 213 mm. Mean temperature in the breeding season (October-March) is 8.4°C, relative humidity is 82.3 % and total precipitations reach 234 mm (Hajek and di Castri 1975).

Chiloé Island (41°S and 73°W) Chiloé is a continental island, distant 2–5 km from the continent. Antipredatory experiments and vocalization recordings were conducted in two large forest blocks, Senda Darwin Biological Station and Fundo "Los Cisnes", at the northern tip of the island where predominate Valdivian and Nordpatagonian forests. Both study sites include large fragments of regenerating evergreen forests of *Drimis winteri*, *Nothofagus nitida*, and several myrtaceous species (Aravena et al. 2002) surrounded by agricultural landscape (Willson and Armesto 1996). The understory included dense *Chusquea spp.* (bamboo) thickets and saplings. Precipitation reaches 2097 mm per year and the mean annual temperature is 10.0°C (Carmona et al. in prep.).

The mean relative humidity is 82 % (data from Castro, 42°S and 73°W, Chiloé; Hajek and di Castri 1975). During the non-breding season (April-September), precipitations reach 1405 mm, relative humidity is 86.5 % and mean temperature reaches 8.6 °C. During the breeding season (October-March), total precipitation reaches 692 mm, relative humidity 78.2 % and mean temperature 11.4°C (Hajek and di Castri 1975; Carmona et al. in prep).

Mocha Island (38°S and 73°W) Located 34.2 km west from the continent, it has three predominant tree species: *Aextoxicon punctatum* and *Drimys winteri* in humid substrates and Mirtáceas (*Luma apiculata* and *Myceugenia planipes*) in intermediate and lower layers. Dense shrublands of *Fuchsia magellanica* and *Aristotelia chilensis* occur in the boundary between forest and farmlands (Lequesne et al. 1999). Precipitation reaches 1373 mm per year, with a relative humidity of 88 % and a mean annual temperature of 12.6 °C, with a strong oceanic influence (Hajek and di Castri 1975).

Cerro Manquehue (33°S and 70°W) Records of vocalizations were conducted at Granja Educativa Manquehue located in the northern border of Santiago city. Fragments of sclerophyllous forests at Cerro Manquehue are remnants of a large extension of forests dominated by *Cryptocarya alba* and scarce understory. Climate is mediterranean with a mean annual precipitation of 356 mm with a relative humidity of 72 % and mean temperature is 13.9°C (Hajek and di Castri 1975).

Cerro Santa Inés (32°S and 71°W) Is a relict isolated Valdivian forest located on the west-facing slope of the coastal mountain range (400–800 m elevation) characterized by an absolute dependence of coastal fog that increase the level of precipitations inside the forest. It is located 60 km from the closest forests. The forest is composed predominantly by *A. punctatum* and *Myrceugenia correifolia* (Perez and Villagrán 1985) although associations of *A. punctatum* and *Lomatia dentata* or only *A. punctatum* are frequent (Francois 2004). The climate is mediterranean-arid, with dry hot summers and cool and rainy winters and mean annual precipitation is 384 mm per year, with a relative humidity of 83 % and mean annual temperature of 14.2 °C (data from Zapallar 32°33'S and 71°S30', altitude 30 m; Hajek and di Castri 1975).

Vocalizations

It can be differentiate four types of vocalizations in Rayaditos and I called them: (i) mobbing call, (ii) contact call, (iii) loud trill, and (iv) repetitive trill. Contact calls were excluded from the present analysis because the social context in which they are emitted (family and/or flock) difficult the identification of individual/s that are calling. Both, male and female sing all types of calls and songs.

The analysis was enterely based on tape recordings made with a digital recorder (DAT Sony PCM-M1) and a Sennheiser ME 66 microphone, with a sampling rate of 48 kHz. Recordings were made principally during spring (reproductive season), before 13:00 PM. Aditionally, in Navarino and Chiloé I made recordings in autumn and winter (non-reproductive season). The methodology used to detect and record songs and calls of Rayaditos consisted in one observer walking at constant speed along different transects or trails until hearing some vocalizations (no playbacks were used to stimulate songs). Then, I approached to the signal and recorded it. Finally, I moved away a minimum of approximately 200 m in the opposite direction. Each site was visited only once per season. No sex differentiation was possible during recordings because Rayaditos are not sexually dimorphic (Moreno et al. 2005, 2007) and, although birds with color bands sometimes were recorded, identification was difficult due to dense vegetation. Signal acquisition and spectrogram analysis were made with the sofware Raven 1.2 (Cornell Bioacoustics Laboratory, Cornell, USA).

Song description

To characterize vocalizations of Rayaditos I adapted a methodology used by several authors (Haavie et al. 2004, Fichtel et al. 2005, Garamszegi et al. 2005, Seddon 2005), using the following variables 1) Duration of each trill or note, according to type of signal, 2) Number of notes per trill or call, 3) Minimum frequency, 4) Maximum frequency, 5) Peak frequency (frequency in the call or song with the most energy), and 6) Bandwidth (difference between minimum and maximum frequency). In some cases, I included the variable time of three consecutives notes (in mobbing calls). A note is any continuous trace on the audiospectrogram (Baptista 1977).

Because the three types of vocalizations are different in structure and emission form, I described and analyzed each one in a separate way. Mobbing call is a series of repetitive notes that can last up to several minutes (S. Ippi pers. obs.). For this reason, I selected a period of 3 s with the higher rate of emission of notes for analyses. In this period, I counted the number of notes and recorded the minimum, maximum, peak frequency and bandwith in kHz. A trill was defined as a regular pattern of rapidly alternating phases of high and low amplitude for a relatively broad frequency range (Slabbekoorn et al. 1999). Three repetitive trills of each individual were averaged and analyzed considering the same bioacustics parameters already mentioned. The remaining acoustic signal analyzed, the loud trill, was not repetitive, thus I analyzed it separately with the same bioacoustical parameters already mentioned.

Antipredator vocalizations

In order to analyze vocal responses of Rayaditos when faced to different predators in Navarino and Chiloé populations, I conducted experiments using taxidermic mounts of different avian predators: An Austral Pygmy Owl or Chuncho (70–80 g) (*Glaucidium nanum*), a predator of small birds (Jiménez and Jaksic 1989); Monito del Monte (*Dromiciops gliroides*) (20–40 g) a marsupial that predate eggs and chicks (Jiménez and Rageot 1979), and a Rufous collared Sparrow or Chincol (20–23 g) (*Zonotrichia capensis*) as a control because, to my knowledge, it is not a threat for Rayaditos (see e.g., Dunn et al. 2004, Stenhouse et al. 2005, for similar approach). Nest boxes were monitored since October to the end of the breeding season. Adults were captured and banded with a unique combination of colored rings and a metal numbered band (National Band and Tag, Co., Newport, KY, model 1242–3) with authorization by the Servicio Agricola y Ganadero, Chile. Trials were conducted when chicks were 4 days old, mounts were presented in successive days (weather permitting) and the order of control and treatments was chosen randomly. Trials consisted of 2 minutes of habituation (to avoid Rayaditos response to previous human disturbance) and 10 minutes of behavioral observations and recordings of vocalizations. Trials were stopped when Rayaditos attacked models more than five times. This situation only occurred with control mounts. The microphone was mounted 0.5 m above the ground level on a tripod at a distance of 2–3 m from the nest. Trials were conducted between 6:50 and 13:00 h.

During antipredator experiments mobbing calls of both parents overlapped, and therefore it was not possible to separate periods of 3 s for each parent in order to analyze them, such as previously explained in the *song description* section. Thus, I analyzed three consecutives notes for each individual and compared the means of each bioacoustic parameter including the duration time of three notes. Three consecutive notes were selected considering the quality and principally, that they not overlap with notes from the other parent. To analyze duration time of vocalizations during trials, I calculated the proportion of experimental time that Rayaditos emitted loud trills and mobbing calls. I calculated the proportion of time of mobbing calls by only one parent, proportion by both parents simultaneously and the sum of both (total duration time of vocalizations).

Sound transmission

In Navarino and Chiloé a series of six trills of Rayaditos obtained from the commercially available CD "Voces de Aves Chilenas" (Unión de Ornitólogos de Chile, Santiago), were broadcasted from a loudspeaker (Sony Mega Bass SRS-A47) at 1.3 m above ground and recorded at a distance of 20 m with a digital recorder (DAT Sony PCM-M1) and a microphone (Sennheiser ME 66) mounted at the same height. This protocol was maintained invariable in all repetitions, and experiments were repeated 10 times in each study site. Each site was selected because some recordings of Rayaditos' vocalizations were made there as well, but the precise point and orientation of the 20 m transect were selected at random. In addition, measurements of habitat features were measured: number of trees with a diameter at breast high (dbh) > 10 cm, number of obstacles (i.e. trunks, branches and leaves) between loudspeaker and microphone, the sum of longitude of these obstacles, and assessment of canopy height and cover at each recording point. Acoustic measurements (minimum, maximum and peak frequency, bandwidth, duration of trill, and maximum amplitude) of the six trills were averaged and compared between the two regions.

Statistical analysis

Statistical analyses on acoustic variables were conducted using SPSS for Windows (Version 13.0; SPSS Inc., Chicago, USA) and STATISTICA 6.0. Shapiro-Wilks and Levene tests were conducted to address normality and variance homogeneity of the variables (Sokal and Rohlf 1995). Non-normal variables were transformed with a log transformation or a box-cox transformation performed using Rundom Box-Cox freeware (Rundom BC version 1.0, http://pjadw.tripod.com/bc.htm). Differences in acoustic variables among populations from different regions were evaluated with one way MANOVA and Tukey post hoc test, or ANOVA test when Tukey test was not possible to perform (Quinn and Keough 2002). Additionally, a discriminant function analysis were made on data from repetitive trills to explore the possibility to correctly classify the different populations using acoustic variables (Quinn and Keough 2002). To evaluate acoustical response to different models in Navarino and Chiloé two way MANOVA were conducted, and variables of time vocalizations were analyzed with Friedman ANOVA test, because data did not have normal distribution.

Finally, I conducted one way MANOVA on habitat data from Navarino and Chiloé with a post hoc ANOVA test. These tests permitted to select habitat variables that differed significantly between both places. On these variables I conducted a parametric correlation test to know how related they are. On the other hand, a MANOVA test was made on the acoustical data from the same trill broadcasted in Navarino and Chiloé, and selected the significant variables with ANOVA tests. Multivariate regressions among the habitat variable and these acoustic variables were conducted to investigate if habitat characteristic could predict the variation on the acoustic signal transmission. For all tests involving multiple comparisons, a sequential Bonferroni correction was used.

Results

Vocalizations

Records of Rayadito vocalizations sum approximately 48.42 h, equivalent to 40 sampling days since 7:00–8:30 AM to 13:00 PM. I recorded and analized three types of vocalizations of Rayaditos: (i) mobbing call, (ii) loud trill, and (iii) repetitive trill.

Mobbing call. The mobbing call is a very loud and repetitive call, easy to hear by humans in the temperate southern forest (Fig. 1), and Rayaditos emitted it in presence of potential predators or threat. Mobbing calls were recorded in the spring in Cerro Manquehue, Chiloé, Isla Mocha, and Isla Navarino, and its minimum frequency were 2.82 kHz (SD = 0.74 kHz), maximum frequency were 13.01 kHz (SD = 3.34) and peak frequency were 6.02 kHz (SD = 0.64), recorded in 13 individuals (Table 1). Note rate was very high, with 6.13 notes/s and duration of this call could extend for as long as the predator or threat was present. In order to study possible differences among these four populations I analyzed periods of 3 s of mobbing calls per individual. Variables were normally distributed (Shapiro-Wilks test; p>0.1). Differences among populations were marginally significant (MANOVA; $F_{12, 16.2} = 2.407$; p = 0.051). Post-hoc univariate tests (ANOVAs) showed that only the number of notes during three seconds was significantly higher in Cerro Manquehue compared to Chiloé island ($F_{3, 9} = 7.09$; p = 0.010).

Table 1. Acoustic parameters in alarm call of Rayaditos in four different populations and in all together. Sample size is in parenthesis. Mean ± SD. * indicates significant differences obtained with a post hoc univariate test.

