PATRONES, ESTRATEGIAS Y SÍNDROMES DE DISPERSIÓN EN POBLACIONES DEL RAYADITO *Aphrastura spinicauda* (FURNARIIDAE) EN DOS AMBIENTES CONTRASTANTES DEL CENTRO Y SUR DE CHILE

Tesis

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A mi mamá, por ayer, hoy, mañana y siempre. Ninguna frase alcanza.
A Sandra, mi motor y mi compás.

Esteban Botero Delgadillo

Esteban nació en Bogotá, Colombia, y estudió Biología en la Universidad Militar "Nueva Granada" (2002-2008). Ornitólogo de formación, Esteban logró adquirir muchísima experiencia en estudios de ecología y monitoreos poblacionales de aves migratorias Neárticas Neotropicales y especies endémicas a Colombia. Su experiencia en estudios sobre la distribución de aves amenazadas de extinción de los Andes colombianos y de la increíble y frágil Sierra Nevada de Santa Marta lo llevaron a preguntarse cuales son los factores responsables de la vulnerabilidad de las poblaciones y las especies, motivándolo a indagar sobre la variación geográfica de rasgos de historia de vida y comportamiento. En un curso internacional de anillamiento y monitoreo de aves del cuál era instructor, Esteban conoció a un estudiante chileno, quién le habló de las interesantes posibilidades de estudiar aves a lo largo de un impresionante gradiente de variación ambiental en el país más largo del mundo. Su tesis, llevada a cabo en el centro-norte y extremo sur de Chile, no solo le mostró la increíble diversidad ambiental de este país, sino que le ayudo a reconciliar la idea de que los patrones a escalas regional y ecológica son el producto de procesos a escalas local e individual. Esto, en última instancia, le ratificó sus intereses a futuro: la variación individual e inter-poblacional como motores de cambio de los rangos de distribución de las especies.

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RESUMEN

Es sabido que los patrones y estrategias de dispersión de una especie pueden variar entre ambientes y evidencia reciente sugiere que rasgos fenotípicos de los individuos correlacionados con la conducta dispersiva (i.e., síndromes dispersivos) también varían en función del contexto ambiental. Es por ello que los estudios centrados en una sola población proveen una visión limitada de los efectos de variación ambiental sobre los patrones y los síndromes dispersivos en una especie. Debido a su rango geográfico extenso con poblaciones establecidas en áreas ecológicamente disímiles, este trabajo utiliza al rayadito (*Aphrastura spinicauda*) como modelo para evaluar una posible covariación inter-poblacional entre la conducta dispersiva y condiciones ambientales. Para ello, se consideró una población aislada en el Parque Nacional Fray Jorge, centro-norte de Chile, caracterizada por un ambiente fragmentado, densamente poblado y con altos niveles de estrés fisiológico, y una población menos densa y con menores niveles de estrés en isla Navarino, sur de Chile, la cual habita un ambiente relativamente continuo. Combinando datos de captura-marcaje-recaptura (CMR), análisis genéticos y experimentos conductuales, se determinó que la sobrevivencia, la dinámica espacial local, la estructura genética a fina escala y las causas y consecuencias de la dispersión natal y reproductiva varían de forma predecible de acuerdo al contexto ambiental. La dispersión natal en Navarino mostró un patrón aleatorio y no afectó la condición física o la reproducción de hembras y machos dispersantes, lo que explicaría la ausencia de diferencias en los patrones de dispersión entre sexos. Por el contrario, la dispersión natal en Fray Jorge exhibió un marcado sesgo hacia las hembras, con machos filopátricos que conformaron agrupaciones de individuos relativamente emparentados, probablemente debido a los altos costos asociados con dispersar. La dispersión reproductiva fue menos frecuente en ambas poblaciones, pero implicó mayores costos en Fray Jorge, con un incremento en la mortalidad de las aves que dispersaron con mayor frecuencia durante su vida, además de una disminución en el éxito reproductivo de los machos. Los síndromes dispersivos también variaron en función del contexto ambiental, observándose una relación entre rasgos de personalidad y dispersión reproductiva únicamente en Fray Jorge, lo que podría haber surgido como una estrategia para reducir los costos de la dispersión en dicha localidad. Los resultados de este estudio indican que los patrones, estrategias y síndromes de dispersión varían conjuntamente en función del ambiente local y no son características necesariamente compartidas entre poblaciones, resaltando la importancia del contexto ambiental en la determinación de la conducta dispersiva de los organismos, como ocurriría con cualquier rasgo de historia de vida.

SUMMARY

It is known that dispersal patterns and strategies can vary in distinct environments, and recent evidence suggest that phenotypic traits that are correlated with dispersal behavior (i.e., dispersal syndromes) also show context-dependent variation. Therefore, studies focused on single populations provide a limited insight into the effects of environmental variation on species dispersal behavior. Given its wide geographic distribution with populations occurring along ecologically differing localities, this study uses the Thorn-tailed Rayadito (*Aphrastura spinicauda*) as a study model to assess a potential interpopulation covariation between dispersal behavior and environmental conditions. Two contrasting environments were considered for this, including an isolated population in Fray Jorge National Park, north-central Chile, which represented a fragmented and densely populated environment with high levels of physiological stress, and an uncrowded population with lower stress levels in Navarino Island, southern Chile, which inhabits a relatively continuous environment. Combining capture-mark-recapture data (CMR), genetic analyses and behavioral experiments, it was observed that survival rates, local spatial dynamics, fine-scale genetic structure and the causes and consequences of natal and breeding dispersal predictably vary according to the environmental context. Natal dispersal in Navarino showed a random pattern and did not affected the physical condition or the breeding performance of dispersed females and males, which would be in accordance with the absence of sex-biased dispersal. On the contrary, natal dispersal

in Fray Jorge was female-biased, with highly philopatric males conforming clusters of genetic relatives, probably due to the higher costs of dispersal. Breeding dispersal was far less frequent in both populations, but implied higher costs for birds in Fray Jorge, with an increase in mortality rates for those individuals frequently engaging in dispersal throughout their lives, and also a decrease of males' breeding success. Dispersal syndromes also varied according to the environmental context, and a relationship between personality traits and breeding dispersal was observed only in Fray Jorge, which could have arisen as a strategy to reduce dispersal costs in this locality. Results from this study suggest that dispersal patterns, strategies and syndromes covary as a function of the local environment and are traits not necessarily shared between populations, highlighting the importance of the environmental context as a causal factor of dispersal behavior, as should occur with any life history trait.

INTRODUCCIÓN

La dispersión es considerada como un atributo conductual de los individuos y un rasgo de historia de vida con múltiples consecuencias a distintas escalas espaciales y temporales, desde la colonización de un ambiente nuevo por unos pocos individuos hasta la estructuración espacial de poblaciones y la dinámica de los rangos de distribución de las especies (Duckworth y Badyaev 2007, Cote et al. 2010, Clobert et al. 2012). Esta conducta puede involucrar el movimiento de un individuo desde su área natal hacia una eventual área reproductiva (i.e., *dispersión natal*), o el desplazamiento entre áreas reproductivas sucesivas (i.e., *dispersión reproductiva*). La dispersión implica numerosos riesgos, ya que los dispersantes incurren en una serie de costos que pueden deberse a una conformación del paisaje que desfavorezca el desplazamiento y asentamiento, a un alto gasto energético en la búsqueda de un parche de hábitat adecuado, a la inadecuada selección de un área y/o a la falta de familiaridad con el hábitat, entre otros (Clobert et al. 2001, 2012, Bowler y Benton 2005). Dados los múltiples costos, se ha propuesto que la dispersión evolucionaría en las poblaciones como una estrategia que permitiría (i) evitar las interacciones competitivas entre parientes o co-específicos, (ii) evitar los efectos adversos generados por la endogamia y (iii) responder de forma adaptativa a ambientes variables espacial o temporalmente (Bowler y Benton 2005, Matthysen 2012, Starrfelt y Kokko 2012). Una vez que la dispersión ha evolucionado, múltiples factores próximos podrían generar que los individuos dispersen de un lugar a otro, incluyendo las interacciones intra e inter-específicas, la razón de sexos poblacional, el grado de parentesco entre individuos, la calidad del hábitat, las características del paisaje, entre otras (Bowler y Benton 2005, Clobert et al. 2004, 2009).

Los patrones (i.e., frecuencia, distancias y sesgos en la dispersión) y estrategias de dispersión en poblaciones naturales suelen ser el producto de una compleja interacción entre múltiples factores ambientales (i.e., extrínsecos) y rasgos de historia de vida de las especies (i.e., intrínsecos). Dicha interacción puede afectar los costos y beneficios asociados con la dispersión, generando en última instancia diferencias inter-individuales en la propensión a dispersar, además de variaciones inter-poblacionales (Matthysen 2012). La dispersión sesgada al sexo, por ejemplo, dependerá de las diferencias entre hembras y machos en las presiones ecológicas y sociales que afectan el comportamiento dispersivo, las que a su vez variarán en función del tiempo/energía invertidos en la competencia por territorios o parejas versus el esfuerzo parental individual (*hipotesis de sistemas de apareamiento*; Arcese 1989). Esto quiere decir que las diferencias observables entre poblaciones o especies en la dispersión sesgada al sexo pueden ser producto de la estacionalidad en la formación de parejas, los roles sexuales en la defensa territorial y la selección de áreas para la reproducción, la contribución relativa de ambos sexos al esfuerzo parental, la saturación del hábitat, y las oportunidades para reproducirse (Wolff y Plissner 1998, Arlt y Pärt 2008). En especies socialmente monógamas, por ejemplo, la presencia de un leve sesgo hacia las hembras o la ausencia de diferencias entre sexos es el patrón dominante (e.g., Clarke et al. 1997), lo que se explicaría por una relativa simetría en los roles de cada sexo en la competencia por territorios reproductivos y/o en el cuidado parental.

En general, la dispersión natal es más común que la dispersión reproductiva en las poblaciones, además de involucrar un mayor número de individuos y abarcar mayores extensiones geográficas (Greenwood y Harvey 1982). La fidelidad al lugar natal es menor que a los sitios reproductivos en varias especies de aves y mamíferos (Greenwood 1980), y al menos en aves, el grado de filopatría parece incrementar con la edad (Greenwood y Harvey 1982, Clarke et al. 1997). La dispersión natal ocurre como respuesta a numerosas causas (véase arriba) y su preponderancia se explicaría por la mayor movilidad, mayor propensión al riesgo y carencia de territorios y/o recursos para defender por parte de los individuos jóvenes (*principio de protección de recursos*; Clark 1994). La dispersión reproductiva, en cambio, está más ligada a la calidad del hábitat seleccionado para la reproducción, al éxito reproductivo de los individuos o de sus vecinos y a la sobrevivencia de los miembros de las parejas sociales/reproductivas (Greenwood y Harvey 1982). El hecho de no responder necesariamente a los mismos factores implica que la dispersión natal y reproductiva podrían estar sujetas a distintas presiones en una misma población, mostrando patrones contrastantes (Hinde 1956).

Además de la conocida influencia de la edad y el sexo sobre la propensión a dispersar (Bowler y Benton 2005, Matthysen 2012), es sabido que otros aspectos afectan la probabilidad de dispersión de los individuos, incluyendo rasgos fenotípicos variados (Ronce y Clobert 2012), la condición física y las condiciones ambientales (Bowler y Benton 2005, Matthysen 2012). La asociación entre rasgos fenotípicos y dispersión ha sido observada en varios organismos y es denominada *dispersión fenotipo-dependiente* (Bowler y Benton 2005, Clobert et al. 2009). A su vez, al conjunto de rasgos fenotípicos consistentemente asociados con la conducta dispersiva de los individuos se les denomina síndromes dispersivos (Cote y Clobert 2012, Ronce y Clobert 2012). La asociación entre la dispersión y la morfología ha sido muy bien documentada en plantas e invertebrados, pero en vertebrados existe poca evidencia de ello (e.g., la rata-topo desnuda *Heterocephalus glaber*; O'Riain et al. 1996). En contraste, la co-variación con rasgos fisiológicos o de historia de vida ha sido descrita en estos tres grupos (Bonte et al. 2012, Ronce y Clobert 2012). En cuanto a los rasgos conductuales, varios autores sugieren que la dispersión está relacionada con la variabilidad conductual de los individuos (Ronce y Clobert 2012); los individuos no dispersantes suelen ser menos agresivos (Duckworth y Badyaev 2007, Duckworth 2008), más sociales (Cote y Clobert 2007), más propensos a colaborar (Sinervo y Clobert 2003), menos exploradores (Dingemanse et al. 2003), más aversos al riesgo (Dingemanse y de Goede 2004) y menos audaces (Fraser et al. 2001) que los dispersantes.

Los estudios sobre dispersión fenotipo-dependiente están restringidos a pocas especies y/o poblaciones de una misma especie, lo que limita la generalidad de sus conclusiones (Cote et al. 2010). En aves, solo dos especies han sido estudiadas con relativo detalle, habiéndose descrito la existencia de síndromes dispersivos en ambas (Cote et al. 2010, Ronce y Clobert 2012). Estudios en el carbonero común *Parus major* en Europa indican que las distancias de dispersión están relacionadas con la conducta exploratoria de los individuos, donde individuos con mayores índices de exploración en aviarios experimentales recorren mayores distancias durante la dispersión natal (Dingemanse et al. 2003). En el azulejo de garganta azul *Sialia mexicana* en Norteamérica, los machos dispersantes que inmigran a un área para establecer un territorio muestran mayores niveles de agresividad que aquellos que eclosionaron o se han reproducido anteriormente allí (i.e., residentes; Duckworth 2006, 2008, 2009, Duckworth y Badyaev 2007). En ésta última especie se ha encontrado, además, que la variación en algunos rasgos morfológicos (e.g., longitud del tarso y del ala) entre residentes y dispersantes se asocia con sus patrones de uso del espacio y su éxito reproductivo en los tipos de hábitat seleccionados (Duckworth 2006a). La teoría y evidencia empírica asociada no solo sugiere que la propensión a dispersar es heredable (Hansson et al. 2003, Sinervo et al. 2006, Doliguez et al. 2009), sino que al estar correlacionada con la habilidad para dispersar (Verhulst et al. 1997), los síndromes dispersivos también serían heredables, dada la integración genética y funcional entre dispersión y algunos rasgos morfológicos y conductuales (e.g., agresividad, conducta exploratoria; Duckworth y Kruuk 2009, Duckworth 2012, Korsten et al. 2013). Sin embargo, también es sabido que las condiciones ambientales experimentadas por un individuo a lo largo de su ontogenia influencian su propensión a dispersar, un fenómeno denominado *dispersión condición-dependiente* (Ims y Hjermann 2001). Algunos trabajos en reptiles (Sinervo et al. 2006) y aves (Le Galliard et al. 2003, Tschirren et al. 2007, Duckworth 2009, Duckworth et al. 2015) han mostrado que las condiciones ambientales experimentadas por hembras reproductivas afectan el fenotipo de su progenie a través de efectos maternos, regulando la expresión de los rasgos asociados con la dispersión y su probabilidad de dispersar. La información que un individuo obtiene de su hábitat (i.e., información externa) y su condición física (i.e., información interna) también pueden tener efectos sobre subsecuentes decisiones relacionadas con dispersar, flexibilizando las estrategias individuales (Ims y Hjermann 2001).

Si bien la dispersión ha sido tradicionalmente concebida como un rasgo fijo de poblaciones y especies, evidencia creciente sugiere que se trata de una respuesta flexible a las condiciones ecológicas y sociales imperantes (Bowler y Benton 2005, Cote y Clobert 2012, Duckworth et al. 2015). Por ejemplo, diferencias en los niveles de competencia o heterogeneidad ambiental entre poblaciones pueden incrementar la variabilidad en los costos asociados a la dispersión (Wheelwright y Mauck 1998, Ward y Weatherhead 2005). Además, ambientes más competitivos podrían promover la expresión de mayores diferencias fenotípicas entre dispersantes y no dispersantes, mientras que dichas diferencias se cancelarían si las presiones sobre la dispersión son menores (Spinks et al. 2000, Aragón et al. 2006). Por ende, la variabilidad ambiental puede afectar las causas y consecuencias asociadas a la dispersión (Verhulst et al. 1997, Eeva et al. 2008, Terraube et al. 2014), las características de los individuos dispersantes y la variación en la expresión de los síndromes dispersivos (Cote y Clobert 2012), y consecuentemente, los patrones de dispersión local (Hawkes 2009, Matthysen 2012). Esta variación asociada al ambiente se conoce como *dispersión contexto-dependiente* (Clobert et al. 2012).

Dada esta aparente flexibilidad en la conducta dispersiva (véase Clarke et al. 1997), los estudios centrados en una sola población proveen una visión limitada de los efectos de un ambiente cambiante sobre los patrones y los síndromes dispersivos en una especie (Spinks et al. 2000, Bonte y Saastamoinen 2012). Algunos trabajos han mostrado como condiciones ambientales variables afectan las causas y consecuencias de la dispersión (e.g., Eeva et al. 2008, Terraube et al. 2014), pero las comparaciones inter-poblacionales en respuesta a la calidad del ambiente local y la densidad poblacional aún son escasas (e.g., Verhulst et al. 1997, Spinks et al. 2000). Adicionalmente, no hay evidencia concreta sobre co-variación de patrones, estrategias y síndromes de dispersión en distintas poblaciones, lo cual proveería un visión única para (i) inferir si las diferencias entre poblaciones implican la variación conjunta de múltiples rasgos fenotípicos (Matthysen 2012); (ii) determinar la prevalencia de distintos patrones bajo escenarios contrastantes (Clarke et al. 1997); (iii) entender las bases ecológicas y conductuales de las decisiones individuales respecto a la dispersión (Bowler y Benton 2005); (iv) comprender cómo la variabilidad ambiental mantiene el polimorfismo en estos rasgos a lo largo de la distribución de una especie (Matthysen 2012); y (v) predecir la respuesta de las poblaciones a variaciones en las fuentes de estrés ambiental que pueden encontrarse en el espacio o el tiempo (Le Galliard et al. 2012). Debido a su amplio rango geográfico con poblaciones establecidas en áreas ecológica e históricamente disímiles (González y Wink 2010, Quirici et al. 2014), el rayadito *Aphrastura spinicauda* (Furnariidae) es un excelente modelo para comparar la dispersión natal y dispersión reproductiva en localidades contrastantes.

El rayadito es un ave distribuida en los bosques templados del centro y sur de Chile y el sur-occidente de Argentina, llegando hasta las islas Malvinas, el archipiélago de Cabo de Hornos y la isla Diego Ramírez (Figura 1). Esta aparente capacidad de colonizar hábitats remotos son características poco comunes en los miembros de la familia Furnariidae (Remsen 2003). Algunas de las poblaciones del borde norte del rango de distribución continental experimentan aislamiento con respecto a las demás poblaciones (González y Wink 2010, Yáñez 2013), habitando remanentes de bosques húmedos completamente rodeados de matorral sub-xerofítico, como es el caso de la población del Parque Nacional Bosque Fray Jorge (Villagrán et al. 2004, del Val et al. 2006). Si bien la vegetación de bosque exhibe altos grados de fragmentación al sur de Fray Jorge, hasta la VI y VII región, las poblaciones más australes, desde las zonas cordilleranas de la VII región hasta la región de Magallanes, incluyendo las islas cercanas al continente como Tierra del Fuego y Navarino, se ubican en áreas con mayor continuidad de la vegetación boscosa nativa (véase Luebert y Pliscoff 2006).