	Navarino (1)	Chiloé (3)	Mocha (3)	C. Manquehue (6)	Total (13)
Minimum frequency (kHz)	2.62	3.31 ± 0.57	2.98 ± 1.39	2.52 ± 0.39	2.82 ± 0.74
Maximum frequency (kHz)	17.25	10.96 ± 3.49	13.27 ± 1.76	13.19 ± 3.80	13.01 ± 3.34
Bandwidth (kHz)	14.63	7.65 ± 4.05	10.29 ± 2.31	10.67 ± 4.04	10.19 ± 3.72
Peak frequency (kHz)	5.68	6.40 ± 0.50	5.63 ± 1.06	6.09 ± 0.47	6.02 ± 0.64
# of notes in 3 seconds	18	15.67 ± 1.53*	17.67 ± 1.15	20.17 ± 1.47*	18.38 ± 2.26

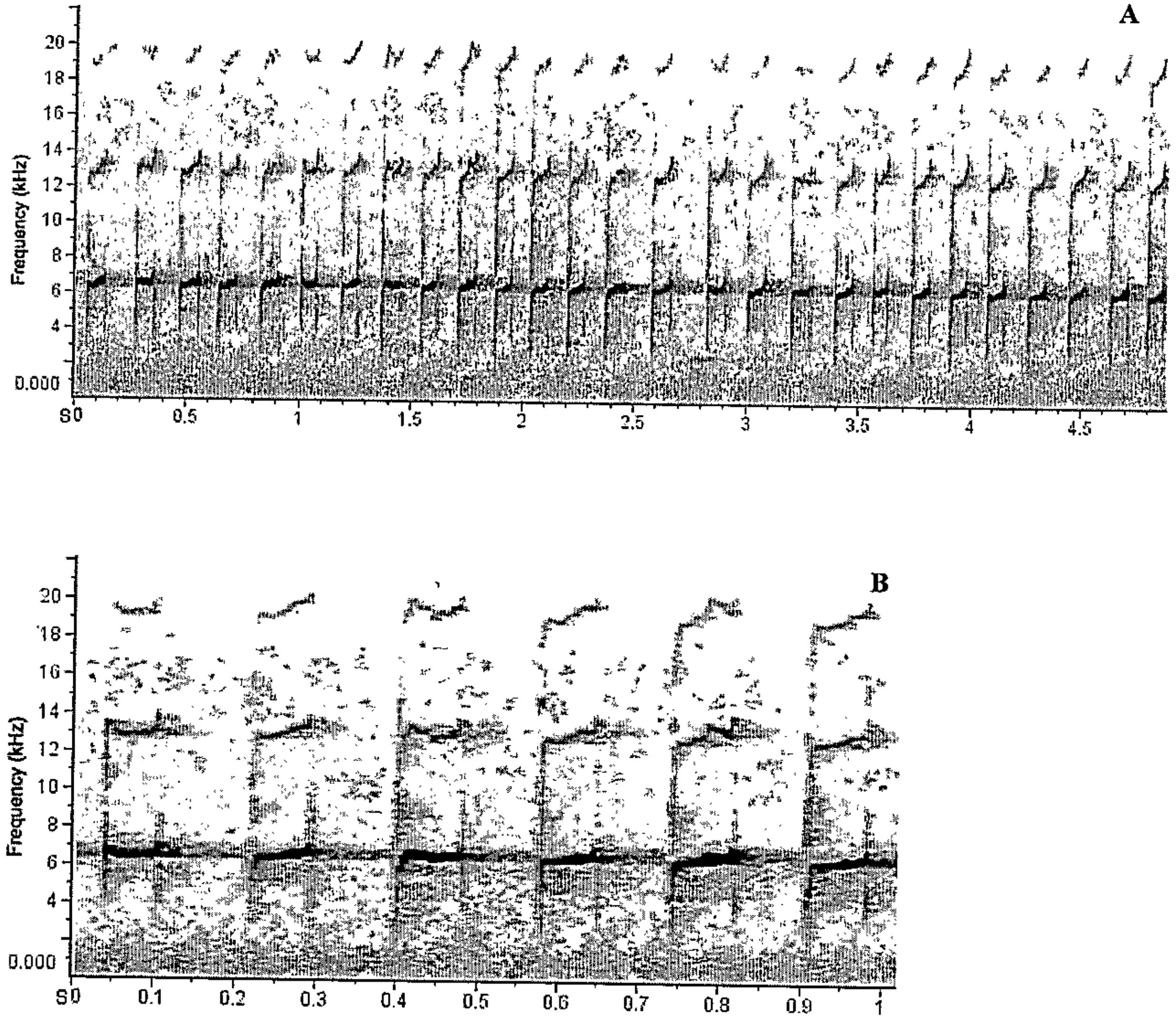

Fig. 1. Representative sonograms of (A) mobbing alarm calls and (B) detail, emitted by a Rayadito in Chiloé population.

Loud trill. The loud trill is an acoustic signal with possible different functions, because it was heard (i) when Rayaditos were in the presence of a suddenly threat close to the nest, (ii) when one parent replaced the pair during incubation, (iii) during territorial aggressive interactions and, also, (iv) in the non-breeding season (Fig. 2). Recordings obtained from 15 individuals showed that the duration of this trill was somewhat variable (mean = 3.22 s; SD = 1.65), minimum frequency was 1.65 kHz (SD = 0.47), maximum frequency was 12.2 kHz (SD = 2.37), bandwidth was 10.55 kHz (SD = 2.16) and peak frequency was 4.96 kHz (SD=0.75). No significant differences were detected among Cerro Manquehue, Chiloé, Navarino, Santa Inés and Mocha populations (MANOVA; $F_{16, 22} = 0.944$; $p = 0.539$; Table 2).

Table 2. Acoustic parameters in loud trill of Rayaditos in five different populations Sample size is in parenthesis. Mean ± SD.

	Navarino (5)	Chiloé (1)	Mocha (3)	C. Manquehue (3)	C. Santa Inés (3)	Total (15)
Minimum frequency (kHz)	1.41 ± 0.36	1.24	1.88 ± 0.13	1.77 ± 0.05	1.83 ± 0.95	1.65 ± 0.47
Maximum frequency (kHz)	11.24 ± 1.14	12.85	13.76 ± 2.23	13.65 ± 3.18	10.56 ± 2.90	12.2 ± 2.37
Bandwidth (kHz)	9.83 ± 0.92	11.61	11.88 ± 2.16	11.88 ± 3.21	8.73 ± 1.95	10.55 ± 2.16
Peak frequency (kHz)	4.81 ± 0.45	5.25	5.05 ± 1.18	5.43 ± 0.17	4.54 ± 1.17	4.96 ± 0.75
Duration of trill (s)	3.46 ± 0.96	4.7	1.52 ± 0.59	3.63 ± 2.46	3.62 ± 2.19	3.22 ± 1.65

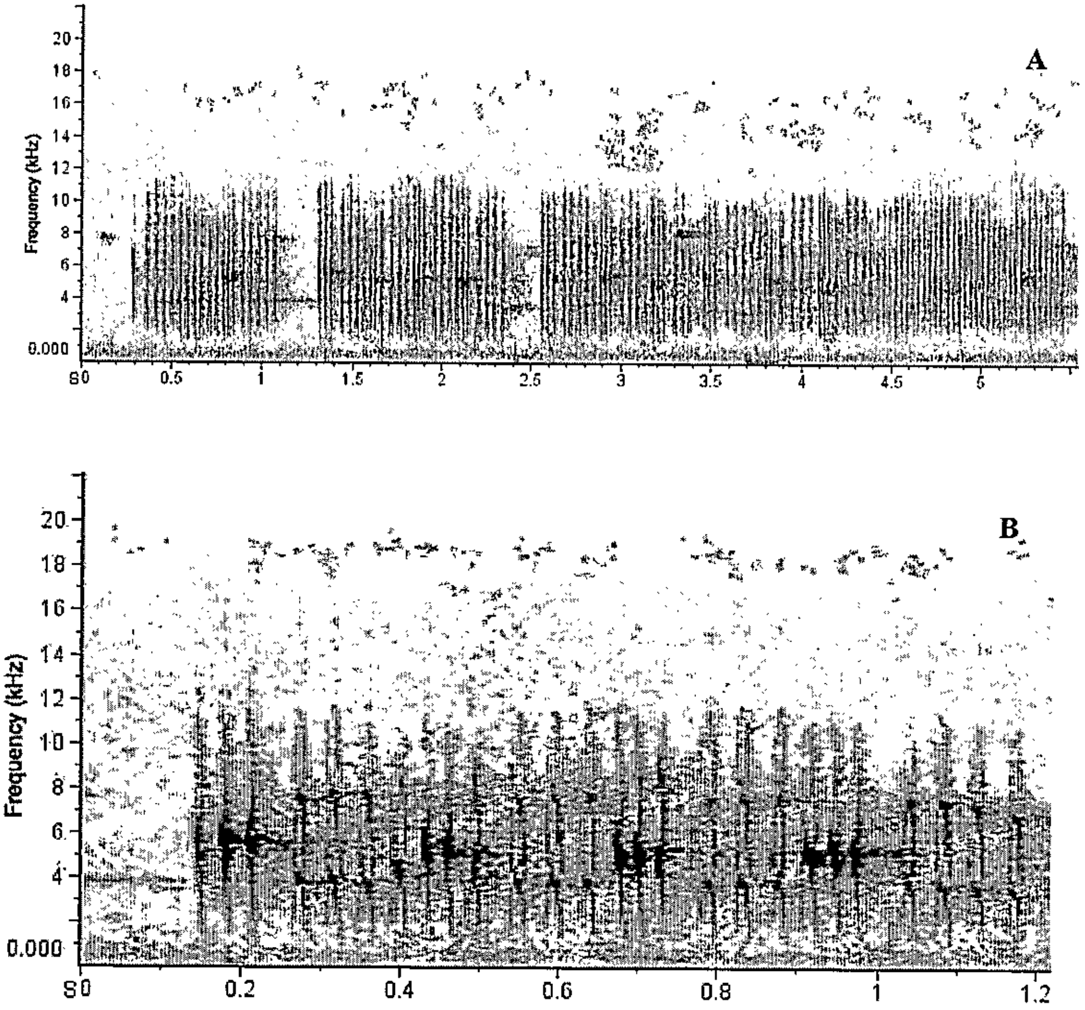

Fig. 2. Representative sonogram of (A) loud trills and (B) detail emitted by a Rayadito in Navarino population.

Repetitive trill. This trill differed from the previous because it was shorter, and emitted during several minutes at regular pauses, being each trill of similar structure with the following ones (Fig. 3). Trills recorded from 69 individuals had a mean duration of 0.63 s (SD = 0.09) with 12.44 notes per trill (SD = 2.18) (Table 3). Mean time between each trill was 4.85 s ± 3.92 (N = 61; range 0.98–21.90 s) (Table 3). Recordings of this type of song were made in the five regions. Analysis were conducted on mean of trills obtained per individual, choose in function of its quality in the spectrogram, that indirectly depends on recording distances. Non-normal variables were transformed with a log transformation for statistical analyses. Repetitive trills showed significant differences among populations (MANOVA; $F_{24, 207} = 3.220$; $p < 0.001$; N = 69). These differences were explained by the differences in peak frequency between Isla Mocha and Navarino (Tukey test; $p = 0.006$) and by the differences in number of notes per trill between Chiloé and Isla Mocha (Tukey test; $p = 0.040$).

Table 3. Acoustic parameters of repetitive trills of Rayadito in five different populations. Sample size is in parenthesis. Mean ± SD. * indicates significant differences obtained with a post hoc Tukey test.