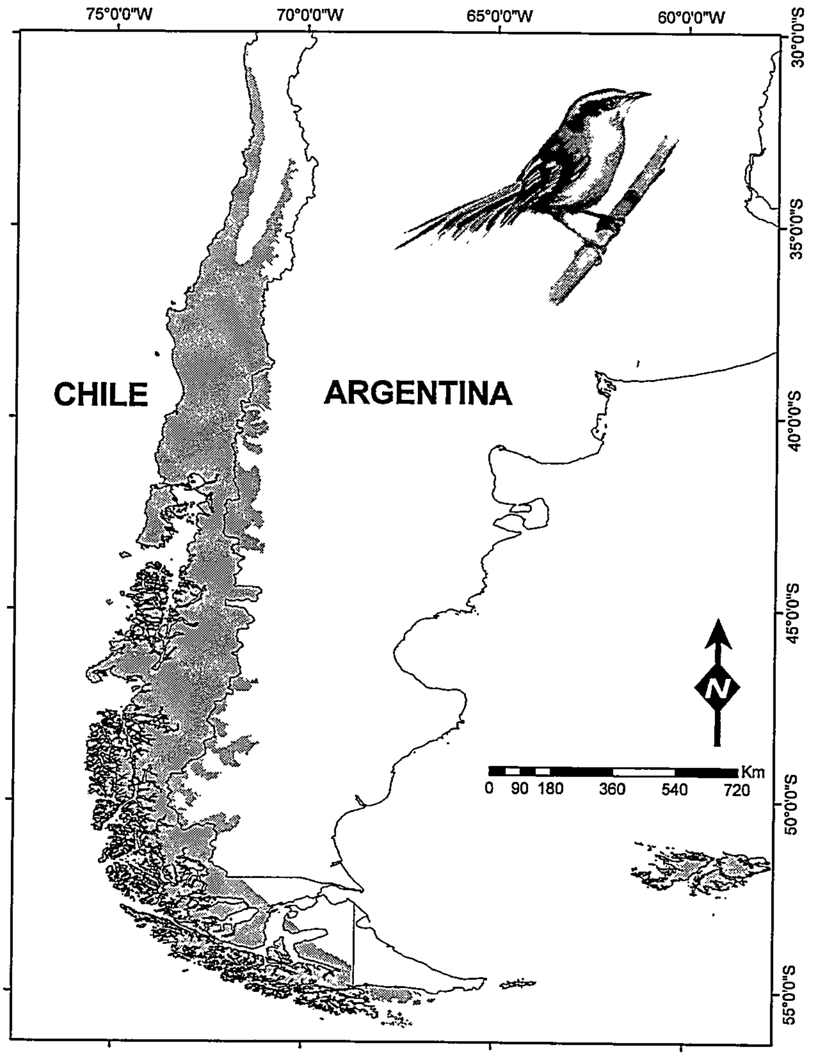

Figura 1. Distribución del Rayadito *Aphrastura spinicauda* a lo largo de Chile, el occidente de Argentina y las islas Malvinas. Basado en Jaramillo (2003).

Similar a otras aves socialmente monógamas, el rayadito carece de dimorfismo sexual evidente y los roles parentales son compartidos (Moreno et al. 2007). La conducta territorial se presenta solo durante la temporada reproductiva, ya que durante las semanas posteriores conforman bandadas familiares (véase Moreno et al. 2005, Vergara et al. 2010, Ippi et al. 2011); durante el resto del año, se observan en bandadas de co-específicos de hasta 15 individuos o bandadas mixtas (Ippi y Trejo 2003). Debido a que los machos reproductivos deben establecer su territorio anualmente, es probable que la competencia entre ellos se centre en la búsqueda de áreas de alta calidad y el rápido establecimiento de territorios; las hembras por su parte, podrían competir por cavidades de alta calidad y un rápido inicio de la reproducción (véase Greenwood 1980, Greenwood y Harvey 1982). Por ende, los costos en los que incurriría un individuo dispersante pueden ir desde el desconocimiento de la ubicación de zonas de alimentación y nidificación en un territorio nuevo hasta un retardo en el inicio de la reproducción (véase Greenwood y Harvey 1982).

Se ha sugerido que las distancias de dispersión en poblaciones del rayadito del centro de Chile serían de ca. 300m (Vergara et al. 2010), por lo que la fragmentación del hábitat parece actuar como un importante filtro para su desplazamiento, afectando además su éxito reproductivo (Vergara et al. 2013). Su densidad poblacional parece estar limitada por la disponibilidad de cavidades (Tomasevic y Estades 2006), siendo la calidad de las mismas y la conectividad del paisaje los factores más relevantes para la selección de los sitios de nidificación (Cornelius 2008, Vergara et al. 2010). Aparentemente, la fragmentación del paisaje boscoso implica una mayor exposición de los rayaditos a la escasez de alimento, depredación de nidos y costos más elevados para dispersar (Vergara y Marquet 2007, Vergara et al. 2010).

Un monitoreo a largo plazo de la biología reproductiva del rayadito ha permitido estudiar la variación intra-específica de aspectos tan variados como el repertorio vocal (Ippi et al. 2011), la conducta anti-depredatoria (Ippi et al. 2013) y el estrés fisiológico en respuesta al contexto ambiental (Quirici et al. 2014). Algunas de las localidades de estudio cuentan con información de captura/recaptura de individuos de ocho años y se encuentran ubicadas en los bordes norte y sur de su distribución geográfica (véase Quirici et al. 2014). Esto brinda una oportunidad única para documentar y comparar las estrategias y patrones de dispersión natal/reproductiva a escala local y determinar la existencia de síndromes dispersivos en el rayadito. Este trabajo plantea examinar la variación inter-poblacional de la conducta dispersiva y sus correlatos en dos ambientes contrastantes en el centro y sur de Chile: el Parque Nacional Bosque Fray Jorge (30°38'S, 71°40'W), en la IV región y la isla Navarino (55°4'S, 67°40'W), en la XII región. Fray Jorge corresponde al borde norte del rango geográfico y representa una discontinuidad climática y vegetacional con respecto a las demás poblaciones continentales (Luebert y Pliscoff 2006; Figura 2A), en tanto Navarino, se encuentra al sur de la población continental más austral, pero la variación espacial de la vegetación y el clima es más homogénea en toda la región (González y Wink 2010, Ippi et al. 2013, Quirici et al. 2014; Figura 2B). La extensión de vegetación boscosa disponible en las dos áreas de estudio (FJ: 2.4 km^2 o ca. 45% del área estudiada; Nav: 3.3 km^2 o ca. 77%; véase **Capítulo 1**) y estimaciones de densidad de individuos reproductivos (FJ: 8.2 parejas/ha, véase Vergara y Marquet, 2007; Nav: 2.9 parejas/ha, Botero-Delgadillo, datos sin publicar) sugieren que Fray Jorge albergaría una población más hacinada respecto a Navarino. Las tasas de ocupación de cajas nido entre 2008 y 2015 (FJ: 17%; Nav: 10%; Botero-Delgadillo, obs. pers.), aunque deben ser interpretadas con cautela, podrían reflejar una mayor disponibilidad de cavidades naturales en Navarino.

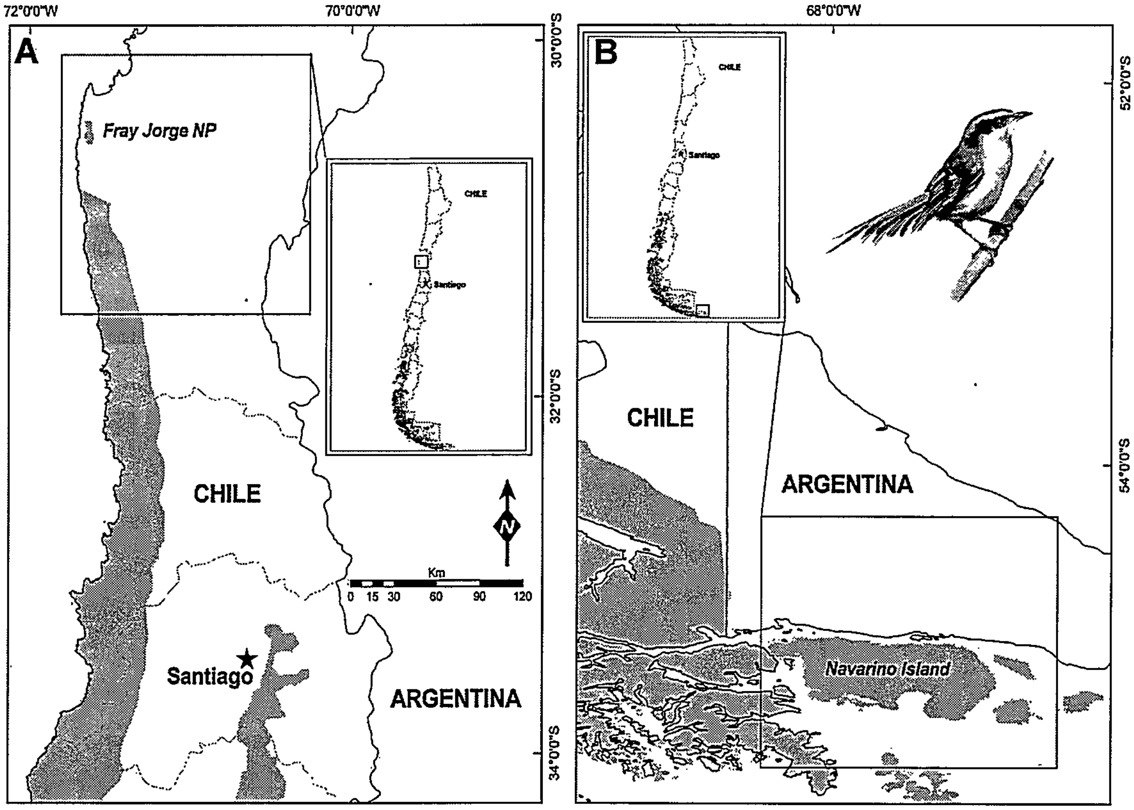

Figura 2. Poblaciones de Rayadito *Aphrastura spinicauda* consideradas en este estudio: **(A)** Parque Nacional Fray Jorge; **(B)** isla Navarino. El área gris representa la distribución de la especie en Chile. Basado en Jaramillo (2003).

Además, estimaciones de la concentración plasmática de corticosterona para adultos y pollos (FJ: 0.79, 0.92 ng/ml; Nav: 0.49, 0.83 ng/ml; valores Log reportados para corticosterona) y su relación negativa con la longitud telomérica sugieren que los niveles de estrés son mayores en Fray Jorge que en Navarino (Quirici et al. 2014, 2016). De hecho, se ha propuesto que Fray Jorge sería un ambiente estresante debido a una eventual saturación poblacional (Quirici et al. 2014). En conjunto, los antecedentes sugieren que ambas poblaciones ofrecen dos contextos ambientales contrastantes, siendo Fray Jorge una población más aislada y un ambiente más fragmentado, densamente poblado y con mayores niveles de estrés que Navarino.

Objetivos

Objetivo General: Evaluar las estrategias, patrones y síndromes de dispersión en el rayadito *Aphrastura spinicauda* y su variación inter-poblacional en dos localidades ambiental y ecológicamente contrastantes en el centro-norte y sur de Chile.

Objetivos específicos:

1. Determinar y contrastar los patrones locales de dispersión natal y dispersión reproductiva en dos poblaciones de rayadito expuestas a ambientes contrastantes en los límites norte y sur de su distribución.
2. Identificar y contrastar las potenciales causas y consecuencias de la dispersión natal y dispersión reproductiva a escala local en dos poblaciones de rayadito expuestas a ambientes contrastantes en los límites norte y sur de su distribución.
3. Determinar la asociación entre dispersión reproductiva local y el fenotipo conductual en el rayadito y contrastar estos síndromes en dos poblaciones expuestas a un contexto ambiental contrastante.

Hipótesis y predicciones

Las hipótesis y predicciones fueron formuladas de acuerdo a los patrones esperados para aves socialmente monógamas, de acuerdo a la teoría y evidencia asociada relevante (Greenwood y Harvey 1982, Clarke et al. 1997, Wolff y Plissner 1998, Arlt y Pärt 2008), y teniendo en cuenta los antecedentes antes descritos sobre la biología reproductiva y ecología espacial del rayadito.

Hipótesis 1. Los patrones locales de dispersión natal y dispersión reproductiva de hembras y machos son dependientes del contexto ambiental local y son más contrastantes en poblaciones que ocupan paisajes más heterogéneos o habitan ambientes densamente poblados.

Predicciones:

a. En un ambiente continuo y menor densidad poblacional (Navarino), la dispersión natal no estará sesgada al sexo y la distribución de distancias de dispersión seguirá un patrón aleatorio; por el contrario, se espera un marcado sesgo hacia las hembras y movimientos no aleatorios en un ambiente fragmentado y densamente habitado (Fray Jorge).
b. Los movimientos asociados a dispersión reproductiva serán más restringidos que la dispersión natal en ambas poblaciones, pero con un sesgo hacia las hembras más marcado en un ambiente fragmentado.
c. La estructura genética a escala fina en cada población reflejará los patrones locales de dispersión natal, esperándose una distribución espacial de genotipos no aleatoria en un ambiente fragmentado.

Hipótesis 2. La importancia de los factores que determinan la dispersión y sus consecuencias a escala local son contexto-dependientes y reflejan diferencias en las presiones ecológicas y sociales sobre la conducta dispersiva entre poblaciones ubicadas en áreas expuestas a ambientes contrastantes.

Predicciones:

a. Factores como la evitación de la endogamia y/o la evitación de competencia intra-específica serán las causas más probables de dispersión natal en un ambiente fragmentado y densamente habitado (Fray Jorge), pero no en un ambiente continuo y con menor densidad poblacional (Navarino), donde la información pública es probablemente un mejor predictor.

b. La consecuencias negativas en el éxito reproductivo o la condición física de los individuos después de la dispersión natal son esperables en un ambiente fragmentado y densamente ocupado, pero no en un ambiente continuo donde la densidad poblacional es menor.

c. Independiente del contexto ambiental, la probabilidad de que un individuo incurra en dispersión reproductiva será mayor luego de un fracaso reproductivo (o bajo éxito reproductivo) o posterior a la pérdida de su anterior pareja social.

d. Las consecuencias negativas de la dispersión reproductiva sobre los componentes de la adecuación biológica (éxito reproductivo y sobrevivencia) serán mayores en un ambiente fragmentado y densamente ocupado que en un hábitat continuo y con menor densidad poblacional.

Hipótesis 3. La relación entre la conducta dispersiva individual y el fenotipo conductual (i.e., personalidad) depende del contexto ambiental local y las diferencias entre dispersantes y no dispersantes se incrementan en ambientes más heterogéneos o densamente habitados.

Predicciones:

a. Los individuos de un ambiente continuo y con menor densidad poblacional (Navarino) serán en promedio más exploradores, más agresivos y más audaces que individuos en un ambiente fragmentado y densamente ocupado (Fray Jorge).
b. En un ambiente con menores restricciones a la dispersión, es decir, más homogéneo y con menor densidad poblacional, no se esperan diferencias marcadas entre individuos dispersantes y no dispersantes; no obstante, en un ambiente fragmentado y densamente habitado, donde los costos de la dispersión son presumiblemente mayores, los dispersantes debiesen exhibir una conducta más exploratoria, mayor agresividad y mayor propensión al riesgo en relación a los no dispersantes.

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CAPÍTULO I

DISPERSAL IN CONTRASTING ENVIRONMENTS: SPATIAL AND GENETIC DATA REVEAL POPULATION-SPECIFIC PATTERNS IN A PASSERINE BIRD

MANUSCRITO ENVIADO A ANIMAL BEHAVIOUR (MS ANBEH-D-16-01007)

DISPERSAL IN CONTRASTING ENVIRONMENTS: SPATIAL AND GENETIC DATA REVEAL POPULATION-SPECIFIC PATTERNS IN A PASSERINE BIRD

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ABSTRACT

Dispersal is considered a plastic response to the local ecological and social environment. Given its facultative nature, it is surprising the lack of studies testing for predictable differences in dispersal patterns in contrasting environments. Here, we combine capture-mark-recapture data from eight years (2008-2015) and molecular genetics to examine local natal and breeding dispersal patterns of a passerine bird, the Thorn-tailed Rayadito (*Aphrastura spinicauda*), in two localities of Chile: Navarino Island, a continuous and uncrowded habitat, and Fray Jorge National Park, a fragmented, densely populated and more stressful environment. Natal dispersal in Navarino showed no sex bias and birds exhibited a random pattern of territory settlement. In contrast, female-biased natal dispersal and restricted male movement was observed in Fray Jorge, where delayed breeding also appeared to occur. Spatial genetic autocorrelation analyses using 13 polymorphic microsatellite loci confirmed this pattern, as fine-scale genetic structure was detectable for male birds in Fray Jorge for a distance up to 450 m. Furthermore, two-dimensional autocorrelation analyses and estimates of genetic relatedness indicated that genetically related males tended to be spatially clustered. Breeding dispersal was restricted in both populations and showed no sex bias, although nesting-site fidelity was more frequent for breeding adults in Fray Jorge. Taken together, our results indicated that apparent survival, local spatial dynamics, and within population genetic structure can predictably vary in localities with contrasting conditions. Our data also suggested that local dispersal patterns in this passerine bird are context-dependent.

Keywords: Breeding dispersal; capture-mark-recapture; fine-scale genetic structure; interpopulation differences; natal dispersal; Thorn-tailed Rayadito

INTRODUCTION

The patterns of dispersal behaviour have been studied in a wide variety of species (Clobert, Baguette, Benton, & Bullock, 2012). Among birds, the frequency and extent of dispersal is usually sex-biased (see Clarke, Sæther, & Røskaft, 1997; Greenwood, 1980), depending on the timing of pair formation, the sex roles in territory establishment and selection of the breeding site, asymmetries in parental effort, habitat saturation, breeding site availability, and reproductive opportunity (Arlt & Pärt, 2008; Wolff & Plissner, 1998). Most of the socially monogamous birds studied up to date exhibit female-biased dispersal, whereas polygynous, colonial breeding and cooperative breeding birds tend to show male-biased dispersal (Greenwood & Harvey, 1982; Clarke et al. 1997). The interplay between sex differences in the amount of time/energy invested in competition for territories and/or mates versus the amount of parental effort is the most invoked explanation for the extent and direction of such biases ('Mating system hypotheses' sensu Arcese, 1989). Other hypotheses propose that population demography, social dominance, and inbreeding avoidance could also act as causal factors of sex-biased dispersal (Arcese, 1989; Szulkin & Sheldon, 2008).