	Navarino	Chiloé	Mocha	C. Manquehue	C. Santa Inés	Total
Minimum frequency (kHz)	2.21 ± 0.44 (18)	2.32 ± 0.32 (8)	2.14 ± 0.44 (26)	2.19 ± 0.21 (10)	1.73 ± 0.52 (7)	2.15 ± 0.43 (69)
Maximum frequency (kHz)	12.45 ± 2.39 (18)	10.65 ± 3.12 (8)	10.71 ± 2.58 (26)	12.95 ± 4.50 (10)	11.97 ± 4.28 (7)	11.61 ± 3.17 (69)
Bandwidth (kHz)	10.24 ± 2.36 (18)	8.33 ± 3.17 (8)	8.57 ± 2.65 (26)	10.75 ± 4.58 (10)	10.24 ± 4.70 (7)	9.46 ± 3.26 (69)
Peak frequency (kHz)	5.03 ± 0.39 (18)*	5.03 ± 0.43 (8)	4.67 ± 0.30 (26)*	4.87 ± 0.29 (10)	4.86 ± 0.23 (7)	4.85 ± 0.36 (69)
Duration of trill (s)	0.58 ± 0.09 (18)	0.64 ± 0.05 (8)	0.64 ± 0.10 (26)	0.66 ± 0.14 (10)	0.63 ± 0.09 (7)	0.63 ± 0.10 (69)
Number of notes per trill	12.17 ± 1.79 (18)	13.87 ± 1.01 (8)*	11.51 ± 2.33 (26)*	13.55 ± 2.37 (10)	13.40 ± 1.62 (7)	12.44 ± 2.18 (69)
Longitude of pauses (s)	5.49 ± 4.24 (17)	5.21 ± 4.16 (7)	5.03 ± 4.37 (23)	3.7 ± 2.84 (10)	3.03 ± 1.24 (4)	4.85 ± 3.92 (61)

Discriminant analyses were conducted with all the data of repetitive trill in order to investigate if trills could be classified correctly for each population. The discrimination among populations was highly significant (Wilks' Lambda = 0.330; $F_{24, 207} = 3.2202$, $p < 0.001$; N = 69) including all six variables in the model: peak frequency (partial lambda = 0.945; p = 0.498), number of notes per trill (partial lambda = 0.608; $p < 0.001$), duration of trill (partial lambda = 0.667; $p < 0.001$), minimum frequency (partial lambda = 0.903; p = 0.194), bandwidth (partial lambda = 0.898; p = 0.169) and maximum frequency (partial lambda = 0.910; p = 0.229). Classification matrix showed that 60.87 % of total cases were correctly assigned; trills from Isla Mocha were those with the highest score (84.62 %), followed by Navarino (66.67 %), Santa Inés (42.86 %), Manquehue (30.00 %) and Chiloé (25.00 %) (Table 4).

Recordings of repetitive trills were made during the non-breeding season (autumn and winter) in Navarino and Chiloé, to compare with vocalizations in the breeding season (spring). Trills from the non-reproductive season did not differ between both populations ($F_{6, 18} = 1.703$; p = 0.178). In Chiloé, there were no differences between both seasons (ANOVA test; $F_{6, 10} = 0.900$; p = 0.520). To the contrary, in Navarino, there were significant differences ($F_{5, 28} = 5.640$; p = 0.001), being the minimum frequency lower in the breeding season meanwhile the maximum frequency and bandwidth were higher during the breeding season (Table 5).

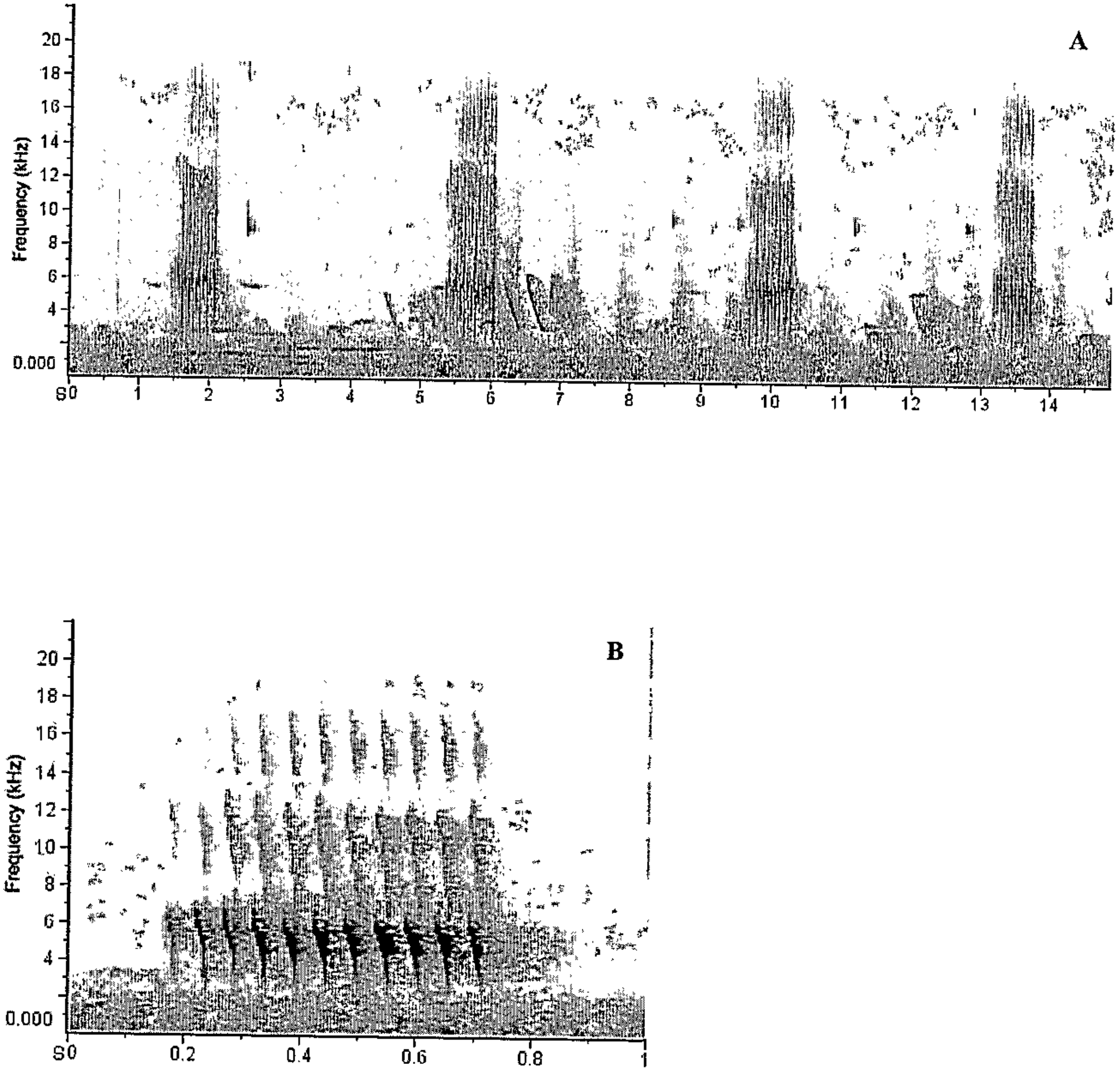

Fig. 3. Representative sonogram of (A) repetitive trills and (B) detail by a Rayadito in Manquehue population.

Table 4. Classification matrix of repetitive trills of Rayadito from five different populations. Rows showed the classification with discriminant function and p indicates the probability to assign trill to each population in function of sample size.

	Percent correct	Navarino p=0.26	Chiloé p=0.12	Mocha p=0.38	C. Manquehue p=0.14	C. Santa Inés p=0.10
Navarino (18)	66.67	12	0	2	2	2
Chiloé (8)	25.00	4	2	1	1	0
Mocha (26)	84.62	1	1	22	1	1
C. Manquehue (10)	30.00	2	2	3	3	0
C. Santa Inés (7)	42.86	2	0	1	1	3
Total (69)	60.87	21	5	29	8	6

Vocal responses to different predators. During antipredatory experiments, Rayaditos used mobbing calls, loud trills and, in a lower proportion, repetitive trills. Therefore, repetitive trill was eliminated from the analysis due to scant sample size. In the analysis I included data of 2006 and 2007 from Chiloé experiments (25 nests). Three notes of mobbing call per individual were selected from each experiment and averaged to analyze acoustical data among different models. Data were normalized with a box-cox transformation. Acoustical responses to different predators in Navarino and Chiloé were analyzed with a two way MANOVA. Data did not show differences in acoustic parameters among Chuncho, Monito del monte or Chincol ($F_{12, 220} = 1.516$; $p = 0.120$) nor interaction between population and models ($F_{12, 220} = 1.398$; $p = 0.168$), but there were differences between Navarino and Chiloé ($F_{6, 110} = 3.919$; $p = 0.001$). Univariate a posteriori tests between both populations showed the differences relied on the duration of each note ($F_{1, 115} = 8.410$; $p = 0.004$) and the duration of three consecutive notes of mobbing calls ($F_{1, 115} = 14.961$; $p < 0.001$), being longer in Chiloé than in Navarino (Fig. 4).

Table 5. Acoustic characteristics of repetitive trills during the breeding and the non-breeding season, in Chiloé and Navarino islands. Data show mean ± SD (sample size). * indicates significant differences obtained with a post hoc univariate test.

		Breeding season	Non-breeding season
Chiloé	Minimum frequency (kHz)	2.32 ± 0.32 (8)	2.31 ± 0.43 (9)
	Maximum frequency (kHz)	10.65 ± 3.12 (8)	10.25 ± 1.76 (9)
	Bandwidth (kHz)	8.33 ± 3.17 (8)	7.94 ± 1.77 (9)
	Peak frequency (kHz)	5.03 ± 0.43 (8)	4.99 ± 0.27 (9)
	Duration of trill (S)	0.64 ± 0.05 (8)	0.56 ± 0.16 (9)
	number of notes per trill	13.88 ± 1.01(8)	11.59 ± 2.49 (9)
Navarino	Minimum frequency (kHz) *	2.21 ± 0.44 (18)	2.66 ± 0.40 (16)
	Maximum frequency (kHz) *	12.45 ± 2.39 (18)	8.84 ± 2.50 (16)
	Bandwidth (kHz) *	10.24 ± 2.36 (18)	6.18 ± 2.63 (16)
	Peak frequency (kHz)	5.03 ± 0.39 (18)	4.97 ± 0.54 (16)
	Duration of trill (S)	0.58 ± 0.09 (18)	0.54 ± 0.09 (16)
	number of notes per trill	12.17 ± 1.79 (18)	12.28 ± 1.77 (16)

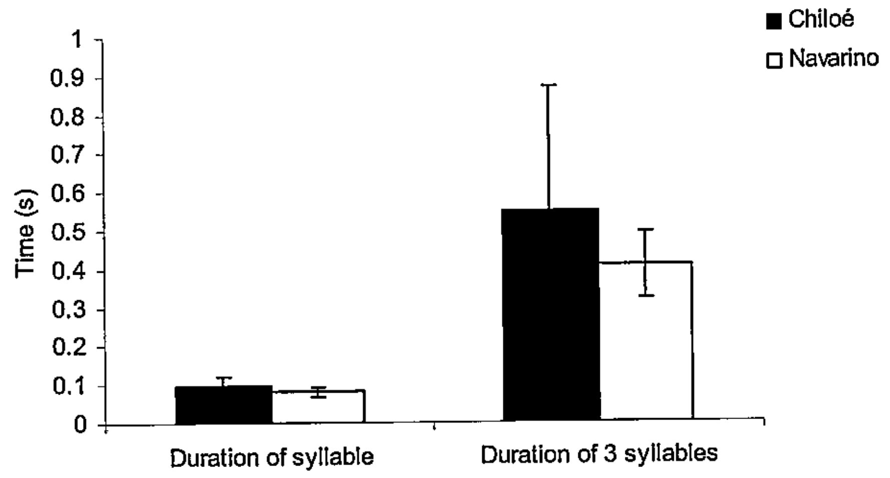

Fig. 4. Duration time (mean ± SD) of mobbing calls notes of Rayaditos during experiments with two different predator and a control, in Chiloé and Navarino. The three consecutive syllables include time between them.

Variables related to the duration of vocalizations were not normal, thus I conducted non-parametric tests on these data. In Chiloé, total time of vocalizations and time of mobbing calls of both parents simultaneously were significantly higher in response to Chuncho than to Monito del monte or Chincol (Friedman ANOVA χ^2 = 20.462; N = 13; df = 2; $p < 0.001$; and χ^2 = 16.449; n = 13; df = 2; $p < 0.001$, respectively). Mobbing calls emitted by only one parent ($\chi^2 = 0.275$; n = 13; df = 2, p = 0.872) and duration of loud trills ($\chi^2 = 1.897$; n = 13; df = 2; p = 0.387) did not differ between the three experiments. In Navarino, total time of mobbing calls during experiments were not different ($\chi^2 = 4.667$; N = 3; df = 2; p = 0.097), likewise as mobbing calls duration of one or two parents ($\chi^2 = 4.667$; n = 3; df = 2; p = 0.097 and $\chi^2 = 4.909$; N = 3; df = 2; p = 0.086) and loud trills time duration ($\chi^2 = 0.286$; N = 3; df = 2; p = 0.867). I found that there were no significant differences between experiments from Navarino and Chiloé, analizing each model separately (Table 6).

Table 6. Statistics for differences in proportion of vocalization duration between Chiloé and Navarino. Mean ± SD (sample size) are shown. No test was significant after sequential Bonferroni correction.

Model		Proportion of vocalization time of			
		one parent	both parents	loud trills	total
Monito del Monte	Chiloé	0.23 ± 0.21 (22)	0.23 ± 0.26 (22)	0.004 ± 0.008 (22)	0.46 ± 0.34 (22)
	Navarino	0.27 ± 0.22 (4)	0.25 ± 0.26 (4)	0.004 ± 0.008 (4)	0.51 ± 0.46 (4)
	Mann-Whitney U	36.5	42.5	43	37
	p	0.593	0.914	0.940	0.619
Chuncho	Chiloé	0.17 ± 0.24 (20)	0.79 ± 0.25 (20)	0.002 ± 0.003 (20)	0.96 ± 0.12 (20)
	Navarino	0.01 ± 0.02 (3)	0.99 ± 0.02 (3)	0.0006 ± 0.001 (3)	0.999 ± 0.0002 (3)
	Mann-Whitney U	9	6	28	6
	p	0.054	0.028	0.830	0.028
Chincol	Chiloé	0.27 ± 0.27 (17)	0.04 ± 0.17 (17)	0.003 ± 0.005 (17)	0.48 ± 0.37 (17)
	Navarino	0.55 ± 0.43 (4)	0.15 ± 0.25 (4)	0.025 ± 0.038 (4)	0.70 ± 0.44 (4)
	Mann-Whitney U	18	23	23	22
	P	0.151	0.217	0.260	0.282

Sound transmission

Experiments were conducted in Navarino (10 times) and Chiloé (9 times) broadcasting the trill six times each. Variables of the six trills per site were averaged and used for statistical analysis. Acoustic variables were different between both populations (MANOVA; $F_{6, 12} = 11.410$; $p < 0.001$). Univariate a posteriori tests showed that the variables that explain the differences were: maximum frequency ($F_1 = 4.991$; $p = 0.039$), bandwidth ($F_1 = 13.559$; $p = 0.002$), duration of trill ($F_1 = 6.535$; $p = 0.020$) and maximum amplitude ($F_1 = 8.470$; $p = 0.010$) (Fig. 5).

On the other hand, habitats were different between Navarino and Chiloé (MANOVA; $F_{5, 14} = 9.749$; $p < 0.001$) and univariate a posteriori test showed that variables that explain differences were number of trees with dbh > 10 cm ($F_1 = 14.407$; $p = 0.001$), and number of obstacles along the transect ($F_1 = 37.096$, $p < 0.001$). Because both variables were correlated ($R^2 = 0.39$; $p = 0.003$; $N = 20$), I used only the number of obstacles along the transect as predictor variable to perform a multivariate regression with acoustic variables that significantly differed between both populations. Multivariate regression was conducted between this variable and acoustic significant variables between both populations ($F_{4, 14} = 4.738$; $p = 0.012$). Bandwidth ($R^2 = 0.26$; $F_{1, 17} = 6.07$; $p = 0.028$; $N = 19$) and maximum amplitude ($R^2 = 0.32$; $F_{1, 17} = 8.15$; $p = 0.011$; $N = 19$) were negatively correlated with the number of obstacles, while duration of trills ($R^2 = 0.15$; $F_{1, 17} = 2.93$; $p = 0.105$; $N = 19$) and maximum frequency were not correlated with habitat features ($R^2 = 0.11$; $F_{1, 17} = 2.04$; $p = 0.171$, $N = 19$). Despite the significances of regressions, the proportion of variation in the dependent variables explained by the model were low, suggesting that other variables might also be important in predicting acoustical "deformation" of the trills in different habitats.

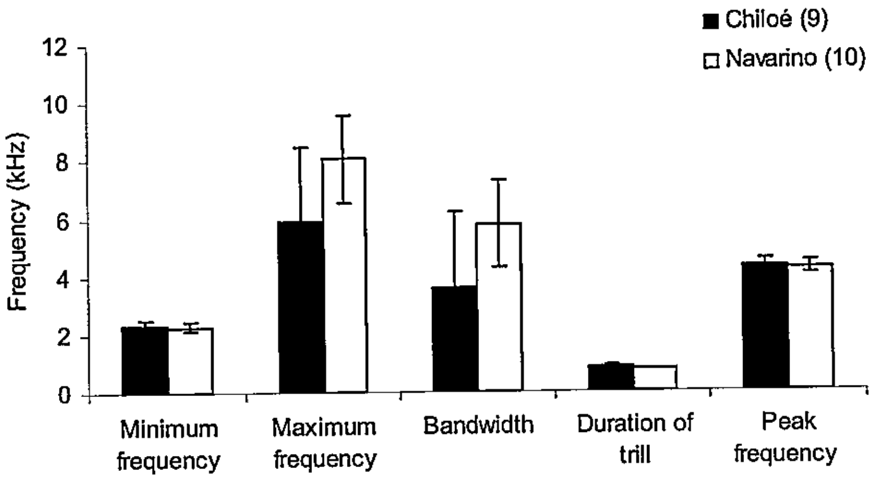

Fig. 5. Acoustic variables (mean ± SD) measured on the same trill emitted in Navarino and Chiloé islands. * = significant differences ($p < 0.05$).

Discussion

Vocalizations of Rayadito analyzed in this study can be divided in four types: mobbing alarm calls, contact calls, loud trills, and repetitive trills. Of these, the mobbing call is, probably, the most recognizable in the temperate southern forests of Chile and Argentina, because they are the first signal we perceive when walking through the forest. Native people (yagans and mapuches) appreciated Rayaditos because they warn about the existence of some threat, like other persons, "warlocks" or dogs, through mobbing alarm calls (Rozzi 2003). My results suggest that only one type of alarm call, that is the mobbing call, is used by Rayaditos when facing different threats which no difference among populations. However, repetitive trills have some variations among populations, although they were no explained clearly by subspecies classification or the acoustic adaptation hypothesis.

Comparisons of each type of vocalization among five populations showed that some variation exist, mainly in repetitive trill, marginally in mobbing calls and no differences were found among loud trills. Rayaditos' vocalizations compared in this study came from five different populations, from south to north: Navarino, Chiloé, Mocha, Cerro Manquehue and Cerro Santa Inés, including the all three subspecies (see Johnson and Goodall 1967, Remsen 2003) and, at least three different types of forests (Armesto et al. 1996b). Valdivian temperate rain forests have a high number of vegetation strata, high stem density and a very high biodiversity and biomass of vascular and non-vascular epiphytes (Armesto et al. 1996a, Arroyo et al. 1996) resulting in a more complex forest than subantartic temperate forests and disturbed sclerophyllous forest. However, Santa Inés relict forest has scattered trees (from 130 to 1500 ind/ha) and little understory (Francois 2004) comparing to Chiloé (2100 ind/ha) (Aravena et al. 2002) and Mocha, and thus, structurally resemble Navarino forests. Acoustic differences in repetitive trills were found between Mocha and Chiloé (for number of notes per trill) and between Mocha and Navarino (for peak frequency). In fact, only trills from Isla Mocha and Navarino were correctly classified in more than 50 % of the cases, being both populations with the higher sample size. Mocha as well as Chiloé and Navarino would be different subspecies, according Johnson and Goodall (1967). Although vocal differences did not corroborate, unequivocally, subspecies division, the Mocha population differed slightly from continental subspecies, represented by Navarino (although also by Manquehue and Santa Inés), and from the third subspecies from Chiloé.

On the other side, acoustic signals can be affected by habitat structure (Morton 1975). My results showed that the same sound (i.e. trill) emitted in two different types of forests (Chiloé and Navarino), suffered modifications in acoustic variables including maximum frequency, bandwidth, sound duration, and maximum amplitude. As predicted by the AAH, higher frequencies were more affected, because their energy is lost through reflections in branches and leaves (Morton 1975), and energy recorded (amplitude) was higher in Navarino were forests are less complex. However, longer trills were recorded in Chiloé than Navarino, and although this result is less clear to explain, reverberations and echoes could have extended it slightly counteracting the attenuation of a more complex habitat. Therefore, acoustical signals transmission is affected differently in Navarino and Chiloé and, thus, songs and long-range acoustic signals would be susceptible to changes that can improve the transmission. Lower frequencies and low rates of notes per second suffer less attenuation and degradation by reverberations in more complex habitats (Richards and Wiley 1980, Slabbekoorn and Smith 2002b) and, thus, songs from Valdivian forest (possibly with the exception of Santa Inés) should have lower frequencies, narrower bandwidth, and lower notes per trill (if duration of each trill not vary), compared to those in Manquehue and Navarino. Maximum frequency and bandwidth did not show significant differences among populations but both variables were lowest in Chiloé and highest in Manquehue (Table 3), meanwhile, the peak frequency was higher in Navarino than in Mocha. However, the number of notes per trill was significantly highest in Chiloé, opposite to AAH predictions. This variable behaves contrary to predictions from the AAH, even in other families, such as Thamnophilidae, because canopy songs have higher number of notes per second than mid- and understory songs (Seddon 2005). Therefore, results suggest that there is no sufficient temporal and/or geographic isolation among these populations that could have produced significant divergence in characteristics of vocalizations in Rayadito, because it is a suboscine passerine, whose songs and calls are innate, and/or that the type of forest is not a selective force enough to change the acoustic parameters of trills in Rayaditos to improve their transmission. That is due to Rayaditos normally sing repetitive trills closer to the canopy (and not at ground level) and thus, frequency attenuation could be similar in different places. However, Rayaditos also feed in edge forests and shrubland habitats, and, in fact, peak frequency of repetitive trills (4.85 kHz, see table 3) is more similar to tropical passerine edge forests bird songs (3.6 kHz for non-oscines and 4.7 kHz for oscines) than upper-forest bird songs (3.1 kHz) (see Morton 1975). Nevertheless, syllables repetition rate and frequency bandwidth of songs are related with body size, beak size and beak gape (Westneat et al. 1993, Podos 2001, Podos et al. 2004b). Therefore, geographical differences in repetitive trills could be associated not only with improvement of signal transmission but with morphological adaptations (Seddon 2005), because body and beak size would be influenced for others ecological factors, such as different food items. Finally, rayadito trills from Chiloé have the same acoustic characteristics in the breeding and the non-breeding season, which make sense because evergreen forest do not change seasonally. However, and contrary to expectations under the AAH, trills from Navarino during the breeding season have higher maximum frequency than during the non-breeding season.

Regarding mobbing calls, these differed among populations though marginally, but univariate tests showed that differences exist between Manquehue and Chiloé, and between Manquehue and Isla Mocha in number of notes of mobbing calls. Again, subespecies would be different among these three regions, and a higher rate of notes per second would be more expected in Manquehue than in another places, because the forest is more open. However, another point to consider is that the Manquehue site is a fragment of secondary forest relatively small, with young trees and scarce natural cavities. Thereby, nest boxes could have enhance breeding densities of cavity nesters, including Rayaditos. For this reason competitive interactions for resources (cavities, territories, and/or food) could resulted also in a higher rate of emission of calls.

However, were trills different because birds emitted different sounds? Or because birds emitted the same sound but different habitats attenuated and modified the sound? If the answer relies in the second question, then changes in trills should be the same that I found when I emitted experimentally the same trill in two different habitats, but I did not find the same pattern. Therefore, birds emit different trills, suggesting that some genetic differences occur, since songs and calls are innate in suboscine birds, and there are no changes by cultural or social influence (Kroodsma 1984, Kroodsma and Konishi 1991). In either case, more detailed experiments are needed to determine the influence of habitat type on songs and calls in Rayaditos, and in order to disentangle how selective forces interact with other traits, like body size, bill size, eavesdropping by predators, among others. Therefore, although differences were not conclusive, the present study shows that acoustic signals, jointly with coloration (Johnson and Goodall 1967) could be expressing certain degree of genetic differentiation among isolated and/or distant populations. Detailed genetic studies would be welcome to confirm or reject this hypothesis.