Dispersal was traditionally considered a fixed trait of populations or species, despite marked intra-specific variation, but most recent studies suggest it is a plastic response to the local ecological and social environment (Bowler & Benton, 2005; Cote & Clobert, 2012; Duckworth, Belloni, & Andersson, 2015). As a result, interpopulation differences in dispersal patterns are expected under distinct environmental contexts (Matthysen, 2012; Hawkes, 2009). Some capture-mark-recapture studies have documented temporal variation in the frequency and the intensity or even the direction of sex-biased dispersal in populations of passerine birds (Eikenaar, Brouwer, Komdeur, & Richardson, 2010; Komdeur et al. 1995). Moreover, recent studies using molecular approaches also show intra-specific differences in dispersal patterns that depend on habitat availability and/or connectivity (Banks & Peakall, 2012). Documenting variation in dispersal behaviour and determining the prevalence of distinct patterns under variable scenarios is necessary to understand the ecological and evolutionary pressures driving such variation (Clarke et al., 1997), and to predict how populations will respond to specific environmental changes (Le Galliard, Massot, & Clobert, 2012). Despite the available studies describing interpopulation differences in avian dispersal (e.g. Payne & Payne, 1993), comparisons of dispersal patterns between populations differing in key factors remain rare. Given the apparent facultative nature of dispersal (Clarke et al. 1997), the lack of studies testing for predictable differences in dispersal behaviour between populations under distinct contexts (e.g. comparing populations inhabiting contrasting environments) is surprising.

Here, we combine capture-mark-recapture (CMR) data and molecular genetics to examine local dispersal patterns of a South American bird, the Thorn-tailed Rayadito (*Aphrastura spinicauda*), a secondary-cavity nester distributed along an extensive latitudinal gradient (30°S-55°S) in Chile and Argentina (Remsen, 2003). Given the vast environmental variation covered by its breeding range, this bird offers an excellent opportunity to assess if dispersal patterns vary predictably between contrasting environments. As other members of the family Furnariidae, rayaditos are socially monogamous and lack obvious sexual dimorphism (Moreno, Merino, Lobato, Rodríguez-Gironés, & Vásquez, 2007). Both sexes incubate the eggs and almost equally share nestling provisioning (Moreno, Merino, Vásquez, & Armesto, 2005). There is no information regarding sex differences in territory establishment and nest-site selection, but it is expected that both sexes are involved, as seems to be the case in other furnariids (see Remsen, 2003). Rayaditos appear to be limited by the availability of natural cavities in secondary-growth and human-altered landscapes (Cornelius, 2008; Tomasevic & Estades, 2006), and also are negatively affected by forest fragmentation at the local scale (Vergara & Marquet, 2007). Although able to colonize distant islands located up to 80-100 km from the continent, rayaditos seldom fly distances longer than 300 m to cross open areas or unsuitable habitat (Vergara, Hahn, Zeballos, & Armesto, 2010).

In this study, we focused on two populations of Rayadito located on opposite ends of its breeding range and differing in habitat heterogeneity, population density and levels of stress. The first population was located in Navarino Island (55°4'S, 67°40'W), southern Chile (hereafter Navarino or Nav), which represents a continuous and less populated environment; the second population, located in Fray Jorge National Park (30°38'S, 71°40'W), north-central Chile (hereafter Fray Jorge or FJ), represents a fragmented and densely occupied habitat (see Methods for a detailed description of each locality). Taking advantage of the differing conditions present in these populations, we used eight-year data on individually marked birds to address the hypothesis that the patterns of local natal and breeding dispersal vary predictably between two contrasting environments. Although natal and breeding dispersal do not necessarily respond to the same factors (Greenwood & Harvey, 1982), several studies report how they would be affected by environmental variability (see below), allowing us to make explicit predictions. Sex-biased natal dispersal is expected to be absent in socially monogamous birds with similar parental roles (Clarke et al., 1997; Greenwood, 1980), especially in continuous environments and uncrowded populations, because dispersal will not be restricted by habitat structure (Winkler et al., 2005) and the costs of movement may be similar for both sexes as breeding opportunities are abundant (Weatherhead & Boak, 1986). In contrast, heterogeneous environments and crowded populations can exert opposite effects, as the first factor can promote longer natal dispersal distances (Matthysen, Adriaensen, & Dhondt, 1995), while the second would favour natal site fidelity (Ward & Weatherhead, 2005; Wheelwright & Mauck, 1998). This could result in female-biased dispersal, because selection may favour male philopatry when breeding opportunities are scarce or when territory quality is highly variable (Ward and Weatherhead 2005). We therefore predicted (i) no sex-biased and unrestricted (i.e. random distribution of dispersal distances) natal dispersal in a continuous and less occupied environment (i.e. Navarino); on the contrary, we expected pronounced female-biased natal dispersal and non-random movement patterns in a fragmented and densely populated environment (i.e. Fray Jorge). Increased territory fidelity in adult monogamous birds commonly result in moderately female-biased or unbiased breeding dispersal (Clarke et al., 1997; Greenwood & Harvey, 1982), although increased male philopatry can be anticipated under crowded conditions and low territory quality (Bensch & Hasselquist, 1991; Ward & Weatherhead, 2005). Accordingly, we predicted (ii) more restricted movements in comparison to natal dispersal in both populations, but with moderately female-biased or unbiased breeding dispersal in the continuous habitat, and more accentuated differences among the sexes in the fragmented environment, with highly philopatric males and dispersing females. Given the expected longer distances resulting from natal dispersal events and the limited effect that breeding dispersal can have on population structure (see Payne & Payne, 1993), we predicted (iii) that the fine-scale genetic structure in each population reflects local natal dispersal patterns (e.g. Beck, Peakall, & Heinsohn, 2008; Double, Peakall, Beck, & Cockburn, 2005), but not movements related to breeding dispersal.

METHODS

Study areas

This study is part of a long-term research on the breeding ecology of the Thorn-tailed Rayadito in Navarino and Fray Jorge, where 171-222 and 101-157 nest boxes have been offered for occupation during 2006-2015 in each locality, respectively. Nest boxes were systematically distributed at regular distances in second-growth forests in Navarino (24 ± 0.6 m between nearest nest boxes; mean ± SE) and forest relicts in Fray Jorge (21 ± 2.6 m), and their position was georeferenced with a 2 m measurement error. The spatial arrangement of nest boxes was defined after considering previous density estimates of breeding birds (e.g. Vergara & Marquet, 2007). The study area plot at Navarino covers ca. 4.3 km^2 in a landscape dominated by sub-Antarctic forests (Rozzi & Jiménez, 2014; see Supplementary Fig. S1), with woodland habitats comprising ca. 3.3 km^2. The study area plot at Fray Jorge covers ca. 5.3 km^2 in a predominantly semiarid landscape, dominated by matorral steppe (Luebert & Pliscoff, 2006; see Supplementary Fig. S1), with a relict forest composed of several fragments located in a coastal mountain range reaching up to 630 m a.s.l. (del Val et al., 2006; Villagrán et al., 2004). Forest fragments range in size between 0.5-22.5 ha and have a combined area of 2.4 km^2 (Cornelius, Cofré, & Marquet, 2000).

While birds from Navarino have maintained recurrent gene flow with other rayadito populations, the Fray Jorge population is isolated (González & Wink, 2010; Yáñez, 2013). Bird density estimates during the breeding season suggest that Fray Jorge harbours a more crowded population (FJ: 8.2 pairs/ha, see Vergara & Marquet, 2007; Nav: 2.9 pairs/ha, Botero-Delgadillo, in prep.), whereas mean rates of nest box use during 2008-2015 indicate there could be a higher availability of natural cavities for nesting in Navarino (FJ: 18%; Nav: 10%; data from this study). These data along with recent estimates of baseline CORT levels for 2010-2011 (FJ: 0.79, 0.92 ng/ml; Nav: 0.49, 0.83 ng/ml; reported Log values for CORT by Quirici et al., 2014) and their negative relation with telomere length (Quirici, Guerrero, Krause, Wingfield, & Vásquez, 2016) suggest that Fray Jorge is a competitive and stressful environment.

Field methods

Data for our study were obtained from eight consecutive breeding seasons (2008-2015) in both localities. Breeding adults were captured inside the nest boxes when nestlings were 12-14 days old (see details in Moreno et al., 2005). For this, we used a manually triggered trap when nestling provisioning took place (Quirici et al., 2014). Adults and nestlings were marked with a lightweight, uniquely numbered, metal ring, and a blood sample was obtained afterwards (ca. 17 μl) by puncturing the brachial vein with a sterile needle (Quirici et al., 2014). Blood samples were stored on FTA™ Classic Cards (Whatman™) for subsequent genetic analyses. Dispersal events were identified based on recaptures of individuals in subsequent years.

Genetic analyses

DNA was extracted from blood samples using a QIAamp® DNA Micro Kit (QIAGEN® #56304). Given the absence of evident sexual dimorphism in rayaditos (Moreno et al., 2007), sex was determined using one chromosome-linked marker (P2/P8; Griffiths, Double, Orr, & Dawson, 1998). All individuals were genotyped at 13 polymorphic microsatellite loci (Supplementary Table S1): species-specific markers As1, As7, As18, As25-1, As25-5, As25-8, As25-10, and As25-14 (Yáñez, Quirici, Castaño-Villa, Poulin, & Vásquez, 2015), and the cross-species amplifying markers Asμ15_ZEST, CcaTgu23 (Olano-Marín et al., 2010), Tgu06 (=CK307697), Tgu05 (=DV946651) (Slate, Hale, & Birkhead, 2007), and marker ZF_AC138573 (van Oosten, Mueller, Ottenburghs, Both, & Kempenaers 2016).

Microsatellite amplifications were performed in multiplex PCR reactions using the Type-it® Microsatellite PCR Kit (QIAGEN® #206246) and primer mixes containing four to five primer pairs (mix 1, 2, and 3; Supplementary Table S1). The forward primer of each pair was fluorescently labelled with 6-FAM™, VIC®, PET® or NED™ (Dye Set G5; Thermo Fisher Scientific). Primer concentrations in these mixes were adapted due to differences in amplification efficiency and dye strength (see Supplementary Table S1). Each 10 µl multiplex PCR contained 15-80 ng DNA, 5 µl of the 2x Type-it® Microsatellite PCR Master Mix, and 1 µl of one of a primer mix. Cycling conditions were: 5 min initial denaturation at 95°C, 23 (mix1 and 2) or 28 cycles (mix 3) of 30 s denaturation at 94°C, 90 s annealing at the temperature given in Table S1, and 1 min extension at 72°C, followed by a 30 min completing final extension at 60°C. After amplification, 1.5 µl of the PCR products were added to 13 µl formamide containing the GeneScan™ 500 LIZ® Size Standard, heat denatured and resolved in POP4 polymer on an ABI™ 3130 Genetic Analyzer (Thermo Fisher Scientific, Darmstadt, Germany). Raw data were analysed and alleles assigned using the GENEMAPPER 4.0 software (Applied Biosystems).

Data analysis - dispersal estimates and CMR data

All analyses of natal and breeding dispersal were based on CMR data obtained during 2008-2015. Natal dispersal was defined as the movement between the natal nest box and the first recorded breeding box, while breeding dispersal comprised movements between consecutive breeding seasons. The frequency of dispersal (% of dispersing individuals) and the distance moved (m) by recaptured birds were both used as descriptors of dispersal behaviour (Clarke et al., 1997). For calculating dispersal frequency, we first applied Dirichlet tessellation (Aurenhammer, 1991) to model the territories of all breeding pairs in both localities for every year (2008-2015), using the spatial patterns of nest box occupation as input data (Adams, 2001; Valcu & Kempenaers, 2008). Mean territory diameters were subsequently calculated for each year/population, and individuals were considered as 'dispersed' if they moved over a distance equal or longer than the upper limit of the 95% confidence interval (CI) of the annual mean territory diameter (see Valcu & Kempenaers, 2008); shorter movements were defined as 'natal/nesting-site shifts', while the absence of movement was referred as 'natal/nesting-site fidelity'. Dirichlet tessellation and estimation of territory diameters were performed in the Analysis tools in ArcGIS 9.3 (ESRI, 2008).

All descriptive analyses and statistical tests were performed with R version 3.3.1(R Core Team, 2016), using $\alpha = 0.05$ for hypothesis testing. Within-population comparisons between the sexes were made for the frequency of dispersal and the distance moved. Fisher-Freeman-Halton tests of independence were used to assess sex and/or age-related differences in the proportions of dispersers/non-dispersers (see Eden, 1987), while Kolmogorov-Smirnov tests were employed to compare the distribution of dispersal distances during natal or breeding dispersal events (Harvey, Greenwood, & Perrins, 1979; Harvey, Greenwood, Campbell, & Stenning, 1984). Because some breeding adults were recaptured more than once, K-S tests for breeding dispersal were performed on two datasets: a first reduced set comprising only the first breeding dispersal distance recorded for every individual, and a second, expanded set, including all distances from some repeatedly recaptured birds (Montalvo & Potti, 1992). We used randomization tests to evaluate the spatial patterns of natal and breeding dispersal for each sex and population, comparing the observed median dispersal distances against null distributions of medians generated by 1000 Monte Carlo simulations to calculate exact probabilities (Wheelwright & Mauck, 1998). Simulated distances were obtained by assigning each breeding individual to any of the 'available' nest boxes during the year of its recapture, with none of them being assigned more than once in every run (see Wheelwright & Mauck, 1998). We tested two null models that varied in the probability of assignment of the 'available' nest boxes for each individual: the first was used for testing if median distances departed from a completely random pattern, using a null uniform distribution for the probability of assignment (i.e. probability of assignment was equal for all nest boxes); the second was used to test if median distances departed from a random-walk search, using an exponential distribution for the probability of assignment that varied as a function of the distance from the natal site (Waser, 1985; Winkler et al., 2005). Exponential null distributions were simulated for each locality based on the regression of the probability of recapture on distance (Winkler et al., 1995). None of these models assumed age-related social dominance (see Wheelwright & Mauck, 1998). All randomization tests were run with the coin package in R (Hothorn, Hornik, van de Wiel, & Zeileis, 2008).

Among-population comparisons were performed to assess if sex-differences in natal/breeding dispersal distances varied between localities, using generalized linear mixed models (GLMM; Bolker et al., 2008). Because density of breeding pairs, and therefore, territory size, can vary between populations and years, the distance moved (m) by dispersing birds might not be directly comparable. Thus, we transformed distances into territory units (Arcese, 1989), using the mean territory diameter estimated for every year and for each study site. For the natal dispersal analysis, the full model included bird sex, population of origin and their interaction as fixed effects, and the natal year and the time interval for recapture (not all nestlings were recaptured the following year as adults) as random effects. The full model for breeding dispersal included the same fixed effects, and as random effects we added year of recapture, bird age (Montalvo & Potti, 1992), and bird identity, given that some birds were recaptured in multiple years (see Ward & Weatherhead, 2005). We fitted negative binomial models with a Log link function using the lme4 (Bates, Maechler, Bolker, & Walker, 2015) package in R. We assessed goodness of fit of a set of candidate models with AICc values using the MuMIn package (Bartoń, 2014), generating a minimum most adequate model by manually removing non-significant parameters (Crawley, 1993).

Finally, to test the critical assumption that dispersal patterns were not affected by sex-differences in mortality rates or probability of recapture (Ward & Weatherhead, 2004), we used two different approaches. For adult birds, we used CMR data to calculate apparent survival probability (φ) and recapture rate (p) using the Cormack-Jolly-Seber model (Sandercock, 2003) as implemented in MARK 5.1 (Cooch & White, 2008; White & Burnham, 1999). We generated different candidate models with different restrictions on the parameters (Lebreton, Burnham, Clobert, & Anderson, 1992), and used AICc values for model selection (Supplementary Table S2). For fledgling survival, we had to use sex-specific recovery rates as an approximation of survival given the low recapture rates (see Results). We corroborated the validity of this approach by calculating the percentage of fledglings recaptured during our study in relation to an estimation of all surviving post-fledging birds in each locality. This was done by first building a static life table (see Gotelli, 2008), using CMR data to compute age-specific survival and fecundity (Supplementary Table S3). Subsequently, assuming no population increase/decrease during the study period, we calculated fledgling survival rates needed to maintain both populations constant (i.e. r = 0; Supplementary Table S3). The ratio of recaptured/surviving nestlings was interpreted as a rough estimate of how representative the recapture rates were.

Data analysis – spatial genetic structure

All genetic analyses were based on genotyped breeding adults that were captured during 2010-2015. We tested for linkage disequilibrium separately on datasets for each sex and population, using exact tests in GENEPOP 4.0 (Raymond & Rousset, 1995). Tests for deviations from Hardy-Weinberg equilibrium (HWE) and estimation of frequency of null alleles were applied on the same datasets in CERVUS 3.0.7 (Kalinowski, Taper, & Marshall, 2007). Details on genetic diversity measures are addressed elsewhere (Yáñez et al., 2015; Botero-Delgadillo, in prep.).

We evaluated sex-differences in dispersal patterns in three ways: (i) spatial autocorrelation analyses and heterogeneity tests were applied to investigate if local spatial genetic structure in each population corresponded to dispersal patterns observed with CMR data; (ii) two-dimensional autocorrelation analyses (2D LSA) were implemented to explore how spatial genetic autocorrelation was distributed in a two-dimensional landscape; and (iii) Mantel tests (Mantel, 1967) of matrix correspondence were used to evaluate if patterns of isolation by distance were present at the local scale. Separated spatial autocorrelation analyses were performed for each sex/population (Nav: 82 females, 79 males; FJ: 69 females, 66 males) based on all genotyped individuals for 2010-2015 (e.g. van Dijk, Covas, Doutrelant, Spottiswoode, & Hatchell, 2015). We repeated the same analyses on 'snapshot' years to check for possible temporal sampling effects due to demographic processes (Foerster, Valcu, Johnsen, & Kempenaers, 2006; van Dijk et al. 2015), selecting the year with the largest number of captured/recaptured adults (Nav: 2014; FJ: 2013). Spatial autocorrelation analyses were conducted in GENALEX 6.5 (Peakall & Smouse, 2012) following the methods described in Peakall, Ruibal, and Lindenmayer (2003), and Banks and Peakall (2012). For calculating genetic correlation coefficients (*r*), GENALEX uses pairwise squared genetic and pairwise geographic distance matrices, and then plots *r* values as a function of distance across different distance class intervals (Peakall, Smouse, & Hubb, 1995). For the geographic distance matrix, UTM coordinates from nest boxes were entered as input data. Given the difficulties to define a representative distance that could reveal the extent of non-random genetic structure, we calculated *r* for increasing distance classes using the Multiple Dclass option in GENALEX to define the first distance interval for traditional correlograms (Peakall et al., 2003). We explored several distance classes ranging from the overall mean territory diameters in Navarino and Fray Jorge (100 and 50 m, respectively) to the maximum distance between nest boxes in each locality (2.9 and 4.2 km). The minimum distance class size for which *r* was significant (150 m; see Results) was subsequently used as the distance interval for traditional correlograms (Peakall et al., 2003). Significance of positive/negative autocorrelation values for traditional and Multi Dclass analyses were assessed by estimating the 95% CI about *r* using bootstrap resampling, and also through 1000 random permutations of bird genotypes to generate estimates of *r* that would be obtained by random (*rp*). We rejected the null hypothesis of no autocorrelation when both estimations indicated significant non-random genetic structure (i.e. the 95% CI around $r \neq 0$ and $r >$ 95% CI around *rp*). Although this is a conservative approach, it is highly recommended when sample sizes are relatively small (Peakall et al., 2003). Nonparametric heterogeneity tests were applied for testing sex-differences in the correlograms by computing the t^2 statistic for each distance class and the correlogram wide 'Omega' (ω) (see Banks & Peakall, 2012; Smouse, Peakall, & González, 2008).

The 2D LSAs were performed separately for each sex/population, estimating the local genetic correlation (*lr*) based on pairwise comparisons between every individual and its *N* nearest neighbours. Calculation of *lr* and standard permutation tests (1000 permutations/run) for significance were conducted in GENALEX as described in Double et al. (2005). We used multiple runs calculating *lr* for four, nine, and 14 nearest neighbours (i.e. subsets of five, 10 and 15 individuals), but only presented results for 14 nearest neighbours, as such subsets comprised an equivalent linear distance to the distance class size used for spatial autocorrelation analyses (see results). Mantel tests were also implemented in GENALEX, using permutation tests (1000 permutations) to assess the significance of correlation between matrices of genetic similarity and geographic distances (Peakall et al., 2003).

Ethical Note

All birds were captured and marked under the authority of Servicio Agrícola y Ganadero (SAG; permits 5193/6295) and Corporación Nacional Forestal (CONAF), Chile. Research was carried with the supervision of the Ethics Committee of the Sciences Faculty, Universidad de Chile.

RESULTS

Natal dispersal patterns

From a total of 565 fledglings marked in Navarino (southern population) up to 2014, 17 (3%) were recaptured at least once as breeding adults, of which eight were females and nine were males. Twelve individuals were recaptured the year after hatching, the remainder after two (N = 3) or three years (N = 2). Based on the distance moved from their natal nest box, all 17 recaptured birds were defined as dispersers. The median distance moved by females (480 m, range: 180-760) and males (420 m, 190-840) were similar, and there were no sex-differences in the distribution of travelled distances (Kolmogorov-Smirnov test: $Z = 0.66$, $N = 17$, $P = 0.52$; see Fig. 1A). Monte Carlo simulations revealed that the median distance moved by either sex was not significantly different from median distances generated by the completely random (females: $P = 0.44$; males: $P = 0.49$) and random-walk models (females: $P = 0.21$; males: $P = 0.28$).

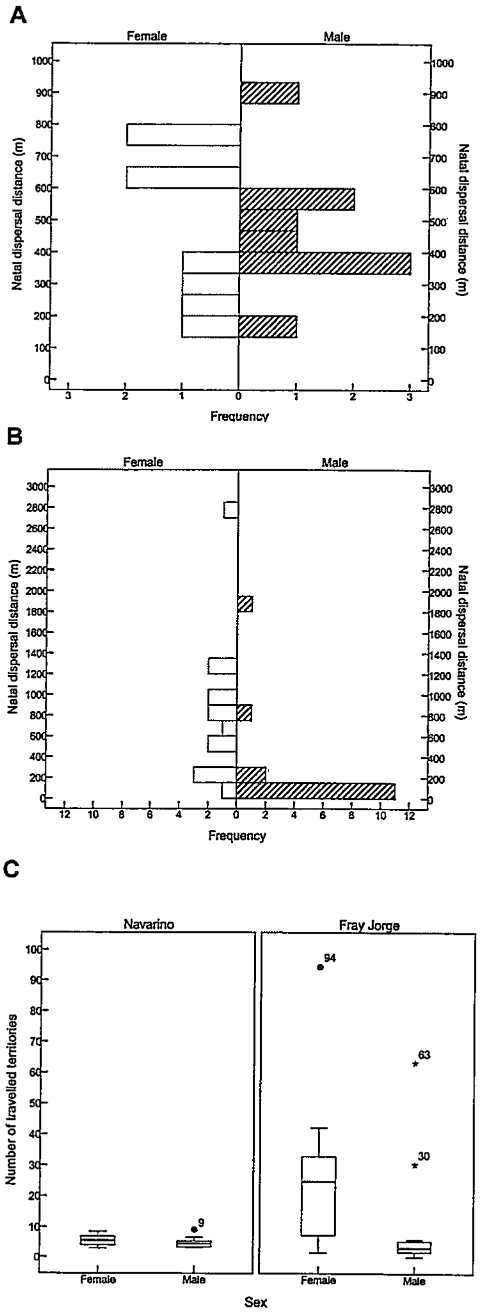

Figure 1. Natal dispersal patterns in two populations of Thorn-tailed Rayadito based on capture-mark-recapture data obtained during 2008-2015. A total of 17 (females: 8, males: 9) and 29 (females: 14, males: 15) post-fledging birds were recaptured in Navarino and Fray Jorge, respectively. Frequency distribution of natal dispersal distances travelled by female and male birds in Navarino Island (**A**) and Fray Jorge National Park (**B**). Natal dispersal was compared between both populations after transforming distances into territory units based on Dirichlet tessellation for each breeding season (**C**).

From 491 marked fledglings in Fray Jorge (northern population) up to 2014, 29 (6%) were recaptured as breeding adults, including 14 females and 15 males. Individuals were recaptured after one ($N = 1$), two ($N = 19$), three ($N = 8$), or four ($N = 1$) years after hatching. Three males were recaptured in their natal box (natal-site fidelity); all other cases were defined as dispersal events. Females travelled longer median distances (740 m, range: 40-2700) than males (100 m, 0-1800), and the distribution of movement distances differed significantly between the sexes (Kolmogorov-Smirnov test: $Z = 1.95$, $N = 29$, $P < 0.001$; see Fig. 1B). Monte Carlo simulations showed that female median distances were not different from values generated by the completely random model, but distances moved by males were shorter than expected (females: $P = 0.35$; males: $P = 0.041$); on the other hand, the random-walk model showed that females moved significantly longer distances than expected, but male movements were not different from values generated under the null hypothesis (females: $P = 0.045$; males: $P = 0.58$).

As expected based on differences in breeding density, adult birds in Navarino occupied larger territories (Dirichlet tiles) than those in Fray Jorge. The upper limit of the 95% CI of the mean territory diameter in Navarino ranged from 63 to 110 m across breeding seasons, while in Fray Jorge it ranged from 29 to 39 m. Comparing natal dispersal distances as territory units (tU), we observed that movements of females (median: 5 tU, range: 3-8) and males (4 tU, 3-9) were similar in Navarino, whilst there was a marked difference between females (25 tU, 1-94) and males (3 tU, 0-60) in Fray Jorge (Fig. 1C). After correcting for random effects (natal year and interval of recapture), the best-fitting model showed a significant sex × population effect on the number of territories moved by natal dispersers (Table 1).

Table 1. Minimal adequate GLMM to test for sex-differences in natal dispersal distances of Thorn-tailed Rayadito in two populations, Navarino Island and Fray Jorge National Park. Main effects were not reported when interactions were significant.

Fixed effects	Estimate*	SE*	Test**	P	Variance^
Intercept	3.31	0.39			
Sex*Population	1.34	0.65	$z_{42} = 2.05$	0.04	
Random effects					
Natal year					7.66 %
Recap. Interval					28.65 %

*Parameter estimates and SE (Standard errors) were estimated relative to 'Female' level in variable 'Sex' and 'Fray Jorge' level for variable 'Population'.

***z* statistic corresponds to the Wald-test.

^The proportion of random variance explained by each random effect.

Breeding dispersal patterns

Within-population patterns of breeding dispersal were similar between the reduced and expanded datasets (see Methods), and therefore, we report descriptive and statistical analyses including all distances, including those from adults that were recaptured more than once (see Montalvo & Potti, 1992).

From a total of 210 captured adults in Navarino, we obtained 127 recapture events of 69 individuals between consecutive breeding seasons (57 recaptures of 35 females, 70 recaptures of 33 males). Of these, 24% were cases of nesting-site fidelity (females: 17%, males: 28%; Fisher-Freeman-Halton exact test of independence $P = 0.21$). Nesting site-shifts (i.e. small movements to adjacent nest boxes) where observed in 59% of all cases, while 17% of recaptures corresponded to breeding dispersal events, which tended to be more frequent in females than in males (females: 24%, males: 11%; F-F-H exact test: $P = 0.07$). The distribution of travelled distances did not differ significantly between the sexes, even though females moved somewhat farther (females: median: 45 m, range: 0-390; males: 30 m, 0-90; Kolmogorov-Smirnov test: Z = 1.23, N = 127, P = 0.07; see Fig. 2A). Monte Carlo simulations suggested that median distances for females and males were shorter than expected under the completely random model (females: P = 0.039; males: P = 0.033), albeit not different from values taken from a random-walk distribution (females: P = 0.64; males: P = 0.68). Recaptured adults had a minimum age of 2-8 years old (exact ages were not always certain), but there was neither a decreasing trend in travelled distances as bird age increased, nor a difference in the frequency of dispersal between age classes (F-F-H exact test, P = 0.21; Fig. 2C, 2E).

From the 197 captured adults in Fray Jorge, 133 recaptures of 81 individuals were obtained between consecutive breeding seasons (67 recaptures of 42 females, 66 recaptures of 39 males). Of these, 57% corresponded to nesting-site fidelity (females: 59%, males: 56%; F-F-H exact test: P = 0.85). Small movements (nesting site-shifts) comprised 27% of all cases, whereas breeding dispersal events were observed in 16% of recaptures and showed no differences between the sexes (females: 17%, males: 14%; F-F-H exact test: P = 0.79), as also did the distribution of travelled distances (females: median: 11 m, 0-270; males: 7 m, 0-270; Kolmogorov-Smirnov test: Z = 0.45, N = 133, P = 0.77; see Fig. 2B). As in the Navarino population, Monte Carlo simulations suggested that median dispersal distances were shorter than randomly generated distances in the two sexes (females, P = 0.028; males, P = 0.012), but not differing from values generated under the random-walk model (females, P = 0.28; males, P = 0.37). Recaptured birds were at least 2-7 years old, and the travelled distances by both sexes tended to be lower in older animals, particularly in males (Fig. 2D). Data also evidenced a difference in the relative frequency of breeding dispersal between age classes (F-F-H exact test, P = 0.03), with an apparent decrease for 4-7 year-old birds (Fig. 2F).

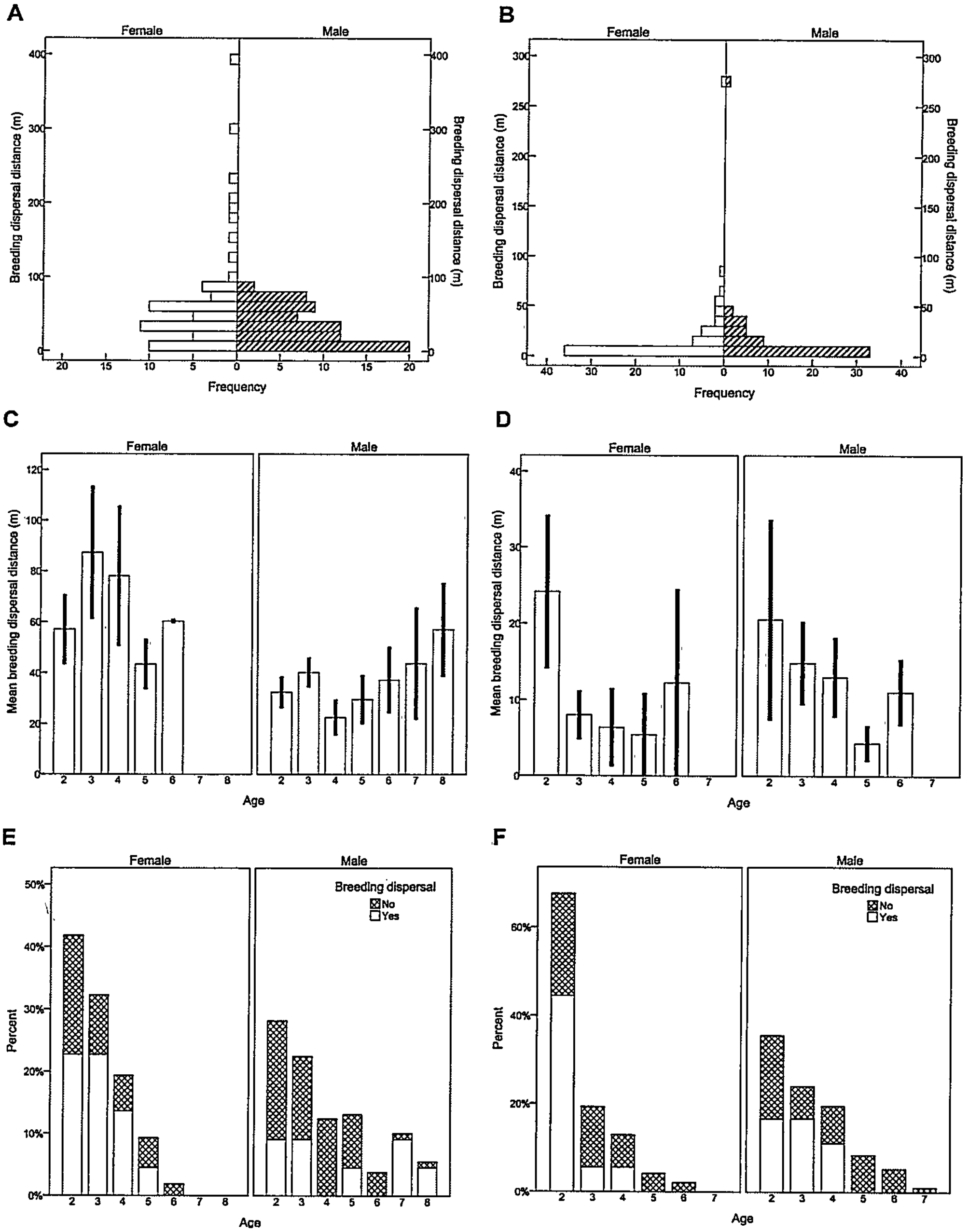

Figure 2. Breeding dispersal patterns in two populations of Thorn-tailed Rayadito based on capture-mark-recapture data obtained during 2008-2015. A total of 127 (females: 57, males: 70) and 133 (females: 67, males: 68) recapture events were obtained in Navarino and Fray Jorge, respectively. Frequency distribution of distances travelled by birds between consecutive breeding seasons in Navarino Island (**A**) and Fray Jorge National Park (**B**). Mean travelled distances (error bars are ± 2 standard errors) between consecutive breeding seasons by birds in Navarino (**C**) and Fray Jorge (**D**) according to their sex and minimum estimated age (exact ages for adult birds were not always known). Frequency of breeding dispersal events for female and male birds in Navarino (**E**) and Fray Jorge (**F**) according to their minimum estimated age.

Overall, females (Navarino: 0.6 tU, 0-4; Fray Jorge: 0.01 tU, 0-46) and males (Navarino: 0.4 tU, 0-1; Fray Jorge: 0.0 tU, 0-9) from both populations tended to move very short distances between consecutive breeding seasons, usually not crossing an entire territory. According to the best model for the among-population comparison, most of the total random variance was attributed to intrinsic differences between individuals, and there was no effect of sex or population on breeding dispersal distances (Table 2).

Table 2. Minimal adequate GLMM to test for sex-differences in breeding dispersal distances of Thorn-tailed Rayadito in two populations, Navarino Island and Fray Jorge National Park. Main effects were not reported when interactions were significant.

Fixed effects	Estimate	SE	Test	*P*	Variance^
Intercept	-0.83	0.26			
Rejected terms					
Sex	-0.35	0.35	$z_{258} = -0.99$	0.32	
Population	-0.18	0.37	$z_{257} = -0.49$	0.62	
Sex*Population	0.47	0.54	$z_{256} = 0.88$	0.38	
Random effects					
Age					0.00 %
Recap. year					0.05 %
Bird identity					49.62 %

*Parameter estimates and SE (Standard errors) were estimated relative to 'Female' level in variable 'Sex' and 'Fray Jorge' level for variable 'Population'.

**z statistic corresponds to the Wald-test.

^The proportion of random variance explained by each random effect.

Apparent survival

For adult birds, the best model only included six parameters and considered temporally-varying values for apparent survival (mean ± SE: φ_1: 0.69 ± 0.04, φ_2: 0.43 ± 0.09, φ_3: 0.47 ± 0.06, φ_4: 0.61 ± 0.08) and recapture rate (p_1: 0.59 ± 0.04, p_2: 0.77 ± 0.07). According to this model, there were no sex-differences in survival probabilities or recapture rates in each population (Supplementary Table S2), although mean apparent between-year survival was higher in Fray Jorge (0.68 ± 0.0002 SE, $N = 197$) than in Navarino (0.55 ± 0.0008, $N = 210$). Recapture rates for post-fledging individuals were almost equal between sexes (see *Natal dispersal patterns*), and also suggested higher survival in Fray Jorge. Vital rates calculated with static life tables indicated that fledgling survival should approximately be 17% in Navarino and 23% in Fray Jorge to maintain both populations constant (Supplementary Table S3). Assuming that the contribution of long-distance immigrants and emigrants to population dynamics is relatively low in comparison to mortality and fecundity (i.e. closed populations), this gave us a rough recovery rate of 18 and 26% of all surviving fledglings that were marked during this study in Navarino and Fray Jorge, respectively.

Spatial genetic structure

There was no evidence of linkage disequilibrium between any pair of loci. With the exception of marker As1 (not included in further analyses), no significant deviations from HWE were detected after applying Bonferroni correction for multiple comparisons (all $P > 0.1$), and frequency of null alleles never exceeded 0.05.

Genetic autocorrelation for increasing distance class sizes for the 2010-2015 dataset (MultiDclass analyses) showed that neither of the sexes in Navarino departed from a random distribution of genotypes at any of the assessed distance intervals (Fig. 3A). Although females in Fray Jorge showed a similar pattern, males exhibited positive genetic structure beyond 300 m (Fig. 3B). Furthermore, r values were above the 95% CI around rp beyond 600 m, but the 95% CI around r was significantly different from 0 only up to 450 m (Fig. 3). Analyses for 'snapshot' years showed similar results, without detectable genetic structure in Navarino (females, $N = 32$; males, $N = 31$), and contrasting patterns in Fray Jorge, where males showed a positive structure, but only beyond 150 m (females, $N = 25$; males, $N = 25$; details not shown).