The most closely related species of Rayadito is the Másafuera Rayadito (*Aphrastura masafuerae*) which is the only other species of genus *Aphrastura,* and it inhabits the island Alejandro Selkirk (33°S and 80°W), 670 km west from the Chilean coast. The Másafuera Rayadito has three types of acoustic signals: alarm call, common call and song (Hahn and Mattes 2000). Alarm calls were characterized by a uniform sequence that could last more than ten minutes, similarly to the mobbing calls of the Thorn-tailed Rayadito. Both species produce this call in the presence of a predatory threat. The alarm calls of the Másafuera Rayadito lie between 1.8 kHz and 7.6 kHz, with 15.2 syllables per second on average, showing somewhat lower but overlapping frequencies, narrower bandwidth, and more notes per second than the Rayadito (Table 1). Common calls of *A. masafuerae*, on the other side, are similar to Rayadito's repetitive trill, produced by both, males and females, with regular pauses between each trill. However, *A. masafuerae* common calls are longer (1.06 s with pauses of 2.1 s) with narrower bandwidth (3–6 kHz) and more rapidly modulated (14–17 notes per trill) than Rayaditos repetitive trills, although all variables overlaped (see Table 3 and Fig. 3). Nevertheless, other behaviors associated with this call in the Másafuera Rayadito is similar to that observed in the Thorn-tailed Rayadito, like searching for food or moving between branches. Because I heard Rayaditos singing repetitive trills more frequently in the breeding season, I suspect that its function is territorial and/or long range mate communication, possibly singing in sex duets. I did not record a sound such as the song described for Másafuera Rayadito, although no field work were conducted before the sunrise. However, a similar song would be emitted during the breeding season by Rayaditos, during darkness previous to the dawn (C. Estades pers. com.). Otherwise, loud trills, very common in Rayaditos, were not described for Másafuera Rayadito.

Vocalizations to different predators

During antipredatory experiments, Rayaditos used mainly mobbing alarm calls. These vocalizations were acoustically the same for aerial and terrestrial predators, and, also in response to a non threatening passerine bird, in Navarino as well as in Chiloé. Also, human approaching to the nest elicited the same vocal response during the breeding season (S. Ippi pers. obs.). However, the aerial predator (Chuncho) elicited a longer vocal response by the two parents. The Chuncho is a small owl that predates above juvenile and adult birds and mice (Jiménez and Jaksic 1989, Rozzi 2003), representing a real threat for Rayaditos, especially when it is near to their nests. Because vocal behavior of Rayaditos differed between Chuncho and control (Chincol) I can conclude that they have the ability to recognize this aerial predator (Welbergen and Davies 2008). In fact, Rayaditos entered to the nest to fed chicks only in two times out of 24 experiments carried out with Chuncho. A similar behavior has been reported for the Másafuera Rayadito, who emit alarm calls for a long time and decrease in almost 50 % the feeding frequency when Másafuera Hawks (*Buteo polyosoma exsul*) were perched close to the nest (Hahn et al. 2004). Interestingly, acoustic parameters as well as duration of vocalizations during mammalian predator and control encounters were not different, neither in Chiloé nor in Navarino, suggesting two possibilities: 1) Rayaditos cannot distinguish between both species, or 2) they distinguish predators but direct nest defense behavior is weak, possibly using nest site selection to counteract this kind of threat (see chapter 1 and Cornelius 2008). Monito del monte is a marsupial considered a living fossil in the fauna of South America, inhabits between 35°S and 44°S and associated with *Nothofagus* forests (Redford and Eisenberg 1992, Muñoz Pedreros and Yañez Valenzuela 2000, Lobos et al. 2005). Monito del monte has an omnivorous diet, including insects, fruits, eggs, and chicks (Jiménez and Rageot 1979). Moreover, sometimes the Monito del monte predates on nests and/or uses the nest boxes to roost, which suggests a potential competition for natural cavities with Rayaditos and other cavity nesters in Chiloé (S. Ippi pers. obs., J. L. Celis-Diez pers. comm.). Unfortunately, vocal recordings from Navarino were very scarce and, hence the lack of differences in vocalizations between Monitos and Chincols should be taken cautiously. There exists the possibility that Rayaditos do not recognize Monito models as predators, possibly because they are nocturnal and/or because the model was inert and non-moving, and given that the Monito is an acrobatic mammal, it might have diminished the response of Rayaditos. Some preliminary experiments not shown here, were conducted with Monito del monte mounts in Chucaos' nests (*Scelorchinus rubecula*), obtaining no response from the parents (M. Willson et al. unpub. data). To the contrary, when alive Monitos del monte were freed close to Chucaos, they tried to attack them (J. L. Celis-Diez pers. com.). Finally, other non-vocal behaviors could be used by Rayaditos to deter nest predation by Monitos such as staying longer inside the nest or select cavities based in the previous breeding attempts or epiphyte cover (Cornelius 2008). Although there is some evidence that Monito del monte can kill adult Rayaditos in their nests (Jiménez and Rageot 1979), risk of themselves would be much lower compared with Chuncho, and Rayaditos would not invest energy in vocalizations but in feeding chicks. Therefore, Rayaditos mobbing behavior would be directed more to adult predators than nest predators (Arnold 2000).

Mobbing behavior is an antipredator strategy that includes a set of behaviors such as prey approaching, repetitive and loudly calls, and sometimes physical attacks attracting, simultaneously, other birds (Curio et al. 1978, Caro 2005). Mobbing behavior of Rayaditos were observed several times in both the breeding and the non-breeding season, involving several individuals of the same and different species. However, during the trials in the breeding season, when predator mounts were close to the nest, approaching of other species was rare (sometimes hummingbirds (*Sephanoides sephaniodes*), White-crested Elaenias (*Elaenia albiceps*) and only once, 3–4 Austral Blackbirds (*Curaeus curaeus*), approached but for a short time) and others Rayaditos were never observed, although their nests could be very close between each other. Therefore, mobbing calls (and associated behaviors) seem very expensive for Rayaditos because they cannot attract other birds to the nest (during trials conducted during the breeding season), making mob durable and ineffective and, on the contrary, increasing their risk (Krama and Krams 2005). Additionally, information about location of their nest would be confirmed by this behavior while other predators can eavesdrop and attack the nest in the future (Searcy and Nowicki 2005). Then, what is the purpose for emitting mobbing calls, loudly and repetitive, during a long period of time, very close to the nest? The first suggestion to explain this behavior is that mobbing alarm calls of Rayaditos would have some characteristics that can confuse aerial predators like a Chuncho. Behavior associated with mobbing calls included permanent change of position, usually moving frequently at 0.50 – 2 m of distance to the model with stereotyped movements of wings and tail (S. Ippi pers. obs.). Frequent changes of position and the high rate of emission of mobbing call notes by both parents simultaneously would contribute to decrease the success of attacks by predators (Curio 1978, Caro 2005). During the analysis of spectrograms of Chuncho experiments, frequently I observed that notes of mobbing calls of both Rayaditos were temporally simultaneous, making more difficult the analysis and the detection of one or both parents emitting alarm calls. Generally, owls are characterized by a high prey detection, because they have a very accurate auditive system (Payne 1971). However, it is possible that synchronized mobbing calls emitted by both parents, necessarily from different positions, could better confuse a predator, thus decreasing the probability of an immediate attack and/or decreasing the probability of a successful attack. During the non-breeding season these confusion effects would be enhanced when flocks of Rayaditos mob predators. Otherwise, high rate of note repetition in the alarm calls could avoid false alarms and, also, the risk that the pair -or flock companion during the non-breeding season- will not hear the alarm (Leavesley and Magrath 2005), meanwhile a greater number of elements in the call could be indicating the proximity of a predator (Leavesley and Magrath 2005). Additionally, I observed that, when parents started to emit alarms, begging vocalizations of chicks stopped immediately, possible making more difficult the exact location of the nest by the predator, a behavior described also for other birds (Curio 1978, Knight and Temple 1988, Caro 2005). Without excluding previous ideas, approaching and mobbing calls of Rayaditos seem to be a costly signal, that honestly communicate the higher quality of the emissary (Zahavi 1975), and deterrent predator to attack. Therefore, mobbing calls of Rayaditos might serve like, for instance, stotting in Thomson gazelles (*Gazella thomsoni*) (Fitzgibbon and Fanshawe 1988), or song of Skylarks (*Alauda arvensis*) when escaping from Merlins (*Falco columbarius*) (Cresswell 1994). Finally, the move-on hypothesis is the most accepted hypothesis that explain the benefits of mobbing behavior (Caro 2005). This hypothesis asserts that while more intense is the mobbing, the sooner the predator should leave the area, and implies that mobbing avoid or decrease the probability of predation and, also, decrease the probability that a predator return to the same area (Caro 2005). Therefore, by these means, Rayaditos not only protect themselves, but also would extend the protection to the near future, when fledglings abandon the nest, thus making the mobbing calls a type of parental investment (Barash 1975, Andersson et al. 1980). Unfortunately, studies about the predator behavior when they are mobbed are lacking, and experimental evidence is needed to support these ideas.

I expected that vocal behavior in response to an unknown mammal predator in Navarino would be different than in Chiloé. However, although acoustics recordings of predator experiments in Navarino were very low, no differences were found among vocalizations between Monito del monte and Chincol, in both populations and, also, no difference existed in vocalizations towards Monito between Navarino and Chiloé. *Nothofagus* forests appeared in the Fuegian-Patagonian region around 8 000 BP and their presence were corroborated by palinology records at 6 000 BP in Navarino Island (Heusser 1998, Coronato et al. 1999, Rabassa et al. 2000, Solari 2007). Therefore, I can suspect that temperate forest avian assemblages arrived to the island with tree forest or shortly after. Isolation and extreme climatic conditions could have avoided (or delayed) colonization of mammal predators. However, because calls are innate, a long period of evolutionary time is also likely to be necessary to change innate predispositions (Hollén and Manser 2007), a period that perhaps has not yet elapsed. Otherwise, a high gene flow between the island and other populations (with coexistent mammalian predators), could also explain the results.

Innate vocalizations of suboscines studied in Thamnophilid antbird species have evolved in response to morphological and acoustic adaptations and species recognition (Seddon 2005). Songs serve as mating signals, thus divergences in these signals could reinforce the isolation in allopatric species or increase the reproductive isolation in isolated populations (Endler 1992, Boughman 2002), even resulting in different subspecies. However, regarding call evolution, patterns are more complex, first, because the enormous quantity of call types occurring in birds, and second, because a strong interspecific component is involved (Magrath et al. 2007). Aerial alarm calls might be heared by conspecifics and other preys but not by predators, contact calls might be heared only by family or flock members, and mobbing calls might attract other possible preys of different species, among others (Marler 2004). Geographic differentiation in calls and trills of Rayaditos were no explained totally neither by AAH nor previous subspecies classification, and also, were no differences in vocal behavior when faced to mammalian nest predator between Navarino and Chiloé. Although connectivity between forests is important for Rayaditos in order to disperse (Cornelius 2006), gene flow could be high through migration or dispersal, producing a situation where vocal phenotypes may not be optimally adapted to each habitat characteristics, at least from an acoustical signal transmission point of view (Lenormand 2002).

DISCUSIÓN GENERAL

El rayadito es una especie abundante que habita a lo largo de aproximadamente 26 grados de latitud, a ambos lados de la Cordillera de Los Andes y también en las islas boscosas del extremo sur de su distribución (Johnson y Goodall 1967, Remsen 2003, Rozzi 2003). Se trata de un ave conspicua tanto por su comportamiento relativamente confiado y gregario, como por sus vocalizaciones. A pesar de la amplia e interrumpida distribución de esta especie, no se encontró una variación geográfica acentuada entre poblaciones tan distantes como Cerro Manquehue e isla Navarino, ni tan aisladas como isla Mocha y Cerro Santa Inés. Esta escasa variación geográfica se detectó tanto en la conducta de defensa del rayadito, como en las características acústicas de las vocalizaciones.