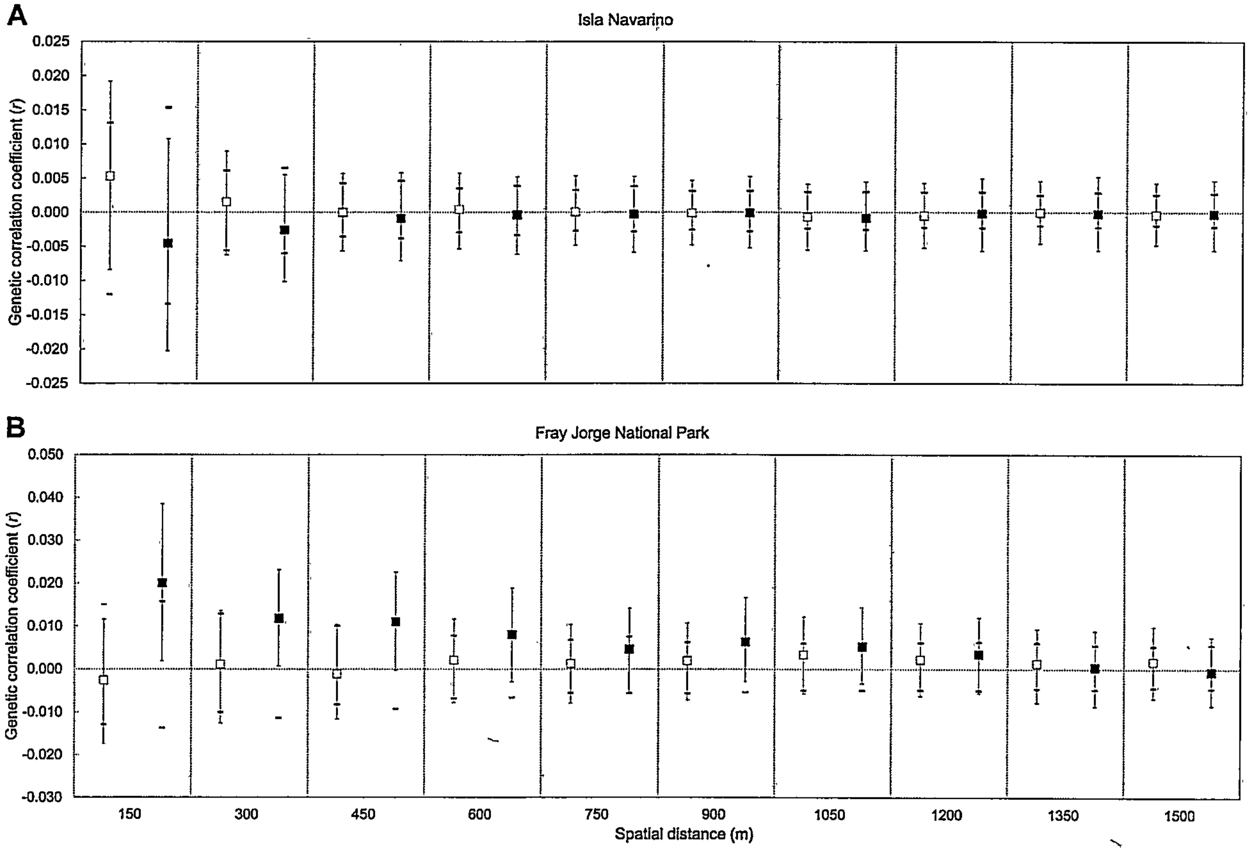

Figure 3. Spatial genetic autocorrelation coefficients (*r*) for increasing distance classes for female and male thorn-tailed rayaditos in Navarino Island (**A**) and Fray Jorge National Park (**B**). Squares represent correlation coefficients (*r*) with 95% confidence error bars determined by bootstrapping; white and black squares represent females and males, respectively. Solid horizontal dashes represent the 95% CI generated by 1000 random permutations assuming a random distribution of genotypes (*r* not different from *rp*).

Traditional correlograms indicated, again, no detectable genetic structure in Navarino, with correlations for both sexes oscillating between positive and negative values (Fig. 4A, 4B). The nonparametric heterogeneity test revealed no significant differences between the *r* values for both sexes at any particular interval (Single-class t^2, all $P > 0.05$), and also no sex-differences when comparing the whole correlograms ($\omega = 5.39$, $P = 0.86$). Similarly to Multi Dclass analyses, correlograms for Fray Jorge suggested no genetic structure for females (Fig. 4C), but positive and significant r values for males (Fig. 4D). The correlograms for females oscillated between high and low autocorrelation, whereas for males they showed a positive structure at 150 m. The heterogeneity test showed that r values differed only significantly at the 150 m interval ($t^2 = 3.03$, $P = 0.04$), but the autocorrelation patterns did not reveal significant sex-differences ($\omega = 12.31$, $P = 0.17$). Analyses for 'snapshot' years confirmed the same patterns as obtained with the whole 2010-2015 dataset (details not shown).

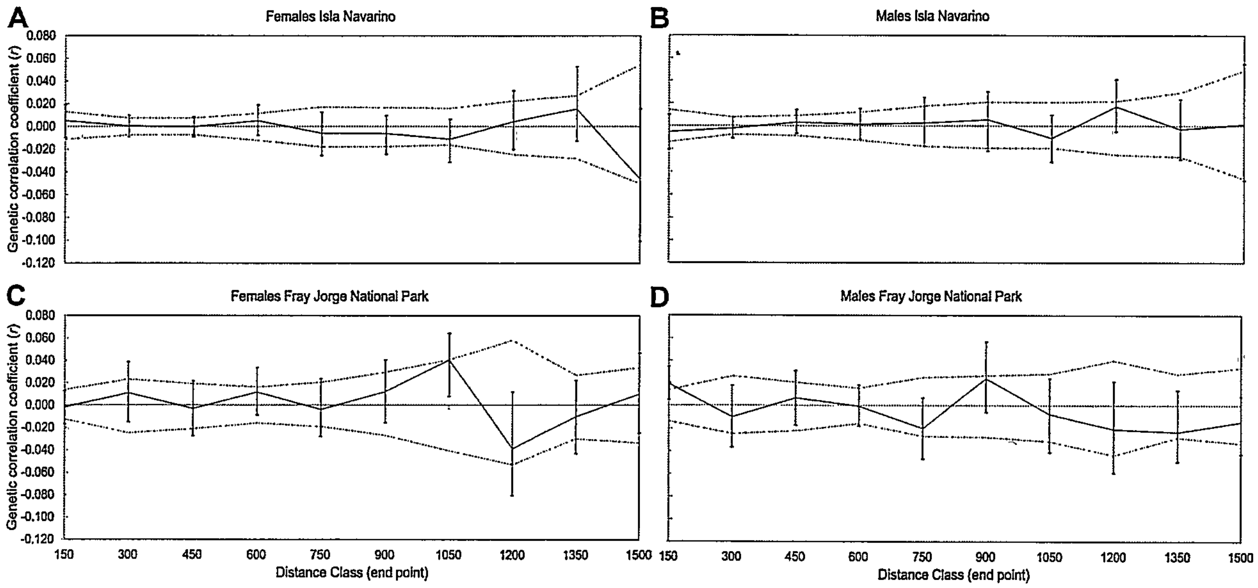

Figure 4. Correlograms showing the genetic correlation (r) as a function of spatial distance for Thorn-tailed Rayadito. Autocorrelation for distance class sizes of 150 m for females (**A**) and males (**B**) in Navarino Island, and females (**C**) and males (**D**) in Fray Jorge National Park. Dotted lines represent the 95% CI assuming a random distribution of genotypes (H_0: r not different from rp). The 95% confidence error bars about r were determined by bootstrapping.

Results of the two-dimensional autocorrelation analyses revealed that for Navarino only 5% and 1% of the lr values were significantly positive for the 89 females (P values for one-tailed tests: 0.006-0.029) and the 72 males ($P = 0.047$) sampled, respectively. Positively-correlated subsets of individuals were not clustered, and there were no significant negative lr values (Fig.

5A, 5B). Although analyses for Fray Jorge suggested a similar pattern for the 69 sampled females (Fig. 5C), with only 4% of positive *lr* values (P = 0.012-0.021), 17% of all *lr* values were significant and positive for the 66 males (P = 0.002-0.048), and three small clusters of correlated subsets of males were distinguishable (Fig. 5D). Again, there were no significant negative *lr* values.

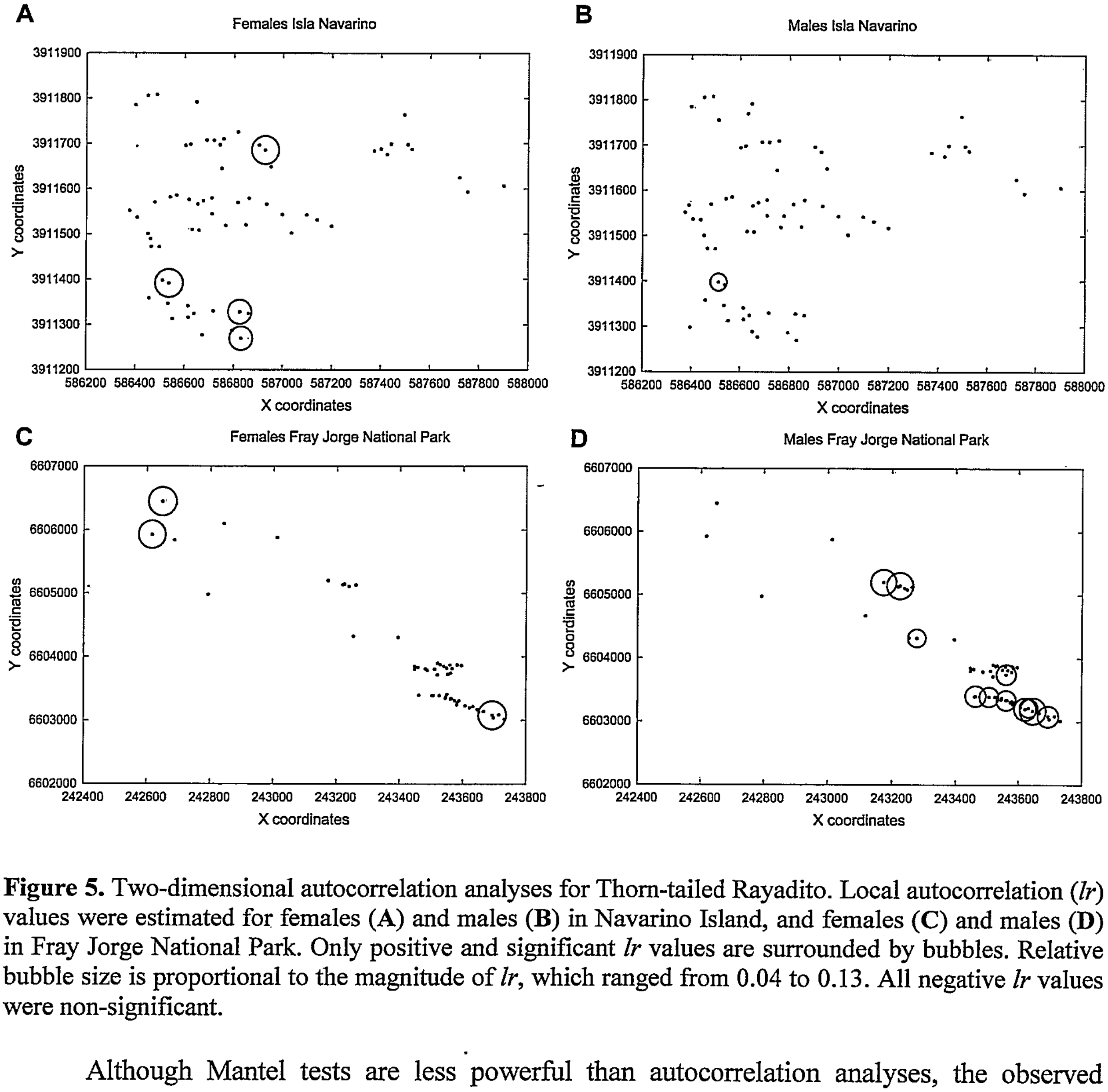

Figure 5. Two-dimensional autocorrelation analyses for Thorn-tailed Rayadito. Local autocorrelation (*lr*) values were estimated for females (**A**) and males (**B**) in Navarino Island, and females (**C**) and males (**D**) in Fray Jorge National Park. Only positive and significant *lr* values are surrounded by bubbles. Relative bubble size is proportional to the magnitude of *lr*, which ranged from 0.04 to 0.13. All negative *lr* values were non-significant.

Although Mantel tests are less powerful than autocorrelation analyses, the observed relationships between pairwise geographic and pairwise genetic distance matrices were consistent with autocorrelation results. Random permutation tests indicated that correlation coefficients were not different from 0 for females (*rxy* = 0.033, *P* = 0.28) and males (*rxy* = 0.009, *P* = 0.41) in Navarino, and for females in Fray Jorge (*rxy* = 0.035, *P* = 0.26); however, there was a weak, but significantly positive correlation for males in Fray Jorge (*rxy* = 0.1, *P* = 0.046).

DISCUSSION

In this study, we compared natal and breeding dispersal between two populations of Thorn-tailed Rayadito to investigate the differences between a continuous, uncrowded and less stressful habitat and a fragmented, densely populated and presumably saturated environment. Overall, we observed that rayaditos travelled relatively short distances during dispersal events, and the combined results from CMR data and population genetic analyses consistently showed that local natal dispersal patterns and sex-specific fine-scale genetic structure varied between the two populations. Local breeding dispersal was far less frequent than natal dispersal, although exhibited a similar pattern in both sites.

Most of our predictions about local dispersal patterns were supported by both CMR and genetic data (see below), indicating that our results were robust. Nevertheless, the observed patterns of natal dispersal should be interpreted cautiously given the reduced dataset (especially in Navarino). However, this does not mean that the dispersal distances reported here are underestimations of the actual dispersal distances, or that the spatial scale of our study was not appropriate. In general, low recovery rates of post-fledging individuals are a common issue in dispersal studies regardless of the spatial scale involved. For instance, nestling recapture rates in studies encompassing smaller (e.g. Payne, 1991) or larger areas (e.g. Matthysen & Schmidt, 1987; Winkler et al., 2005) than ours, ranged between 3 and 5% (but see Potti & Montalvo, 1991). Furthermore, because mortality in altricial birds is much higher for juveniles than for adults (Naef-Daenzer, & Grüebler, 2016), it is likely that most fledglings have died instead of having dispersed long distances (see Birkhead, Eden, Clarkson, Goodburn, & Pellat, 1986; Eden, 1986). Our data support this assumption, with estimated fledgling survival rates (assuming no population growth) being three to four times lower than the rates of adult apparent survival. Despite the impossibility to estimate the distance moved by missed dispersers, we do consider unlikely that the majority of surviving juveniles have moved longer distances than those described here. For example, missed dispersers in Navarino could have moved to nearby forest patches without the need of travelling long distances, and in the case that most of them were moving farther away (e.g. > 1 km), this could have been noticed with genetic analyses given the high polymorphism of microsatellite markers in this population (Yáñez et al., 2015). In the case of missed dispersers in Fray Jorge, they could also have moved to other patches around the study area, but none of these were farther apart than the longest distances between nest boxes. Although long-distance movements outside the study sites do occur, they are infrequent (Botero-Delgadillo et al., in prep.).

Interpopulation differences in natal dispersal

It has been proposed that the costs and benefits of natal dispersal will be relatively similar for males and females when both sexes select a nesting site or establish and defend a territory (Clarke et al., 1997; Greenwood, 1980), leading to no sex-biased dispersal (e.g. Arcese, 1989; Eden, 1986; Enokson, 1987; Kålås and Løfaldli, 1987; Matthysen & Schmidt, 1987). Furthermore, this pattern should hold when there are no differences in sex-specific survival rates (Murray, 1967; Waser & Jones, 1983; Waser, 1985), and when movement is not limited by nesting site availability or habitat saturation (Arlt & Pärt, 2008; Weatherhead & Boak, 1986). However, a saturated and fragmented habitat could increase social competition (see Payne, 1991) and dispersal frequency/extent (Matthysen, Adriaensen, & Dhondt, 1995), generating potentially different responses in each sex depending on the costs and benefits related to dispersal under such conditions (Matthysen, 2012; Starrfelt & Kokko, 2012). Supporting prediction (i), the observed distribution of natal dispersal distances did not differ between the sexes in the more continuous environment (i.e. Navarino), while females moved longer distances than males in the fragmented and saturated environment (i.e. Fray Jorge).

The mechanisms underlying sexual asymmetries in natal dispersal under a more heterogeneous and saturated habitat could be manifold, but some authors propose that dispersing males run higher risks of losing all breeding opportunities due to difficulties of finding and defending suitable breeding sites, and also due to the increased uncertainty regarding the quality of those sites (Bensch & Hasselquist, 1991; Winkler et al., 2005). Females, on the other hand, usually find breeding opportunities as they depend on the presence of an already settled male in a territory, regardless of the female's role in subsequent nest-site selection (Arlt & Pärt, 2008). Once a subtle sex bias in dispersal behaviour has arisen, the social environment could reinforce the asymmetries in dispersal-related costs experienced by each sex (Payne & Payne, 1993), particularly if adult survival is high, as it is the case in Fray Jorge. Because levels of aggression may increase in saturated and stressful environments, dispersal costs for males will also increase due to the difficulty of establishing a territory in an area with unfamiliar neighbours of the same sex (Payne & Payne, 1993). On the contrary, the social incentive for females returning to the natal area will be low, as their already higher dispersal tendency will decrease the probability of encountering a socially familiar place (Payne & Payne, 1993).

We did not find direct evidence for more restricted breeding opportunities in Fray Jorge compared to Navarino, but CMR data and analyses of movement patterns support this idea. While most recaptured fledglings from Navarino were yearlings (70%), nearly all recaptures in Fray Jorge were 2-3 year-old birds (93%), suggesting that both females and males could be delaying their first breeding attempt in the fragmented and densely populated environment (Potti & Montalvo, 1991). Although these birds could have remained undetected while breeding in natural cavities inside the study area during their first year, this is unlikely, because bird counts and searches for marked individuals around the nest boxes were carried out on a weekly basis during all years. We cannot rule out the possibility that these birds bred in nearby forest patches beyond the extent of the study area, but limited breeding dispersal suggests that this is unlikely. Regarding the movement patterns, results from Monte Carlo simulations indicated that unlike Navarino, birds from Fray Jorge would have more restricted options for finding and establishing a breeding territory. A completely random null model assumes that birds are aware of the breeding opportunities in the entire study area, and that the probability of establishing is uniform across the study site; in contrast, the random-walk model assumes that birds search for any available breeding site starting at their natal nest box and moving outwards until an unoccupied area is found (Waser, 1985; Winkler et al., 2005). Natal dispersal in Navarino seemed to follow a combination of both processes, suggesting that birds could be establishing almost anywhere but also could search for a breeding area near their natal site (Payne, 1991; Winkler et al., 2005). On the other hand, the data suggest that females in Fray Jorge did not occupy the first available vacant site, but travelled longer distances following a more random pattern, possibly resulting from trying to find an unpaired territorial male (Arlt & Pärt, 2008; Wolff & Plissner, 1998);

meanwhile, movements of males in Fray Jorge appeared to be restricted to the nearest available area to their natal site (Payne, 1991).

Interpopulation differences in breeding dispersal

Theoretical and empirical studies suggest that adult birds, once they established a territory, may pay higher costs of dispersal than younger birds, who have not yet invested in finding and defending a suitable breeding site (Greenwood & Harvey, 1982; Wheelwright & Mauck, 1998) and thus may have less to lose ('asset-protection' principle; Clark 1994). Compared to natal dispersal, less frequent and shorter movements during breeding dispersal would then be expected. The observed frequency/extent of breeding dispersal in both populations support this.

The expected contrast in breeding dispersal between the two studied populations, as stated in prediction (ii), received partial support. The observed pattern in both localities suggests no sex-biased breeding dispersal, with median dispersal distances being shorter than expected by chance, albeit not significantly different from a random-walk process. There were also no differences between the populations when the uncorrected distances were transformed into territory units. Nonetheless, nesting-site fidelity was twice as frequent in Fray Jorge than in Navarino, and only birds in Fray Jorge apparently decreased the frequency of breeding dispersal as they aged (particularly the males). Taken together, these results indicate that despite high philopatry in breeding adults from both sites, mature birds in Fray Jorge rarely moved away from an established breeding territory ('social constraint' hypothesis; Payne & Payne, 1993), suggesting that habitat fragmentation and saturation also imposes restrictions to breeding dispersal (Bensch & Hasselquist, 1991; Ward & Weatherhead, 2005).