Curiosamente y contrario a lo esperado, la conducta de defensa del nido, es decir, la conducta mostrada frente al monito del monte no fue diferente entre las tres poblaciones. El monito del monte es un marsupial presente desde los 35° S hasta los 44° S, asociado a los bosques de *Nothofagus* (Redford y Eisenberg 1992, Muñoz Pedreros y Yañez Valenzuela 2000, Lobos et al. 2005), principalmente arborícola y de hábitos crepusculares y/o nocturnos. Incluye en su dieta insectos, frutas, huevos y polluelos (Jimenez y Rageot 1979). Además de ser reconocido como depredador de nidos de aves, también podría ser competidor por cavidades, ya que se han registrado numerosos casos en que el monito utiliza las cajas-nido para hibernar y dormir. Además, estadísticamente no se encontraron diferencias entre las respuestas de los rayaditos al monito y al control-chincol en la etapa de cuidado de polluelos, aunque una diferencia notoria es que el monito no fue atacado físicamente, y el chincol sí. Estos resultados sugieren la posibilidad de que el rayadito no reconozca al monito del monte como una amenaza o bien, que poseen otras estrategias para contrarrestarla. Se ha encontrado evidencia que sugiere que el rayadito selecciona activamente las cavidades que utiliza para reproducirse (Cornelius 2008). A partir del año 2006, las cajas anideras de Chiloé se protegieron contra la depredación de mamíferos, específicamente del monito del monte. A partir de dicha temporada la depredación de nidos disminuyó a cero en las cajas protegidas, a pesar de que durante el invierno, los monitos conseguían entrar e hibernar en ellas, aunque en una menor proporción en comparación a las temporadas anteriores al uso de dicha protección. En los años previos a 2006, los rayaditos que sufrieron un evento de depredación no volvieron a utilizar las cajas en la temporada siguiente (C. Cornelius com. pers., y R. A. Vásquez com. pers.), a la vez que la utilización de cajas bajó drásticamente a casi cero en tres años (R. A. Vásquez com. pers). Por otro lado, en las temporadas de 2006 y 2007, aquellas cajas que fueron ocupadas por monitos durante el invierno, no fueron utilizadas por el rayadito en la primavera siguiente, a pesar de que estos monitos fueron reubicados en cavidades naturales y las cajas fueron limpiadas durante julio-agosto (J. L. Celis-Diez y S. Ippi datos no publicados). Lo anterior sugiere que el rayadito es capaz de recordar y evitar aquellas cavidades donde sufrieron depredación o encontraron monitos hibernando durante la época no reproductiva. De hecho, de 43 intentos reproductivos monitoreados durante 2006 y 2007, sólo en una ocasión la caja había sido usada por monitos durante el invierno anterior. Una estrategia de defensa del nido podría ser la selección de cavidades en función de la cobertura de epífitas y follaje en los troncos (Cornelius 2008), junto con la información obtenida de las experiencias reproductivas previas (Hoover 2003) y la memorización de las cavidades utilizadas por el depredador durante el invierno. Esta última idea abriría una interesante línea de investigación acerca del rol de la memoria en la defensa del nido, la conducta antidepredatoria y el aprendizaje en suboscinos.

Es necesario mencionar que existen dos factores metodológicos que pueden haber influido en la conducta demostrada por el rayadito frente al monito del monte. En primer lugar, el monito del monte es un animal crepuscular-nocturno y cabe la posibilidad de que el rayadito no lo reconozca como una amenaza, ya que no lo vería atacar. En segundo lugar, el monito es una especie altamente móvil, y no existen registros de esta especie en actitud de acecho o permaneciendo largo tiempo inmóvil, por lo cual el estímulo utilizado (monito taxidermizado) podría verse disminuido y por lo tanto, la respuesta del rayadito se vería disminuida o anulada. Sin embargo, la utilización de mamíferos taxidermizados como modelos de depredadores de nidos ha sido una metodología comúnmente usada, y en la mayoría de los casos validada por la conducta ante un estímulo control (Knight y Temple 1988, Stenhouse et al. 2005).

Por otro lado, la conducta antidepredatoria de los rayaditos que habitan la isla de Navarino fue más agresiva que la de aquellos de Chiloé y Cerro Manquehue. Es decir, los rayaditos de isla Navarino emitieron llamadas de alarma/acoso por más tiempo y se acercaron a menor distancia del depredador (chuncho), abandonando casi completamente las actividades de cuidado parental y alimentación, a la vez que emitieron llamadas de alarma/acoso por tanto tiempo como permaneció el estímulo en las cercanías del nido. Una mayor agresividad en Navarino podría estar relacionada con una menor duración de la temporada reproductiva, favoreciendo una defensa más activa, dadas las menores posibilidades de renidificación. Algunos estudios también han relacionado una mayor intensidad de la conducta antidepredatoria con un mayor nivel de stress (Thaker et al. 2009), lo que en el caso de la población de Navarino podría estar relacionado con la rigurosidad climática. Por otro lado, la predicción de que la conducta antidepredatoria del rayadito sería equivalente en todas las poblaciones, puesto que habita en simpatría con el chuncho, se hizo bajo el supuesto de que la presión de depredación dada por esta especie sería similar en todas las poblaciones estudiadas. Es posible, sin embargo, que la abundancia de este depredador varíe entre poblaciones y esto genere diferentes presiones para el ensamble de presas. Sin embargo, la escasa literatura que documenta la abundancia del chuncho a lo largo de su distribución en Chile indica que es más o menos constante y común, por lo menos en los sectores centrales y sureños de su distribución (Jiménez y Jaksic 1989). No obstante, la diversidad y abundancia de presas si es diferente en poblaciones más australes (Rozzi et al. 1996a, b, Anderson y Rozzi 2000, Ippi et al. 2009), lo que podría derivar en un aumento del consumo de rayaditos por parte del chuncho. Cabe señalar que en la Isla Navarino no habitan especies de reptiles ni anfibios que puedan ser incorporados en la dieta del chuncho y solo se encuentran dos especies nativas de roedores.

Las comparaciones de las vocalizaciones registradas en las cinco poblaciones mostraron que existen ciertas diferencias, principalmente en los trinos repetitivos y marginalmente en las llamadas de alarma/acoso, aunque no se encontraron diferencias en los trinos fuertes. Las variables acústicas de los trinos repetitivos que difirieron entre las poblaciones fueron la frecuencia de máxima energía (entre isla Mocha y Navarino) y el número de notas por trino (entre Chiloé e isla Mocha). Las tres subespecies descritas para rayadito se encuentran en isla Mocha, Chiloé y el continente, que incluye Cerro Santa Inés, Cerro Manquehue e isla Navarino. Por lo tanto, se detectaron diferencias entre poblaciones que serían subespecies distintas, pero estas diferencias no fueron consistentes, a través de todas las poblaciones. Por otro lado, estos resultados tampoco se ajustaron completamente a lo predicho por la hipótesis de adaptación acústica (Morton 1975), ya que, si bien la frecuencia de energía máxima fue mayor en Navarino que en isla Mocha (Navarino es un tipo de bosque más abierto que isla Mocha), el número de notas por trino fue máximo en Chiloé, donde justamente, la mayor complejidad estructural del bosque aumentaría la degradación de la señal por reverberancia y atenuaría más rápidamente la calidad de la señal. Es decir, la variación geográfica encontrada en los trinos repetitivos no se puede explicar inequívocamente, ni por la actual clasificación de subespecies ni por la hipótesis de adaptación acústica. No obstante, las diferencias vocales encontradas podrían ser causadas por una variación genética subyacente ya que las vocalizaciones en suboscinos son innatas (Kroodsma 1984, Kroodsma y Konishi 1991) y podrían responder a presiones del ambiente, aunque no se puede descartar la posibilidad de que las diferencias sean producto de plasticidad fenotípica (West-Eberhard 2003). La diferenciación vocal y la formación de dialectos entre especies de suboscinos ocurrirían más lentamente que en oscinos, debido a que ésta requeriría de cambios a nivel genético. En cambio, en oscinos, las variaciones vocales que desembocan en la formación de dialectos regionales, podrían reflejar tanto plasticidad fenotípica como adaptación local originada a partir de diferenciación interpoblacional vía aislamiento genético (véase West-Eberhard 2003). La formación de dialectos en los cantos de los paseriformes, particularmente de los oscinos, ha sido considerada como la posible clave que permitió una rápida radiación en este grupo de aves, ya que podría constituir un efectivo mecanismo de aislamiento reproductivo (Nottebohm 1972, Podos et al. 2004). Sin embargo, no se ha encontrado una correlación entre aprendizaje y diversidad específica en aves actuales (Baptista y Trail 1992). Más aún, recientemente se ha encontrado evidencia de que tanto las variables ecológicas relacionadas con la transmisión eficiente del sonido y la morfología del pico (relacionada con la alimentación) como las de reconocimiento vocal de especies (básicamente al momento de formar una pareja reproductiva), habrían influido en la evolución de los suboscinos (Seddon 2005). Por lo tanto, la comparación a escala geográfica de los rasgos conductuales y vocales en aves, sería útil para entender los mecanismos comportamentales que conducen a cambios microevolutivos e incluso a la formación de especies (Foster 1999), en aves con y sin aprendizaje vocal. A este respecto, la variación vocal detectada en los trinos repetitivos del rayadito, sugiere que podrían existir mecanismos de selección divergentes o frecuencia-dependiente entre ellas. Sin embargo, como estas diferencias son escasas y no fácilmente explicables por la hipótesis de adaptación acústica se sugiere que existiría, a la vez, un flujo genético suficiente como para diluir diferencias acentuadas e incluso evitar adaptaciones locales (Lenormand 2002; R. A. Vásquez, datos no publicados).

En el caso de las llamadas de alarma/acoso, éstas sólo difirieron levemente entre las poblaciones, a la vez que no se encontraron diferencias acústicas en la respuesta vocal emitida frente a los distintos estímulos presentados durante la temporada reproductiva. Es decir que, en una primera instancia, sólo existiría un tipo de llamada de alarma/acoso para varios tipos de situaciones de riesgo. Esta llamada de alarma/acoso es parte fundamental del comportamiento de acoso (*mobbing behavior*), el cual constituiría la base de la conducta de defensa del rayadito frente a distintos estímulos, tanto depredadores como competidores, a lo largo de las tres poblaciones estudiadas.

El comportamiento de acoso ha sido descrito principalmente en aves y mamíferos y consiste en la aproximación a un depredador, generalmente inactivo (Altmann 1956, Curio 1978, Curio et al. 1978), aunque también puede ir dirigido a pequeñas especies que no representan peligro alguno para los acosadores (Arnold 2000). En el caso específico del rayadito, el comportamiento de acoso se caracteriza por un acercamiento a la potencial amenaza (depredador o competidor), acompañado de cambios constantes de percha, abertura y cierre de alas, y fuertes y repetidas llamadas de alarma/acoso que se extienden por largo tiempo, todo esto expresado por ambos integrantes de la pareja. Dicha conducta fue observada tanto en despliegues territoriales como antidepredatorios, con ligeras diferencias: los ataques físicos fueron dirigidos prácticamente sólo al chincol y al macho conespecífico y el tiempo durante el cual permanecieron cerca del estímulo realizando despliegues visuales y vocales fue mucho más largo cuando se enfrentaron al chuncho. Dado que estos despliegues son forzosamente costosos, constituirían una señal honesta de calidad individual (Zahavi 1975) que puede ser recepcionada por el propio individuo acosado (depredador o competidor) (Fitzgibbon y Fanshawe 1988, Cresswell 1994), y/o por posibles aliados conespecíficos (Maklakov 2002), o futuras parejas (Arnold 2000). El resultado de esta señalización sería disuadir tanto a depredadores como a competidores, de continuar o comenzar un ataque, mientras que, simultáneamente, individuos de distinto sexo podrían considerar los beneficios de aparearse o aliarse con el acosador. Esta disuasión se potenciaría si participan muchos individuos ya que crearían un efecto de dilución y/o confusión que disminuiría el éxito de un ataque (Altmann 1956, Caro 2005). De esta manera, mientras más intenso es el acoso, el depredador se alejará más rápidamente y a mayor distancia (Pettifor 1990), y disminuirá la probabilidad de que dicho depredador retorne al área en la que fue acosado (Caro 2005). Considerando esta última idea, el rayadito estaría también haciendo una "inversión a futuro" al acosar intensamente a un depredador, porque al evitar su regreso, protegería a sus próximos e indefensos volantones. Es decir, el comportamiento de acoso, no solo funcionaría como estrategia antidepredatoria sino también de defensa del nido, es decir de cuidado parental (Barash 1975, Andersson et al. 1980). Finalmente, las llamadas de alarma/acoso interrumpen las llamadas de los polluelos dentro del nido (S. Ippi, obs. pers.), por lo cual será más difícil localizar el nido para atacarlo, disminuyendo los riesgos involucrados en el reclamo de los polluelos (Leech y Leonard 1997, Fontaine y Martin 2006), un rasgo que se ha descrito también en otras aves (Knight y Temple 1988, Caro 2005). El comportamiento y las vocalizaciones de acoso, por tanto, cumplirían varias funciones simultáneamente (Marler 2004) y serían útiles frente a distintos tipos de amenazas: rivales hetero y conespecíficos, depredadores de adultos y depredadores de nidos. Una estrategia conductual de defensa única y simple podría significar para el rayadito una ventaja a la hora de colonizar exitosamente ambientes nuevos, con distintos ensambles de competidores y depredadores. Si consideramos su elevada abundancia a lo largo de todo su rango de distribución, esto podría efectivamente haber sucedido durante la recolonización de los ambientes boscosos, después de la última glaciación. Experimentos más detallados son necesarios para dilucidar cuáles son las ventajas de utilizar esta conducta, pero, sobre todo, es necesario integrar la respuesta del depredador y/o competidor en el estudio conductual de este tipo de interacciones (Caro 1989, Caro 2005).

Un rasgo inesperado en la conducta del rayadito fue la elevada agresividad demostrada hacia el chincol, el cual supuestamente estimularía una respuesta neutra o basal, dado que es una especie co-existente, que incluso prácticamente no se sobrepone en nicho alimenticio ni en uso de refugios con el rayadito (véase Dunn et al. 2004, Stenhouse et al. 2005, Duckworth 2006, para ejemplos de estudios que utilizan especies neutras como controles experimentales). Dado que prácticamente no se encontraron diferencias estadísticamente significativas entre la conducta territorial frente a un macho conespecífico y un macho de chincol, se sugiere la existencia de territorialidad intra e interespecífica en el rayadito, por lo menos, durante la época reproductiva. La territorialidad intraespecífica constituiría un rasgo adaptativo, dados los altos niveles de competencia que pueden generarse por recursos limitantes, como son las cavidades naturales (Tomasevic y Estades 2006, Cornelius et al. 2008). La territorialidad interespecífica surgiría como un subproducto de la territorialidad intraespecífica (Murray 1981), o en ocasiones, como respuesta a similitudes morfológicas y/o a recursos limitantes compartidos (Murray 1971, Tynkkynen et al. 2006). En relación a los recursos alimenticios, ambas especies tienen cierto grado de omnivoría. El rayadito es principalmente insectívoro aunque puede consumir frutos y/o semillas y el chincol, si bien es principalmente granívoro, también incluye insectos en algunas épocas del año (Grigera 1976, 1982, López-Calleja 1995, Novoa et al. 1996, Estades 2001). Dicha territorialidad interespecífica podría ser también un rasgo que permitiría al rayadito defender su territorio frente a cualquier tipo de amenaza aunque ésta sea desconocida. Aunque esta conducta no estaría exenta de los costos energéticos que conlleva atacar a especies inofensivas, también podría haber sido determinante en el hecho de que el rayadito sea una especie exitosa (i.e., abundante) a lo largo de toda su distribución.

Por lo tanto, este estudio permitió detectar dos características que podrían ser claves en el éxito del rayadito a lo largo de todo su rango de distribución. En primer lugar, el comportamiento de acoso, y en particular la llamada de alarma, constituirían la principal estrategia defensiva en esta especie. En segundo lugar, la existencia de territorialidad interespecífica, la cual es similar a la intraespecífica, tanto en intensidad como en el tipo de los despliegues realizados, permitiría enfrentar exitosamente amenazas desconocidas. Considerando que el rayadito es una especie ampliamente distribuida, que habita diferentes tipos de bosque, y que comparte con un ensamble variable de especies de depredadores y competidores, el mantenimiento de una agresividad relativamente alta, frente a cualquier tipo de amenaza potencial, le permitiría hacer frente a la amplia gama de amenazas que se encuentren a lo largo de su distribución geográfica. Más aún, en conjunto con otros rasgos de historia de vida, le permitiría colonizar otros tipos de ambientes enfrentándose exitosamente a los peligros presentes en cada sitio. Es decir, la selección a favor de una alta agresividad durante la temporada reproductiva frente a "amenazas reales" (e.g., chuncho, rival conespecífico) podría dar como subproducto la existencia de estos comportamientos dirigidos a individuos desconocidos o que no representan una amenaza "real" (e.g., chincol) (Murray 1981). Sin embargo, es necesario realizar estudios incluyendo variables relacionadas con los costos y/o beneficios sobre la adecuación biológica (*fitness*) del rayadito para estimar cuán adaptativos pueden ser estos rasgos.

Resumiendo, la baja variabilidad interpoblacional de las características acústicas de las vocalizaciones del rayadito, sumado a la también baja variabilidad interpoblacional en las conductas de defensa, sugieren que existe un alto flujo génico o un escaso aislamiento temporal y/o espacial, que impide la divergencia conductual entre las poblaciones, limitando la adaptación local (Lenormand 2002). Por lo tanto, la migración y la condición innata de las vocalizaciones en suboscinos podrían ser factores que limitan cambios adaptativos "rápidos" de sus vocalizaciones y, en general, también de las conductas de defensa. Para finalizar, los resultados de esta tesis sugieren que una agresividad generalizada durante la época reproductiva (que podría estar relacionada con las cavidades como un recurso limitante) y el comportamiento de acoso, son componentes principales de la conducta de defensa, y constituirían características fundamentales que determinan que los rayaditos habiten exitosamente un amplio rango latitudinal y una gran variedad de hábitats boscosos.

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APPENDIX I

Table. Presence/absence of bird species seen in edge and interior forest in Navarino and Chiloé Islands. Species listed for Cerro Manquehue are not forest exclusive and no correspond to formal point counts. Aquatic and semi–aquatic species that frequent interior forest were excluded.

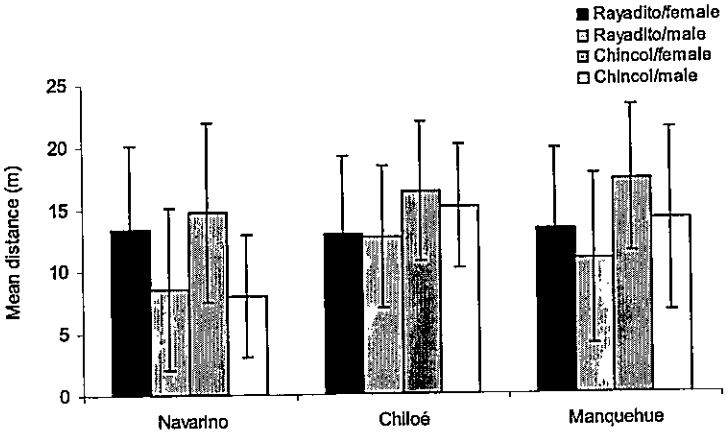
Species	Family	Navarino Island[1]	Chiloé Island[2]	Cerro Manquehue[3]
Cathartes aura	Cathartidae		x	
Coragyps atratus	Cathartidae		x	
Accipiter chilensis	Accipitridae	x		x
Circus buffoni	Falconidae		x	
Parabuteo unicintus	Accipitridae		x	x
Buteo polyosoma	Accipitridae		x	x
Buteo ventralis	Accipitridae		x	
Caracara plancus	Falconidae	x	x	x
Milvago chimango	Falconidae	x	x	x
Falco sparverius	Falconidae	x		x
Falco femoralis	Falconidae			x
Falco peregrinus	Falconidae		x	x
Columba araucana	Columbidae		x	x
Zenaida auriculata	Columbidae			x
Enicognatus ferrugineus	Psittacidae	x	x	
Enicognathus leptorhynchus	Psittacidae		x	
Bubo magellanicus	Strigidae	x	x	x
Tyto alba	Tytonidae	x	x	x
Strix rufipes	Strigidae	x	x	x
Glaucidium nanum	Strigidae	x	x	x
Sephanoides sephaniodes	Trochilidae	x	x	x
Campephilus magellanicus	Picidae	x	x	
Colaptes pitius	Picidae			x
Picoides lignarius	Picidae		x	x
Cinclodes patagonicus	Furnariidae	x	x	
Cinclodes oustaleti	Furnariidae	x	x	
Cinclodes fuscus	Furnariidae	x	x	
Pygarrhichas albogularis	Furnariidae	x	x	
Sylviorthorhynchus desmursii	Furnariidae		x	
Aphrastura spinicauda	Furnariidae	x	x	x
Leptasthenura aegithaloides	Furanariidae		x	x
Pteroptochos tarnii	Rhinocryptidae		x	
Pteroptochos megapodius	Rhinocryptidae			x

Scelorchilus rubecula	Rhinocryptidae		x	
Eugralla paradoxa	Rhinocryptidae		x	
Scytalopus fuscus	Rhinocryptidae			x
Scytalopus magellanicus	Rhinocryptidae	x	x	
Lessonia rufa	Tyrannidae		x	
Coloramphus parvirostris	Tyrannidae	x	x	
Xolmis pyrope	Tyrannidae	x	x	x
Elaenia albiceps	Tyrannidae	x	x	x
Anairetes parulus	Tyrannidae	x	x	x
Tachycineta meyeni	Hirundinidae	x	x	
Pygochelidon cyanoleuca	Hirundinidae	x		
Troglodytes musculus	Trogloditidae	x	x	x
Phytotoma rara	Cotingidae			x
Turdus falcklandii	Turdidae	x	x	
Mimus tenca	Mimidae			x
Curaeus curaeus	Emberizidae	x	x	x
Phrygilus patagonicus	Fringillidae	x		
Diuca diuca	Emberizidae			x
Zonotrichia capensis	Emberizidae	x	x	x
Carduelis barbatus	Fringillidae	x	x	x
Total raptor species		8	13	12
Total species		29	42	32

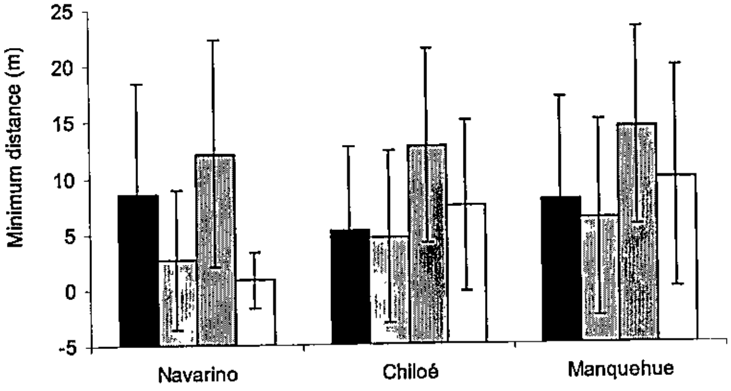
[1] Anderson and Rozzi 2000, Ippi et al. 2009; [2] Rozzi et al. 1996a, Jaramillo 2003; [3] Chicharro et al. 2007, Armesto et al. 2008

APPENDIX II

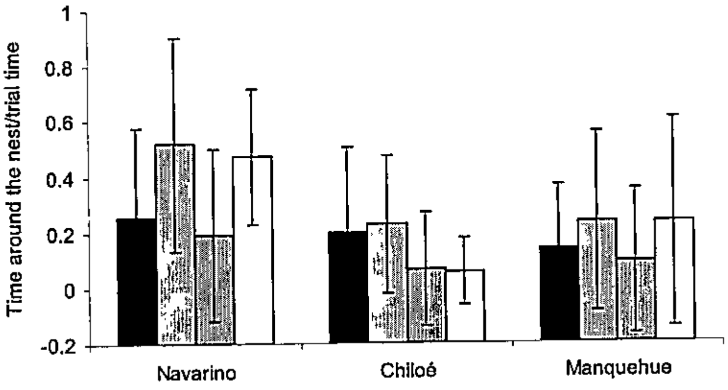
a)



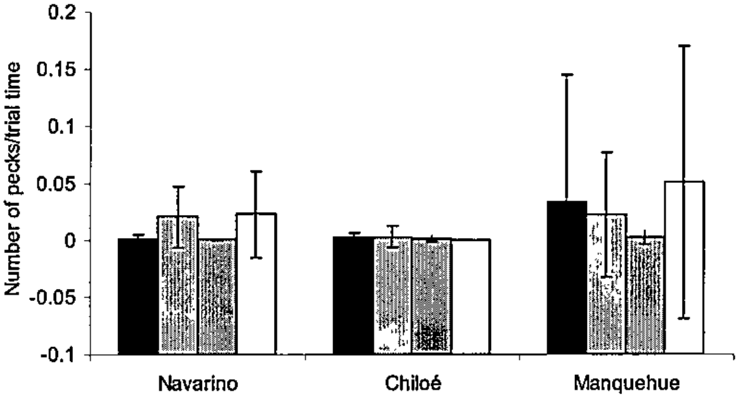
b)