The number of travelled territories during breeding dispersal did not differ between the sexes regardless of the environmental context, and only individual identity seemed to explain some of the observed variation. This points at breeding dispersal as an individually determined trait, which might depend on, for example, genetic variation or differences in breeding experience or phenotypic quality (Matthysen, 2012). However, other factors not considered in this study could also influence breeding dispersal, particularly interactions within the breeding pair. It is well known that pairing status affects breeding dispersal probability, such that in faithful pairs males and females will show a similar degree of philopatry, whereas divorce induces sex-specific (typically female-biased) dispersal (e.g. Calabuig, Ortego, Cordero, & Aparicio, 2008; Harvey et al., 1979, 1984; Payne & Payne, 1993; Valcu & Kempenaers, 2008; Ward & Weatherhead, 2005). This should be considered in future studies intended to assess the costs and benefits of breeding dispersal.

Genetic consequences of dispersal

Spatial genetic structure usually reflects a complex interaction of population demography, social and mating systems, and dispersal behaviour (Double et al., 2005). In contrast to other studies focused on polygynous (Double et al., 2005) or cooperatively breeding birds (Beck et al., 2008; Temple, Hoffman, & Amos, 2006; van Dijk et al., 2015), social interactions are not expected to influence the genetic structure in species with mating systems such as social monogamy (Banks & Peakall, 2012; Peakall et al., 2003). We found no sex-related differences in apparent survival, so potential effects of differences in mortality can also be discarded. Therefore, differences in population genetic patterns can be attributed to different natal dispersal patterns with relative confidence (Banks & Peakall, 2012).

Both analyses with a complete 2010-2015 dataset and those based on 'snapshot' years were consistent with prediction (iii). Results from Navarino supported the hypothesis of non-restricted, perhaps nearly random, natal dispersal in both sexes. Similarly, females in Fray Jorge also showed no fine-scale genetic structure, confirming that despite dispersing over much longer distances than males, their movements were not different from a random pattern. Although rayaditos moved relatively short distances, we still expected no local genetic structure in the aforementioned cases, because positive or negative genetic autocorrelation may only be detectable under strong restricted or exacerbated dispersal, respectively (Goudet et al., 2002).

Males in Fray Jorge showed a pattern of isolation by distance according to Mantel tests, and a positive genetic structure extending not much beyond 450 m (Fig. 3; see Peakall et al., 2003; Double et al., 2005). Considering these results along with the distribution of dispersal distances, it seems that male natal dispersal in Fray Jorge is restricted to within-fragment movements, given that diameters of the largest forest patches in this locality are 150-500 m (Botero-Delgadillo, pers. obs.).

The 2D LSA allowed us to confirm that positive genetic structure for males in Fray Jorge was the result of a patchy signal (Peakall et al., 2003; Double et al., 2005), as would be expected if habitat fragmentation is restricting male natal dispersal. Males were grouped in clusters of local genetic autocorrelation. Moreover, a closer look at the pairwise genetic distances of males composing such clusters revealed that in several cases, half sibs or even full sibs and fathers/offspring tended to be at distances no longer than 100-200 m away from each other (see Supplementary Table S4). Despite a risk of potentially deleterious inbreeding, the higher rate of female movement could override any negative effect (see van Dijk et al., 2015). Whether inbreeding avoidance is a major cause of female natal dispersal in Fray Jorge is beyond the scope of this work, but this would be interesting to study, given the apparent isolation of this population of rayaditos and its relatively low genetic diversity (Yáñez, 2013).

Concluding remarks

Non-migratory movements of passerine birds are usually reported as being < 1 km (see Eden, 1986; Paradis, Baillie, Sutherland, & Gregory, 1998), and in forest-dwelling species occurring in fragmented landscapes these distances can be even shorter (50-600 m; Harris & Reed, 2002). With the exception of females in Fray Jorge, distances travelled by rayaditos seem to follow this pattern, and even dispersal distances transformed into territory units were comparable to distances described for other species showing high site fidelity (see Arcese, 1989). Previous evidence already suggested that movements of rayaditos at the local scale rarely exceed 900 m (Vergara et al., 2010), and that forest fragmentation has consequences for breeding behaviour (Cornelius, 2008) and population density (Vergara & Marquet, 2007). Our results support these findings, and show that apparent survival, local spatial dynamics, and within-population genetic structure varied predictably in areas with contrasting local conditions. It seems that natal dispersal patterns of rayaditos are context-dependent: in a non-isolated, less stressful and continuous-habitat environment, their spatial dynamics resembled the patterns described for other socially monogamous birds. In contrast, in an isolated, crowded, more stressful and fragmented environment, rayaditos showed female-biased natal dispersal and restricted male movements. Although breeding dispersal did not vary markedly between the populations, adult birds from the more crowded environment were also more faithful to their previously established territory.

Further studies should test the effects of habitat fragmentation, population density, and social interactions separately. It would also be interesting to include additional study areas to better represent environmental variation along the distributional range of this bird. We suggest that studies looking at context-dependent dispersal patterns are still needed to fully understand the evolution of distinct dispersal strategies in different taxa (Clarke et al., 1997), ideally focusing on species with varying mating and social systems.

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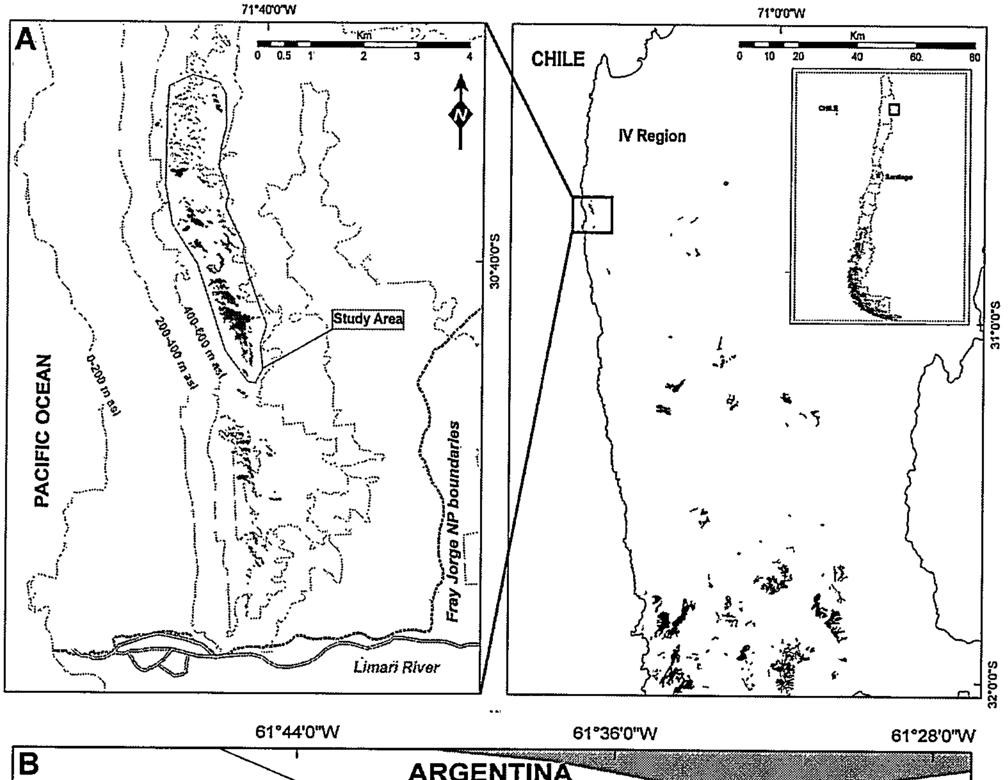
Supplementary Material Figure S1. Details of two study areas for comparing dispersal patterns in two populations of Thorn-tailed Rayadito. Forest relict fragments on the coastal mountain range (grey areas at the left and darker areas at the right) in Fray Jorge National Park (**A**), north-central Chile (IV Region). Sub-Antarctic forest and secondary forest (grey area) in lowland areas of Navarino Island, southern Chile (XII Region).



Supplementary Material Table S1. Details of 13 polymorphic microsatellite loci and one chromosome-linked marker (Ps/P) for Thorn-tailed Rayadito. The first eight loci are species-specific markers. M: primer mixes containing four to five primer pairs. T_a: annealing temperature. C: primer concentration in mix. Size range is in base pairs (bp).

Locus	Fluorescent dye	M	T_a (°C)	C (μM)	Size range (bp)
As1	NED-TTTCCAGTTGTATCTCTCAGCA GAAGAATGGGATCTAAGAAGTC	1	54	0.4	217-245
As7	6FAM-GCTGGGCTTGCATATTCTTC TCTTGTTTTGAAGGGAAGTGGA	2	55	0.36	213-253
As18	VIC-GGAAGCCATCTTAGGCTGTG GGGCATAGATGGTTGCTGAT	2	55	0.6	212-220
As25-1	PET-GGAGGGTATTTGGCAAGGTT AGGATGGCTTGCTAGCTGTG	2	55	0.3	176-208
As25-5	NED-TGGGTTCAGTATCCTGGAAGA GAGTTGCTCTTCTCTCCCTCA	2	55	0.4	172-210
As25-8	PET-AAGAAGCTCACCCGCTACCT TGTTGTCGTGCCTGAAGAAG	1	54	0.5	224-230
As25-10	VIC-GGAGTTATACCAGTTATAAAGG TGCTGTTGTCTGGCTAGCA	1	54	0.4	142-202
As25-14	6FAM-TTTCTGCTGCTGGAAAGGTT GTTCATCCAGGGAGAGTCCA	1	54	0.3	177-239
Asμ15 ZEST	6FAM-AATAGATTCAGGTGCTTTTTCC GGTTTTTGAGAAAATTATACTTTCAG	3	55	0.4	101-133
CcaTgu23	PET-CAAGGMYCATGCCAAAATAA CCCTYCCTCCCTTCAGTTTT	3	51	0.8	120-161
Tgu05	NED-CACAGAAAAGTGAGTGCATTCC TGGGAAAACATCTTTACCATCA	3	51	0.42	252-260
Tgu06	VIC-CGAGTAGCGTATTTGTAGCGA AGGAGCGGTGATTGTTCAGT	3	51	0.34	189-219
ZF_AC138573	NED-ATGYCAACTGAAATGTCAAGGT ATGAGGTCACTGAAAGKTWTAATA	3	51	0.5	134-192
P2/P8	6FAM-CTCCCAAGGA TGAGRAAYTG TCTGCATCGC TAAATCCTTT	2	55	0.6	356-382

Supplementary Material Table S2. Model selection for capture-mark-recapture (CMR) data from two populations (Navarino Island, Nav; Fray Jorge National Park, FJ) of Thorn-tailed Rayadito. Models' goodness of fit was assessed using values of Akaike's Information Criterion corrected for small samples (AICc) where lower values indicated better fit. Model notation: φ = apparent survival; p = recapture rate; FJF = female birds from FJ; FJM = male birds from FJ; NavF = female birds from Nav; NavM = male birds from Nav. Time-dependent variables were denoted with (t), whereas variables that were constant through time were denoted with (.). Equality between populations and/or sexes were denoted with '=', while differences appeared as '≠'.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	No. Par*	Deviance
φFJF(t)=φFJM(t)≠φNavF(t)=φNavM(t) pF(t)=pM(t)	791.91	0.00	0.52	1.00	6	139.19
φFJF(t)=φFJM(t)≠φNavF(.)=φNavM(.) pF(t)=pM(.)	795.06	3.14	0.11	0.21	5	144.39
φFJF(t)≠φFJM(t)≠φNavF(t)≠φNavM(t) pF(t)=pM(t)	800.36	8.45	0.01	0.01	6	153.79
φFJF(t)=φFJM(t)≠φNavF(t)=φNavM(t) pF(.)=pM(.)	805.28	13.37	0.00	0.00	6	142.12
φFJF(t)=φFJM(t)=φNavF(t)=φNavM(t) pF(t)=pM(t)	806.58	14.67	0.00	0.00	14	137.04

*No. Par: number of parameters in the model.

Supplementary Material Table S3. Static life tables for Thorn-tailed Rayadito assuming no population increase/decrease ($r = 0$) in two localities during 2008-2015. Approximated per capita rates of population growth (r) were calculated as $\ln(R_o)/G$ (Stearns, 1992). All survival and fecundity rates for ages 2-8 were estimated from capture-mark-recapture (CMR) data. Numbers in bold represent adjusted vital rates calculated by trial and error until obtaining $r = 0$. a_x = surviving individuals; l_x = age-specific survival rate; m_x = age-specific fecundity (mean number of fledglings produced by a female); R_o = number of fledglings produced by a female during its entire lifetime ($\Sigma\ l_xm_x$); G = generation time ($\Sigma\ x\ l_xm_x/R_o$).

Population	Age	a_x	l_x	m_x	l_xm_x	$x\ (l_xm_x)$
Navarino Island						
	0	**8076**	**1.000**	0.0	0.000	0.000
	1	**1400**	**0.173**	4.4	0.763	0.763
	2	110	0.014	5.1	0.071	0.142
	3	71	0.009	5.4	0.047	0.142
	4	50	0.006	5.4	0.033	0.134
	5	34	0.004	5.3	0.022	0.112
	6	9	0.001	5.2	0.006	0.035
	7	6	0.001	5.1	0.004	0.027
	8	2	0.000	5.0	0.001	0.010
					$R_o = 0.95$	G = 1.40
Fray Jorge NP						
	0	**3788**	**1.000**	0.0	0.000	0.000
	1	**880**	**0.232**	3.0	0.697	0.697
	2	124	0.033	3.1	0.101	0.203
	3	83	0.022	3.2	0.070	0.210
	4	51	0.013	3.1	0.042	0.167
	5	24	0.006	3.1	0.020	0.098
	6	11	0.003	3.0	0.009	0.052
	7	8	0.002	3.0	0.006	0.038
	8	3	0.001	2.9	0.002	0.014
					$R_o = 0.95$	G = 1.51

Supplementary Material Table S4. Pairwise relatedness among breeding male neighbours of Thorn-tailed Rayadito at Fray Jorge National Park (30°38'S, 71°40'W), Chile. Relatedness coefficients were estimated for eleven male clusters of 15 individuals that previously showed local positive genetic autocorrelation (*lr*) in a two-dimensional autocorrelation analysis (2D LSA; Double et al. 2005). For every subset showing significant ($P \leq 0.05$) and positive *lr* values, we estimated maximum estimates of relatedness (*r*) between a reference male and his 14 nearest neighbours. The *r* values for each pair of males were transformed into four relationships (U: unrelated; HS: half-siblings; FS: full-siblings; PO: parent-offspring) using the ML-Relate software (Kalinowski, Wagner, & Taper, 2006) to calculate the log-likelihood of these relationships.

Sample	*lr*	*P*	NN1	NN2	NN3	NN4	NN5	NN6	NN7	NN8	NN9	NN10	NN11	NN12	NN13	NN14
32	0.111	0.002	U	U	U	U	HS	U	U	HS	U	U	U	U	HS	U
20	0.109	0.003	PO	HS	U	HS	HS	U	U	HS	HS	U	U	U	U	U
14	0.102	0.007	U	U	U	HS	U	U	U	U	HS	PO	PO	U	U	U
49	0.068	0.02	U	U	U	U	U	U	U	U	FS	U	U	U	U	U
44	0.079	0.021	U	U	PO	HS	U	U	U	HS	U	U	U	U	U	U
63	0.067	0.026	U	U	U	U	U	U	HS	U	U	U	U	U	U	U
53	0.062	0.035	U	U	U	U	HS	U	U	U	HS	HS	U	U	U	U
26	0.063	0.037	U	U	U	U	PO	U	HS	U	HS	U	U	U	U	U
8	0.061	0.047	U	HS	U	HS	HS	U	U	U	U	FS	U	U	U	U
43	0.054	0.048	U	U	U	U	U	U	U	U	U	U	U	U	HS	U
40	0.051	0.049	PO	U	U	U	U	HS	U	U	U	U	U	HS	U	U

CAPÍTULO II

VARIATION IN THE CAUSES AND CONSEQUENCES OF LOCAL DISPERSAL IN TWO POPULATIONS OF A FOREST BIRD SUGGESTS CONTEXT-DEPENDENT STRATEGIES

MANUSCRITO FORMATEADO PARA ENVIAR A ECOLOGY

Context-dependent dispersal in a forest bird

VARIATION IN THE CAUSES AND CONSEQUENCES OF LOCAL DISPERSAL IN TWO POPULATIONS OF A FOREST BIRD SUGGESTS CONTEXT-DEPENDENT STRATEGIES

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ABSTRACT

Populations exhibit contrasting dispersal patterns in specific environmental contexts, but intraspecific comparisons of dispersal causes and consequences are necessary to gain key insights into the variation of environmental effects on dispersal. Combining capture-mark-recapture (CMR) data from eight years with molecular genetics, we tested for predictable differences in factors promoting local natal and breeding dispersal and their fitness consequences in two populations of a forest passerine bird, the thorn-tailed rayadito (*Aphrastura spinicauda*). Comparisons were made between populations facing contrasting local conditions in north-central and southern Chile. A northern population represented a fragmented, densely populated and more stressful environment, while the southern population corresponded to a continuous forest-dominated landscape and a less occupied and less stressful habitat. A set of 24 variables was selected for representing breeding success and apparent survival, and GLMMs were used to predict the main drivers and the benefits/costs of local dispersal. None of the assessed factors explained variation in the causes and consequences of natal dispersal in the southern population. By contrast, density-dependence and kin competition avoidance predicted natal dispersal distances of females and males in the northern locality, respectively. In addition, a reproductive cost for males was also evident in this population. Breeding dispersal might be an adaptive response of females to bad breeding experiences in previous years, but it appeared costly for males and for newly formed breeding pairs in both localities. High reproductive costs and decreased long-term survival were only detected for adult birds in the northern population. We found sex-specific consequences despite the absence of sex-biased breeding dispersal, which can be explained by sex-specific trade-offs between social and ecological pressures. The correspondence between results and predictions in this study supports our hypothesis that population-specific dispersal patterns can be explained by context-dependent costs and benefits of local natal and breeding dispersal.

Key words: Breeding performance; Chile; contrasting environments; inbreeding avoidance; intraspecific variation; kin competition; long-term mortality; mate and site choice; public information; thorn-tailed rayadito.

INTRODUCTION

Determining the causes and consequences of dispersal is critical to increase our understanding of the evolution and preponderance of dispersal behavior, but also to predict population responses to spatial and temporal environmental variation (Bowler and Benton 2005, Clobert et al. 2012). However, given the differences in dispersal propensity between pre-reproductive and adult individuals and the proximate factors and fitness consequences of their dispersal decisions (Matthysen 2012, Starrfelt and Kokko 2012), natal and breeding dispersal are often studied as separated phenomena by vertebrate ecologists (Johst and Brandl 2000).

Among birds, natal dispersal is not only more frequent than breeding dispersal, but involves more extensive movements with different effects on population spatial dynamics (Greenwood and Harvey 1982, Clarke et al. 1997, Paradis et al. 1998). Natal dispersal (i.e., the movement from the natal site to that of first breeding) is often viewed as a strategy to reduce mating between closely related individuals, or simply to avoid competition among kin ('inbreeding avoidance' and 'kin competition' hypotheses, respectively; see Arcese 1989). Also, natal dispersal can be forced by interactions with older and/or socially dominant conspecifics, or by a decrease in the quality of the natal site as a consequence of high population density ('social dominance' and 'population demography' hypotheses, respectively; see Arcese 1989, Byholm et al. 2003). On the other hand, breeding dispersal (i.e., subsequent move between breeding sites) is commonly regarded as a strategy to increase breeding success by adult individuals (Greenwood and Harvey 1982), particularly after mate loss through divorce or death of one member of a breeding pair, or after breeding failure ('mate choice' and 'site choice' hypotheses; Payne and Payne 1993, Daniels and Walters 2000). Breeding dispersal decisions can also be affected by the quality of an individual's breeding territory in comparison to nearby patches, for which the density and/or breeding productivity of conspecific neighbors can be used as a proxy of habitat quality ('public information' hypothesis; Danchin et al. 2004). Despite the aforementioned differences in their proximate factors, natal and breeding dispersal can have the same potential fitness consequences, as both can affect individual survival rates (Eden 1987, Cilimburg et al. 2002), physical condition (see Calabuig et al. 2008), or breeding success (Pärt 1990, Ward and Weatherhead 2005).

Although the scientific literature is plenty of detailed assessments of the potential costs and benefits of natal and breeding dispersal for numerous bird species (see Clobert et al. 2012), the influence of local environmental variation and the context-dependence of their causes and consequences are still poorly understood, as relevant factors related to dispersal have been mostly studied in specific populations under a particular environmental context (but see Verhulst et al. 1997, Eeva et al. 2008, Terraube et al. 2015). Considering that populations can exhibit differing dispersal patterns in contrasting environments (Lidicker and Stenseth 1992, Spinks 2000), interpopulation comparisons of dispersal strategies may prove valuable to determine how the direction and magnitude of the causes and consequences of natal/breeding dispersal vary depending on local conditions.

In this study, we explicitly test for differences in the factors promoting natal and breeding dispersal and their fitness consequences at a local scale in two peripheral populations of a forest passerine bird, the thorn-tailed rayadito (*Aphrastura spinicauda*). The thorn-tailed rayadito is a secondary-cavity nesting bird that occupies the temperate forests of Chile and western Argentina, covering a long latitudinal gradient (30° S–55° S; Remsen 2003). This species is negatively affected by forest clearance and fragmentation, probably due to the subsequent decrease in the availability/quality of nesting cavities (Cornelius 2008), and also to its reluctance to use relatively small gaps of non-suitable habitat (>300 m; Vergara et al. 2010). A long-term research has revealed differences in relevant ecological factors between two peripheral populations of this bird, which are located in contrasting environments near the northern (Fray Jorge National Park, north-central Chile; 30.63 S, 71.67° W) and southern (Navarino Island, southern Chile; 55.06° S, 67.67° W) limits of its distribution. The northern population occurs in a highly fragmented forest relict surrounded by a vast semiarid matrix (del-Val et al. 2006), resembling an isolated oceanic archipielago (Cornelius et al. 2000), whereas the southern population inhabits a continuous forest-dominated landscape (Luebert and Pliscoff 2006). In addition to this difference in landscape configuration, the northern locality appears as a densely populated and more stressful environment than the southern locality, as suggested by estimates of population density (Vergara and Marquet 2007, see also **Chapter 1**), baseline CORT levels (Quirici et al. 2014), and telomere lengths (Quirici et al. 2016).

As would be expected under these different environmental contexts, a comparison of dispersal behavior between these two populations showed contrasting patterns (see **Chapter 1**): natal dispersal in the northern population is female-biased and male movement is highly restricted, whereas bird movements in the southern locality follows a random pattern with no sex bias; breeding dispersal distances are more restricted than natal dispersal and nesting-site fidelity is more frequent among adult males in both populations, although age-related increased fidelity is only observed in males in the northern locality. These patterns might imply that the costs of dispersal are higher for birds in the northern population relative to those from the southern one and for males compared to females (**Chapter 1**). Combining capture-mark-recapture (CMR) data from eight years and molecular genetics, we address the hypothesis that the causes and consequences of local natal and breeding dispersal for thorn-tailed rayaditos are context-dependent and that local differences in the pressures on dispersal underlie the contrasting interpopulation variation in dispersal patterns. We assessed how kin interactions, density-dependence, habitat quality, mate choice, public information, breeding success and apparent survival are linked to dispersal strategies and how they interact with individual condition (i.e., age and sex) and the local environment (see Table 1).

As restrictions to dispersal and its related costs are expected to be lower in homogeneous environments and uncrowded populations (see Weatherhead and Boak 1986, Wotton et al. 1986, Wheelwright and Mauck 1998, Ward and Weatherhead 2005, Winkler et al. 2005), we predicted density-dependence and relatedness (inbreeding avoidance and/or kin competition avoidance; Bowler and Benton 2005) to be the proximal factors explaining variation in natal dispersal in the fragmented and densely populated environment (northern population), whereas habitat quality would better reflect natal dispersal in the continuous and less occupied habitat (southern population; see prediction 1 in Table 1). Following the same reasoning, adverse consequences on the breeding success or physical condition after natal dispersal were expected in the northern, but not in the southern population, especially in males (prediction 2). Given that most breeding dispersal events take place after mate loss and/or after breeding failure (Greenwood and Harvey 1982), we predicted increased breeding dispersal in both localities for widowed birds and after a poor breeding season (prediction 3), or if neighbor density/breeding productivity was higher in other patches (prediction 4). However, we did expect higher reproductive and/or mortality costs after breeding dispersal in the northern population compared to the southern population, particularly in males (prediction 5).

Table 1. Main predictions, related factors and measured variables for the potential causes and consequences of local natal and breeding dispersal in two populations of thorn-tailed rayadito.

Dispersal type		Prediction[^]	Related factor[‖]	Measured variables[§]	Target
Natal dispersal	Causes	Prediction 1	Natal habitat quality	SD of nestlings weight in natal nest x	Females and males
			Kin competition	Sex ratio in natal nest x	
			Inbreeding avoidance and kin competition	Genetic relat. with female neighbors $x+1$	
				Genetic relat. with male neighbors $x+1$	
			Density-dependence	Density of adult neighbors $x+1$	
	Consequences	Prediction 2	Breeding habitat quality	Condition index $x+1$	Females and males
			Breeding success	Sexual partners $x+1$	Females
				Paternity loss $x+1$	Males
Breeding dispersal	Causes	Prediction 3	Mate choice	Pairing status $x+1$	Females and males
			Past breeding success	Timing of breeding x	
				Breeding performance x	
			Nesting habitat quality	SD of brood weight x	
		Prediction 4	Public information	Density of adult neighbors $x+1$	
				Past breeding performance neighbors $x+1$	
	Consequences	Prediction 5	Breeding site quality	Condition index $x+1$	Females and males
			Breeding success	Sexual partners $x+1$	Females
				Paternity loss $x+1$	Males
			Mortality costs	Apparent survival (long term)	Females and males
			Nesting habitat quality	Territory quality index $x+1$	Breeding pair
				SD of brood weight $x+1$	
				Nest volume $x+1$	
			Breeding success	Timing of breeding $x+1$	
				Breeding performance $x+1$	
				Clutch volume $x+1$	

[^] Detailed description of predictions in the Introduction.

[‖] Factors commonly used for assessing hypothesis of dispersal (for a review see Arcese 1989, Payne and Payne 1993).

[§] Detailed description of variables in the Methods section (see *Measuring the causes and consequences*). Variables were measured either before (year x) or after (year $x+1$) natal/breeding dispersal

METHODS

Study areas

The northern study area was located in Fray Jorge National Park (Coquimbo Region), with an extension of ~4.3 km^2 in a semiarid landscape dominated by matorral steppe (Luebert and Pliscoff 2006). A total of 101–157 nest boxes have been installed between 2006 and 2015 in naturally fragmented remnants of temperate forest that occur at the top of the coastal mountain range at 630 m a.s.l. (del-Val et al. 2006). The southern study area was located in Navarino Island (Magallanes and Chilean Antarctic Region), comprising ~3.3 km^2 of a relatively continuous cover of sub-Antarctic forest and secondary growth (Rozzi and Jiménez 2014). Here, 171–222 nest boxes have been provided for occupation during the same time period. Nest boxes were regularly distributed in both sites after considering density estimates of breeding birds (e.g., Vergara and Marquet 2007), and their position was geo-referenced with 2 m measurement error.

Field procedures

Field data was gathered as part of a long-term monitoring of the breeding ecology of thorn-tailed rayaditos between 2008 and 2015 in both study areas. During each year, nest box occupants (adults and nestlings) were captured and marked with numbered aluminum bands when nestlings were 12-14 days old (Quirici et al. 2014). After capture, birds were measured and weighted (tarsus length, wing chord and tail length, ± 0.05 mm; body mass, ± 0.1 g; see Moreno et al. 2005, 2007), and a ~17 µl blood sample was obtained by puncturing the brachial vein with a sterile needle (Quirici et al. 2014), which were subsequently stored on FTA™ Classic Cards (Whatman™) for subsequent genetic analyses. Nest boxes were checked regularly until fledging, recording in detail the breeding phenology (egg-laying, hatching day, fledging day) and breeding success (clutch size, egg volume, hatching success, fledglings produced) for all occupant birds.

Genetic analyses

A detailed description of DNA extraction and microsatellite amplification analyses is given elsewhere (**Chapter 1**). Briefly, molecular sexing was carried using one chromosome-linked marker (P2/P8; Griffiths et al. 1998), given the lack of obvious sexual dimorphism in rayaditos (Moreno et al. 2007). Individuals were genotyped at 13 polymorphic microsatellite loci, using eight species-specific markers (see Yáñez et al. 2015), and five cross-species amplifying markers: Asμ15_ZEST, CcaTgu23 (Olano-Marín et al., 2010), Tgu06 (=CK307697), Tgu05 (=DV946651) (Slate et al. 2007), and marker ZF_AC138573 (van Osoten et al. 2016). All but one microsatellite marker were included for further estimation of genetic relatedness and parentage analyses (see below), as they showed no significant deviations from Hardy-Weinberg equilibrium (HWE; all $P > 0.1$) and the frequencies of null alleles were below 0.05.

Estimation of natal and breeding dispersal

Estimates of the distance and probability of dispersal were based on capture-mark-recapture (CMR) data obtained during 2008–2015. Local natal dispersal was defined as the distance between the natal nest box and the first recorded breeding nest box. We measured natal dispersal as the linear distance (m) between natal and breeding sites, but it was not treated as a categorical variable, given that movements of post-fledging birds were larger than the threshold values used to categorize them as 'dispersed' or 'non-dispersed' (see below). Natal dispersal analyses were based on 29 recaptures from a total of 491 marked nestlings in the northern population (6%), and

17 out of 565 marked nestlings in the southern population (3%). Although such recovery rates could imply that our dataset was biased towards the less dispersive individuals, this bias was probably low, as estimated mortality rates of juvenile birds in both populations (North: 77%; South: 83%) indicate that our sample comprised ~26% of all surviving fledglings in the northern population and 18% in the southern population (**Chapter 1**). Moreover, local movements reported for rayaditos rarely exceed 900 m long (Vergara et al. 2010), which are far below the maximum distance between nest boxes in the two study plots (North: 4.2 km; South: 2.9 km).

Local breeding dispersal was defined as the distance from one nest box to another between consecutive breeding seasons. Following Forero et al. (1999), we analyzed breeding dispersal both as a continuous (linear distance) and as a dummy variable ('dispersed'/'non-dispersed'), based on 95 (43 females, 52 males) and 133 (67 females, 66 males) adult recaptures in Navarino and Fray Jorge, respectively. To categorize recaptures as dispersed or non-dispersed, we used a measure of territory size as a threshold value (Valcu and Kempenaers 2008). We used Dirichlet tessellation (Aurenhammer 1991) to model and measure breeding territories for all captured adults during each year (Adams 2001). We then calculated the mean territory diameter in each population for every breeding season, in order to obtain a measurement of territory size that was independent of the yearly variation of bird density (Valcu and Kempenaers 2008). Linear distances that were equal or higher than the upper limit of the 95% confidence interval (CI) of the annual mean territory diameter were defined as dispersal events. Tesellation and estimation of territory diameters were performed in ArcGIS 9.3 (ESRI 2008).

Measuring the causes and consequences

To assess the causes and consequences of dispersal, we defined 24 variables that were extracted from the yearly monitoring of breeding success/phenology. These variables are related to a number of factors commonly invoked to explain the costs and benefits of dispersal, and were measured either a year before (year *x*) or after (year *x*+1) dispersal occurred (see Table 1).

The causes of natal dispersal considered five variables that did not discriminate between sexes (Table 1), and included the standard deviation, SD, of nestling weight in the natal nest in year *x* (e.g., Rabenold et al. 1991), the sex ratio in the natal nest in year *x*, the genetic relatedness with adult female/male neighbors established in the natal site in year *x*+1 (e.g., Wheelwright and Mauck 1998), and the density of adult neighbors in the natal site in year *x*+1 (measured as the mean distance from the three nearest breeding pairs). Maximum likelihood coefficients of pairwise genetic relatedness (*r*) between all sampled birds were calculated using the ML-Relate software (Kalinowski et al. 2006), and then a distance-weighted mean relatedness coefficient was computed between every breeding adult and the nearest three female/male neighbors around its natal site, using the linear distances between them as relative weights.

The consequences of natal dispersal included general and sex-specific variables (Table 1). While the influence of habitat quality in the first breeding territory was tested for both sexes (physical condition index for each bird in year *x*+1, calculated as the residuals from the regression of weight on tarsus lenght[3]; see Montalvo and Potti 1992), the effect of dispersal on breeding success was assessed separately for females (confirmed sexual partners in year *x*+1, categorized as 'one' or 'two or more mates') and males (paternity loss in year *x*+1, measured as the percentage of extra-pair young, EPY; e.g., Valcu and Kempenaers 2008). The number of mates per breeding female and estimates of paternity loss were obtained after performing parentage analyses, combining assignment and exclusion approaches (*sensu* Jones et al. 2010).

We first performed parentage analyses as implemented in CERVUS 3.0.7 (Kalinowski et al. 2007) based on 12 microsatellite loci (combined probability of exclusion in both populations, $P > 0.999$), using the logarithm of odds (LOD score) and critical Delta for assigning paternity. Results from these analyses were subsequently checked to confirm/exclude paternity. Assignment was confirmed whenever the most likely parent showed no loci mismatches with putative offspring and there was 95% confidence around the assignment based on LOD or Delta scores (i.e., strict confidence; Kalinowski et al. 2007). If the social father was the most likely candidate and showed no mismatches, assignment was still confirmed regardless of the confidence around it. If a set of candidates that did not include the social father showed no mismatches and positive LOD scores, but certainty around the assignment was below 80% (relaxed confidence), the whole set was excluded. Because EPY were not always confidently assigned to any of the sampled males, paternity gain was not certain in several cases, and thus we did not include this variable.

The causes of breeding dispersal comprised six variables focused on both sexes (Table 1), including the potential effects of 'past breeding performance' (brood size/clutch size*100 in year *x*), the SD of brood weight during the last breeding attempt (i.e., year *x*), timing of breeding during the last year (hatching date in year *x*, estimated as the number of days after the first recorded hatching date in the season; see Montalvo and Potti 1992), the density of adult neighbors in year *x*+1 and their 'past breeding performance' (e.g., Calabuig et al. 2008), and pairing status in year *x*+1 (e.g., Harvey et al. 1979, 1984, Blakesley et al. 2006). Due to the low frequency of divorce (Nav: 2%; FJ: 6%), we excluded these cases from further analyses and only considered two categories of pairing status: 'reunited pairs' and 'widowed birds'.

Similar to natal dispersal analyses, we used the same three variables for assessing the consequences of breeding dispersal on individual physical condition and breeding success in year $x+1$ (Table 1), but also considered rates of adult apparent survival as an estimation of the potential long term mortality costs (e.g., Pakanen et al. 2016; see details in *Statistical analysis*). Additionally, six variables were used to evaluate the effects of dispersal on reproductive success and settlement decisions of breeding pairs (Table 1), including timing of breeding in year $x+1$, 'breeding performance' in year $x+1$, clutch volume in year $x+1$ (calculated as the sum of egg volumes for the entire clutch; see Moreno et al. 2005), a territory quality index for year $x+1$ (percentage of years of successful occupation of a nest box corrected by the total number of years monitored; Forero et al. 1999), the SD of brood weight in year $x+1$, and nest volume in year $x+1$ (cm^3), a potentially adaptive trait of nest architecture for rayaditos (Botero-Delgadillo et al. 2017) linked to habitat quality for birds in general (Mainwaring et al. 2014). Given the difficulties to separate the potentially combined effect of both members of the breeding pair on these variables (e.g., clutch size, brood size, brood weight; Clutton-Brock 1988), we first tried to include female and male identity as crossed random factors in the analyses (see Valcu and Kempenaers 2008), but this prevented mixed models to converge. We thus decided to analyze these factors at the pair level, for which we categorized breeding pairs in two levels according to the number of dispersed members ('none'/'at least one'). Although discriminating between pairs with one and two dispersers would be ideal, this was not possible due to the difficulty to confirm the dispersal history of all pair members, for example in cases were recaptures with known dispersal status paired with new birds entering into the study plots.

Statistical analyses

With the exception of adult apparent survival (see below), the causes and consequences of dispersal were assessed by fitting generalized linear mixed models (GLMM; Bolker et al. 2008), using different error distributions and link functions depending on the response variable (see Results). All GLMMs were performed in R version 3.3.1 (R Core Team, 2016), using the packages lme4 (Bates et al. 2008), MASS (Venables and Ripley 2002), pscl (Jackman 2015), and MuMIn (Bartoń 2014).

For modeling the potential causes of natal dispersal, we considered individual travelled distances (log transformed) as the response variable and sex and locality as interacting factors, while the hatching year of every individual (Winkler et al. 2005) and age at recapture were included as random effects. A full model included all the measured variables as fixed effects (see Table 1), from which non-significant factors were removed by a backward stepwise procedure, subsequently obtaining a minimal most adequate model that was selected based on values of the corrected Akaike's Information Criterion AICc (Crawley 1993). To test the consequences of natal dispersal, we fitted separated GLMMs for each sex to assess the effects of travelled distances on birds' physical condition and sex-specific variables of breeding success (Table 1). These models also included locality as interacting factor and the aforementioned random effects.

In general, model building and selection for breeding dispersal followed the same logic applied to natal dispersal analyses. We preliminarily assessed the relationship between dispersal distances (log transformed) and probability of dispersal (dummy variable) with the pairing status of individual birds through linear and log-linear models (Christensen 1997), respectively. Both locality and pairing status were introduced as cofactors in all GLMMs to assess their interaction with predictor variables and potential effects on dispersal behavior. Analyses were carried out separately for female and male birds, mainly to avoid both members of reunited pairs to contribute twice (see Calabuig et al. 2008). For those variables related to breeding success (i.e., 'breeding performance'; SD of brood weight; 'past breeding performance' of neighbor adults; clutch volume; nest volume), we used relativized values in order to reduce heteroscedasticity, calculating the proportional value of each data point in relation to the population annual modal value. Only variables that were a relative measure *per se* (e.g., hatching date) were not transformed. Since all observations from every recaptured bird were entered in the models at the individual level, individual identity was included as a random factor, along with birds' estimated age and year of recapture. Analyses at the breeding pair level included pairing status as a cofactor (see above), and year of recapture and nest box identity as random effects.

For testing long-term mortality costs, we used CMR data to calculate adult apparent survival (φ) and recapture rate (p) using the Cormack-Jolly-Seber model (Sandercock 2003) in MARK 5.1 (White and Burnham 1999). We fitted different candidate models with variable restrictions on the parameters (Lebreton et al. 1992), including the individual cumulative linear distance across years and the number of breeding dispersal events as covariates. Given the difficulties to obtain parameter estimates and calculate effect sizes from a model using discrete individual covariates (Cooch and White 2017), we used separate models for females and males in each population instead of grouping individuals by 'Sex' and 'Locality'. Covariates were corrected by the total number of individual recaptures before performing the analyses. The most adequate models were selected based on AICc (Appendix S1: Table S1).