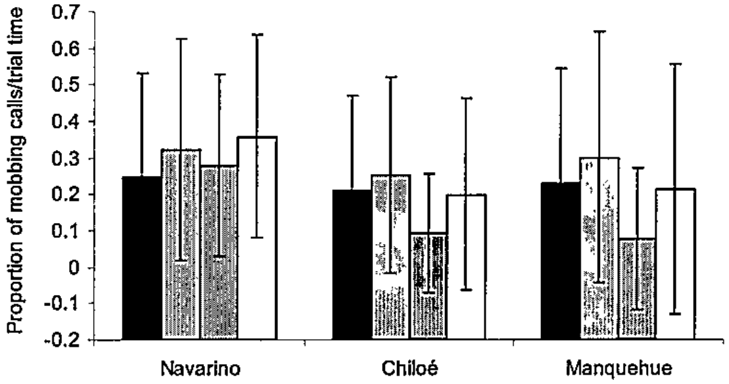
c)



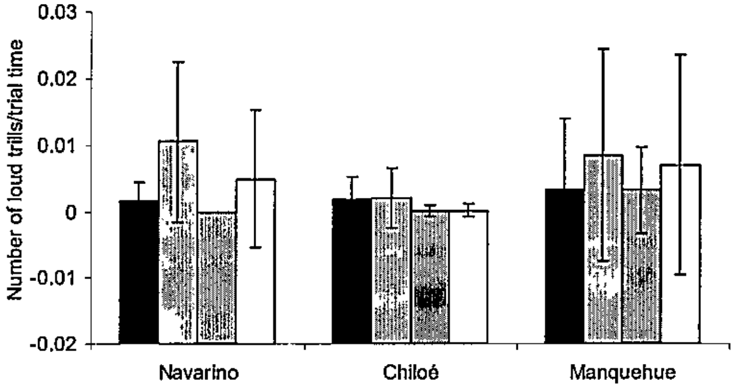
d)


Number of pecks/trial time
0.2
0.15
0.1
0.05
0
-0.05
-0.1
Navarino
Chiloé
Manquehue

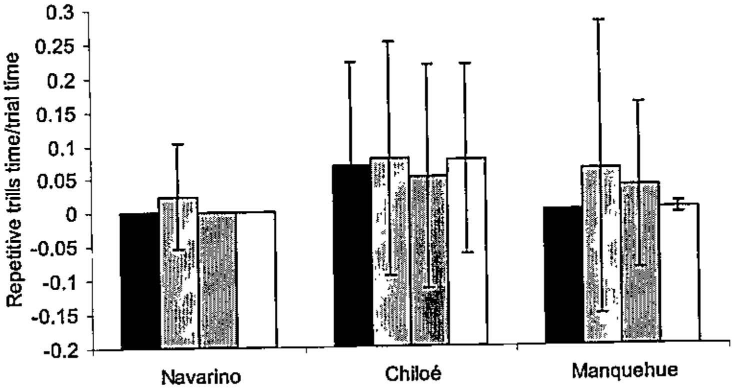
e)


Proportion of mobbing calls/trial time
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
-0.1
-0.2
Navarino
Chiloé
Manquehue

f)


Number of loud trills/trial time
0.03
0.02
0.01
0
-0.01
-0.02
Navarino
Chiloé
Manquehue

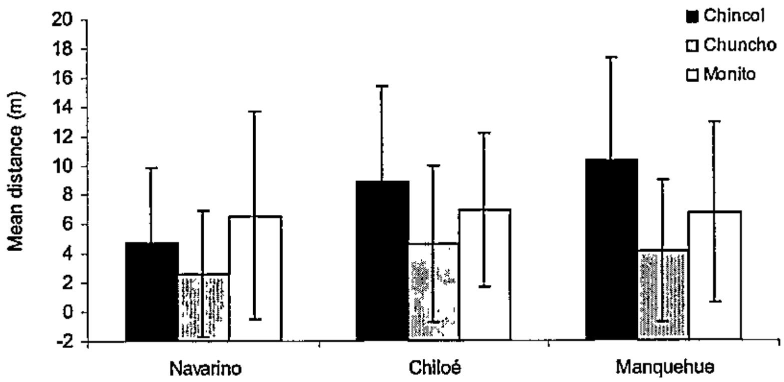
g)



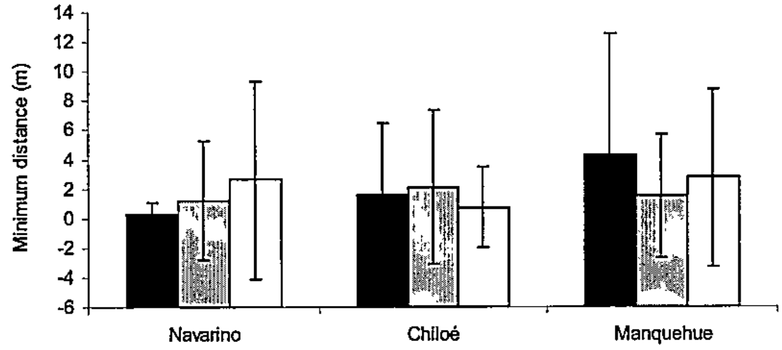
Appendix II (Fig. a-g) Territorial response variables in Navarino Island (N = 10), Chiloé Island (N = 21) and Cerro Manquehue (N = 13 for Chincols; N = 12 for Rayaditos) during laying stage (2006-2007). Data represent the mean value ± SD of different variables for male and female behavioral responses when facing the Chincol and the Rayadito male stimuli.

APPENDIX III

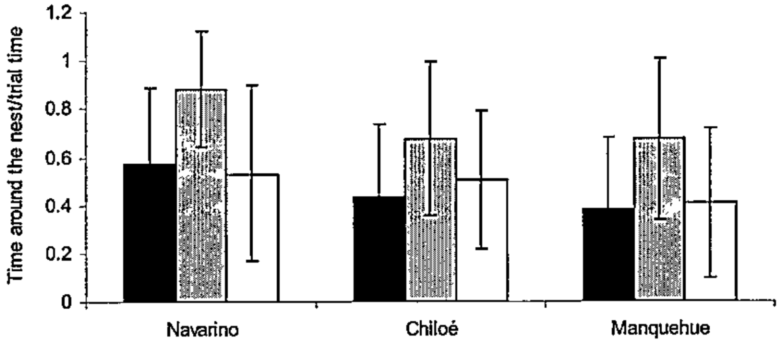
a)



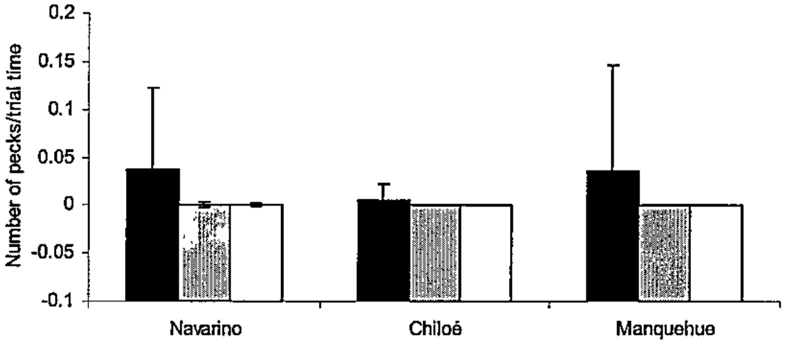
b)



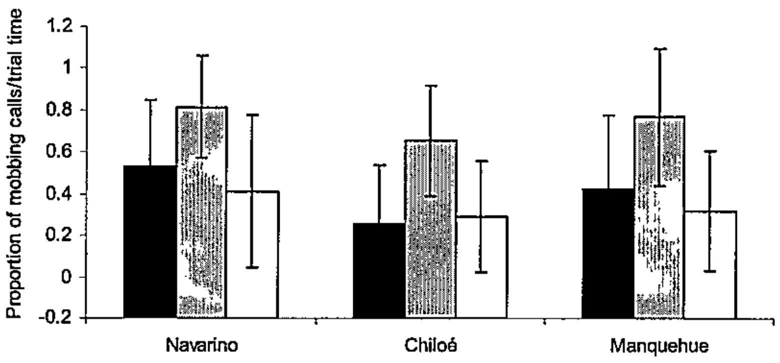
c)



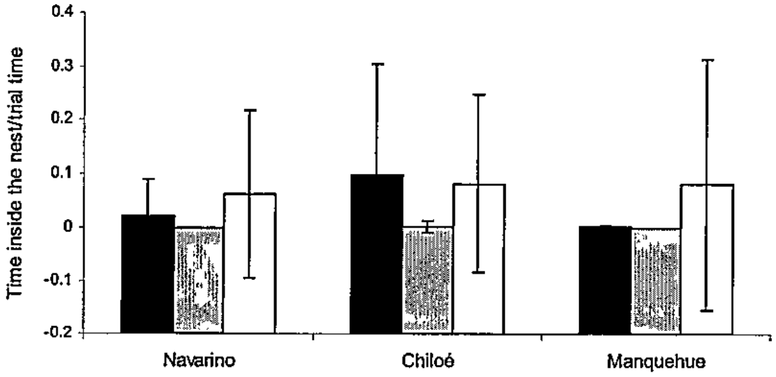
d)


Number of pecks/trial time
0.2
0.15
0.1
0.05
0
-0.05
-0.1
Navarino
Chiloé
Manquehue

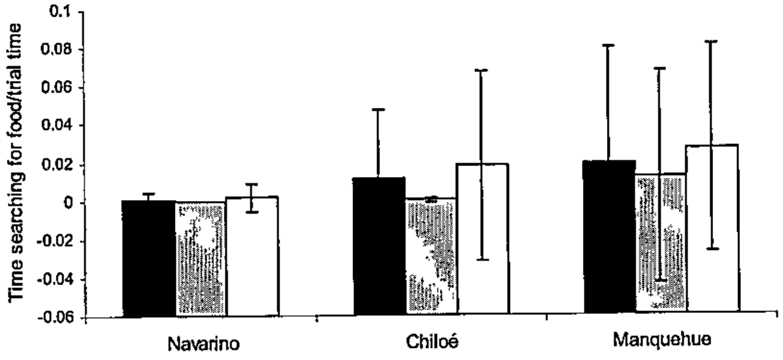
e)


Proportion of mobbing calls/trial time
1.2
1
0.8
0.6
0.4
0.2
0
-0.2
Navarino
Chiloé
Manquehue

f)


Time inside the nest/trial time
0.4
0.3
0.2
0.1
0
-0.1
-0.2
Navarino
Chiloé
Manquehue

g)



Appendix III (Fig. a-g) Antipredator response variables in Navarino Island (N = 22 for Chincol; N = 24 for Chuncho and Monito), Chiloé Island (N = 52) and Cerro Manquehue (N = 24 for Chincol; N = 22 for Chuncho and Monito) during nestling stage (2006-2007). Data represent the mean value ± SD of different variables for Rayaditos behavioral responses when facing the two predator stimuli (Monito del monte and Chuncho) and a control (Chincol).

Antipredator and territorial behavior in the Thorn-tailed Rayadito (*Aphrastura spinicauda*): interpopulation comparisons in vocal and defensive behavior

Tesis
Entregada a La
Universidad de Chile
En Cumplimiento Parcial De Los Requisitos
Para Optar Al Grado De

Doctor en Ciencias con mención en Ecología
Y Biología Evolutiva

Facultad de Ciencias

Por
Silvina G. Ippi Oporto

Septiembre, 2009

Director de Tesis
Dr. Rodrigo Vásquez S.

FACULTAD DE CIENCIAS

UNIVERSIDAD DE CHILE

INFORME DE APROBACIÓN

TESIS DE DOCTORADO

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

Silvina Graciela Ippi Oporto

Ha sido aprobada por la comisión de Evaluación de la tesis como requisito para optar al grado de Doctor en Ciencias con mención en Ecología y Biología Evolutiva, en el examen de Defensa de Tesis rendido el día 31 de julio de 2009.

Director de Tesis:

Dr. Rodrigo A. Vásquez S. ____________________

Comisión de Evaluación de la Tesis:

Dr. Pablo Sabat ____________________

Dr. Juan J. Armesto Z. ____________________

Dr. Cristian Estades F. ____________________

Dr. Rigoberto Solís ____________________

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