RESULTS

Proximate causes of natal dispersal

In the northern population, females moved longer linear distances (739.9 m, 875.9; median, interquartile range IQR) than did males (95.5 m, 121.1), whilst in the south, distances of females

(485.7 m, 452.7) and males (417.5, 239.1) were relatively similar (see **Chapter 1** for a detailed comparison of dispersal patterns). Only two predictor variables explained the variation in natal dispersal distances for post-fledging birds, although in interaction with locality and sex (Table 2). In the northern population, females dispersed longer distances when the natal patch was more densely occupied by breeding adults during the year of establishment (year x+1; Table 2, Fig. 1a), whereas males moved farther from their natal site as relatedness with adult neighbors of the same sex increased (Table 2, Fig. 1b). No such effects were detected for birds in the southern population (Fig. 1a, 1b).

Fitness consequences of natal dispersal

Dispersal distances did not explained variation in the physical condition of post-fledging birds in any of the populations studied (Table 4). Because all tested females had one sexual partner during their first breeding attempt, this variable was not assessed (Table 4). However, a significant interaction effect of natal dispersal and locality on paternity loss was detected: while the percentage of extra-pair young (EPY) in year x+1 increased as a function of dispersal distance for post-fledging males in the northern population, paternity loss was almost negligible in the southern population (Table 4, Fig. 1c).

Proximate causes of breeding dispersal

Dispersal events (i.e., movements longer than the upper limit of the 95% CI of the annual mean territory diameter) represented 32% from all recapture events in the northern population, and 42% in the south. Territory diameters in the north ranged from 29 to 33 m during the study period, and 25% of all movements between breeding seasons were above that range. In the southern population, only 8% of all movements were longer than the estimated territory diameters, which ranged from 63 to 110 m. Because linear distances above the range of estimated territory diameters exhibited low variability, models using breeding dispersal as a continuous or as a dummy variable yielded similar results (but see Forero et al. 1999). Therefore, we only present analyses on the categorical predictor/response.

The relationship between breeding dispersal and social status differed between both sexes (see Table 3). The minimal most adequate log-linear model for females (Log-likelihood ratio test: $\chi^2_2 = 0.96$, $P = 0.61$) indicated that despite the relative frequency of non-dispersers was higher in the northern population, widows were more prone to leave their previous breeding territory than remated females regardless of the locality (Table 3). The most adequate model for males (Log-likelihood ratio test: $\chi^2_4 = 4.23$, $P = 0.37$) showed that dispersal and pairing status varied independently, and more importantly, that non-dispersers were more frequent than dispersing individuals in both populations (Table 3).

According to GLMMs, all responses to potential causes of breeding dispersal were dependent on the pairing status of adult birds (Table 2). Although variation in the probability of dispersal among reunited pairs was not predicted by any of the independent variables, widowed birds of each sex exhibited variable responses. Overall, widowed females were more prone to disperse in year x+1 when breeding productivity of local neighbors during the last breeding season was low (Table 2, Fig. 2a). Significant interaction effects also indicated that dispersal probability of widowed females in the northern population increased after a late start of the last breeding attempt (not shown), and also following a poor breeding performance in year x (Table 2, Fig. 2b).

Table 2. Minimal adequate GLMMs for individual proximate causes of natal and breeding dispersal in two populations of thorn-tailed rayadito. Main effects or first order interactions were not tested when second order interactions were significant.

Dispersal type	Sex	Explanatory terms[§]	Estimate	SE	Test[‖]	P
Natal dispersal	Both	Intercept	2.16	3.63		
		Locality	-1.03	3.71	Not tested	
		Sex	0.05	4.27	Not tested	
		Sex*(log)distance to neighbors x+1	-0.23	2.30	Not tested	
		Sex*mean relatedness male neighbors x+1	-1.10	4.57	Not tested	
		Locality*Sex*(log)distance to neighbors x+1	-1.14	0.49	t_{25}=-2.11	0.045
		Locality*Sex*mean relatedness male neighbors x+1	10.98	4.95	t_{25}=2.21	0.036
Breeding dispersal	Females	Intercept	-0.14	1.27		
		Locality	-1.95	1.96	Not tested	
		PairStatus	17.67	10.21	Not tested	
		Locality*PairStatus	-26.04	11.55	Not tested	
		PairStatus*Timing of breeding x	-16.18	9.42	Not tested	
		PairStatus*Past breed. performance neighbors x+1	11.86	6.81	z_{156}=2.29	0.021
		Locality*PairStatus*Timing of breeding x	23.18	10.3	z_{156}=2.25	0.024
		Locality*PairStatus*Breed. performance x	10.88	5.15	z_{156}=1.99	0.048
	Males	Intercept	2.19	3.51		
		Locality	-9.91	6.01	Not tested	
		PairStatus	-14.34	6.81	Not tested	
		Locality*Timing of beeding x	-4.21	2.40	Not tested	
		Locality*(log) distance to neighbors x+1	4.92	2.41	Not tested	
		PairStatus*Timing of breeding x	0.16	0.07	z_{96}=2.16	0.030
		Locality*PairStatus*(log)distance to neighbors x+1	-0.37	-0.16	z_{96}=-2.23	0.025

Linear distance (log) and occurrence of dispersal ('dispersed'/'non-dispersed') were used as response variables for the natal and breeding dispersal models, respectively. Models for natal dispersal used a Gaussian distribution error and an identity link. Models for breeding dispersal used a binomial error structure and a log link. Variables were measured either before (year x) or after (year x+1) natal/breeding dispersal. Random factors in mixed models included: bird age (natal/breeding dispersal), hatching year (natal dispersal), individual identity (breeding dispersal), and year of recapture (breeding dispersal).

[§] Parameter estimates and SE (standard errors) were estimated relative to 'Navarino' (southern population) level in variable 'Locality', 'female' level in variable 'Sex', and 'reunited' level in variable 'Pairing status'.

[‖] z statistic corresponds to the Wald-test (H_o: parameter/SE = 0).

Table 3. Minimal adequate log-linear models testing the association of pairing status and breeding dispersal of female and male thorn-tailed rayaditos from two populations.

Pairing status		Dispersal status	Locality	Most adequate log-lineal model				
Reunited	Widowed			Explanatory terms[§]	Estimate	SE	Test[‖]	P
A. Females				Intercept	2.84	0.22		
35	10	Non-dispersed	North	Locality	0.67	0.25	z_2=12.95	0.008
11	11	Dispersed		PairStatus	-1.09	0.28	Not tested	
16	7	Non-dispersed	South	Dispersal	-0.45	0.34	Not tested	
12	8	Dispersed		Locality*Dispersal	-0.57	0.40	z_2=-1.43	0:151
				PairStatus*Dispersal	0.90	0.41	z_2=2.17	0.029
B. Males								
31	14	Non-dispersed	North	Intercept	3.01	0.17		
10	11	Dispersed		Locality	0.23	0.18	z_4=1.28	0.198
17	15	Non-dispersed	South	PairStatus	-0.41	0.18	z_4=-2.19	0.028
13	7	Dispersed		Dispersal	-0.63	0.19	z_4=-3.26	0.001

Full models included all main effects (Locality + PairStatus + DispersalStatus) and all first/second order interactions to explain the observed frequencies. The minimal most adequate model was selected using AICc values.

[§] Parameter estimates and SE (standard errors) were estimated relative to 'Navarino' (southern population) level in variable 'Locality', 'reunited' level in variable 'Pairing status', and 'non-dispersed' level in variable 'Dispersal'.

[‖] z statistic corresponds to the Wald-test (H_o: parameter/SE = 0).

In both populations, widowed males tended to disperse after a late breeding attempt in year *x* (Table 2, Fig. 2c), but there was an opposite response to the local density of adult neighbors: males in the north were more likely to move towards denser areas, whilst in the south, they tended to disperse to patches with lower density of adult neighbors (Table 2, Fig. 2d).

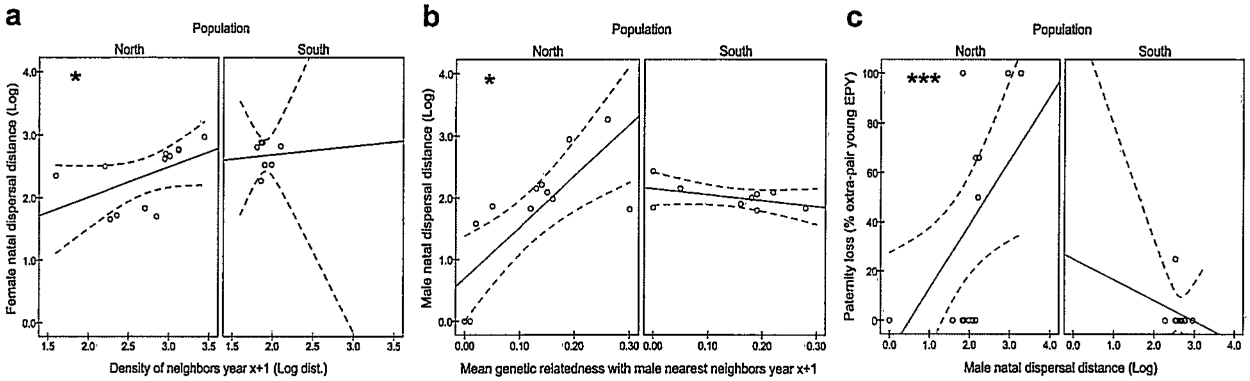

Figure 1. Causes and consequences of natal dispersal in a northern population (Fray Jorge National Park) of thorn-tailed rayadito. Variation in female natal dispersal distances as a function of density of adult neighbors in year x+1 (a), and relationship of male dispersal and mean genetic relatedness (r) with male neighbors in year x+1 (b). Paternity loss as a function of dispersal distance in post-fledging males (c). Levels of significance are marked for first and/or second order interactions: * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

Fitness consequences of breeding dispersal

Analyses of the fitness consequences of breeding dispersal revealed that the number of mates per breeding female in year x+1 increased for dispersers, although this relationship was dependent on the locality and pairing status of birds (Table 4, Fig. 2e). In the southern population, dispersal lead to an increase of sexual partners of both widowed and remated females, but such apparent benefit was only evident for widowed females in the northern locality (Fig. 2e). In the case of males, breeding dispersal represented a reproductive cost that also interacted with pairing status and locality (Table 4).

Table 4. Minimal adequate GLMMs for individual fitness consequences of natal and breeding dispersal in two populations of thorn-tailed rayadito. Main effects or first order interactions were not tested when second order interactions were significant. Response variables are in bold.

Dispersal type	Models by factors§	Females				Males			
		Estimate	SE	Test$^{\Vert}$	P	Estimate	SE	Test$^{\Vert}$	P
Natal dispersal	**Physical condition index x+1**								
	Intercept	-0.41	3.52			4.41	3.67		
	Locality	2.66	3.77	t_{18}=0.70	0.490	-3.46	3.74	t_{20}=-0.92	0.366
	log(travelled distance)	0.32	1.33	t_{18}=0.34	0.809	-1.18	1.37	t_{20}=-0.86	0.397
	Locality*log(travelled distance)	-0.55	1.41	t_{18}=-0.39	0.701	1.16	1.39	t_{20}=-0.83	0.416
	Sexual partners/Paternity loss x+1								
	Intercept	Not assessed^				-6.05	4.59	Not tested	
	Locality					1.24	0.01	Not tested	
	log(travelled distance)					0.98	0.21	Not tested	
	Locality*log(travelled distance)					1.02	0.22	t_{20}=1.89	< 0.001
Breeding dispersal	**Physical condition index x+1**								
	Intercept	1.18	0.23			2.59	0.11		
	Dispersal	0.91	0.34	Not tested		-0.21	0.14	z_{117}=2.17	0.140
	Locality*Dispersal	-1.14	0.39	Not tested			Not included in model^^		
	PairStatus*Dispersal	-0.29	0.28	Not tested			Not included in model^^		
	Locality*PairStatus*Dispersal	0.98	0.45	z_{103}=4.64	0.031		Not included in model^^		
	Sexual partners/Paternity loss x+1								
	Intercept	0.19	0.54			3.78	0.31		
	Dispersal	-3.07	1.29	z_{105}=5.65	0.017	-2.77	0.45	Not tested	
	Locality*Dispersal	0.56	0.87	z_{105}=0.41	0.522	-29.48	0.34	Not tested	
	PairStatus*Dispersal	0.57	1.15	z_{105}=0.24	0.620	0.79	0.38	Not tested	
	Locality*PairStatus*Dispersal	Not included in model^^				-2.39	0.40	z_{111}=34.47	< 0.001

Models for physical condition used a Gaussian distribution error and an identity link. Models for number of sexual partners (females) and % paternity loss (males) used a binomial negative error structure and a log link. Variables were measured either before (year x) or after (year x+1) natal/breeding dispersal. Random factors in mixed models included: bird age (natal/breeding dispersal), hatching year (natal dispersal), individual identity (breeding dispersal), and year of recapture (breeding dispersal).

[§] Parameter estimates and SE (standard errors) were estimated relative to 'Navarino' (southern population) in variable 'Locality', 'reunited' in variable 'Pairing status', and 'non-dispersed' in variable 'Dispersal'.

[‖] z statistic corresponds to the Wald-test (H_o: parameter/SE = 0).

^Variables that showed no inter-individual variability were not assessed (see text).

^^Variables that were not included in the minimal most adequate models based on AICc values.

Although in the southern population the costs of paternity loss after dispersal were only evident for widowed males, dispersers in the northern population had higher percentage of EPY in their own nests, independent of their pairing status (Fig. 2h).

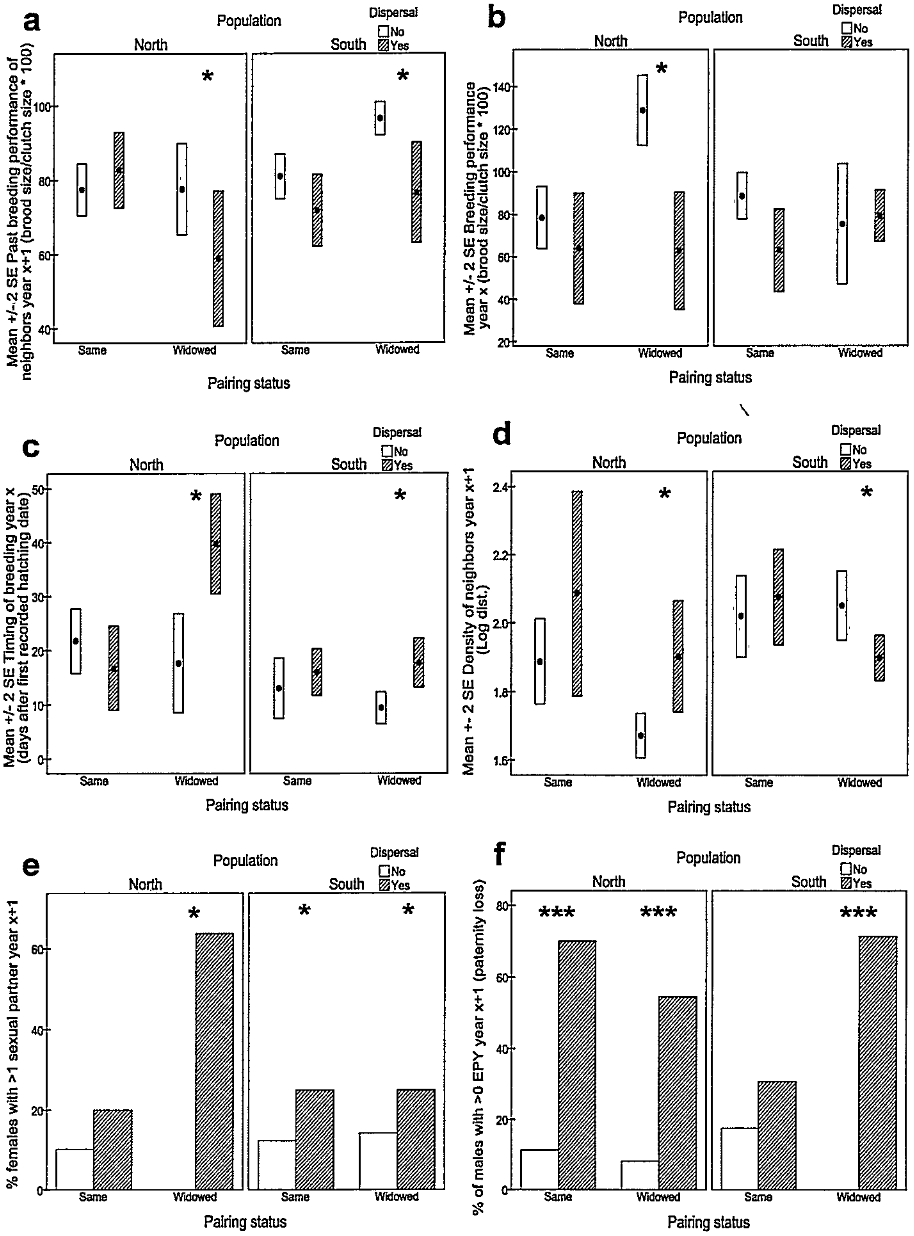

Figure 2. Causes and consequences of breeding dispersal in two populations of thorn-tailed rayadito in the northern and southern part of its distribution. The first four panels (a-d) depict proximate factors affecting breeding dispersal in females (a, b) and males (c, d). Reproductive consequences for females (e) and males (f) are also shown. Levels of significance are marked for first and/or second order interactions: * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

The analyses for mortality costs of breeding dispersal showed contrasting results between populations. The most adequate models for both sexes in the southern population suggested that values of apparent survival varied temporally, but none of the two covariates of breeding dispersal were included (Appendix S1: Table S1). Individual mean apparent survival rates in this locality during years 2008–2015 were 0.65 ± 0.1 for females and 0.66 ± 0.2 for males (mean ± SE). By contrast, the best models for both sexes in the northern population included apparent survival as a constant term, and included the number of breeding dispersal events (BDE) as a covariate (Appendix S1: Table S1). The negative effect of dispersal was expressed by the following equations: $\text{logit}(\varphi) = 1.27 - 0.57 \times (\text{BDE})$, for females, and $\text{logit}(\varphi) = 1.29 - 0.45 \times (\text{BDE})$, for males. Individual mean apparent survival rates estimated for females and males in the northern locality corresponded to 0.78 ± 0.04 and 0.78 ± 0.05, respectively.

A total of 67 breeding pairs from the northern population and 55 from the south were analyzed, from which 51 and 54% consisted of reunited pairs in each locality, including cases with none (North: $N = 17$; South: $N = 26$) or at least one dispersed adults (North: $N = 13$; South: $N = 8$). The remainder cases corresponded to pairs formed by widowed females and males, also with none (North: $N = 8$; South: $N = 16$) or at least one confirmed disperser (North: $N = 25$; South: $N = 9$). Results from GLMMs suggested no negative consequences of dispersal in the southern population, other than a decrease in the territory quality occupied by widowed pairs in year $x+1$ (Table 5, Fig 3a). In the north, all dispersed pairs settled in less productive territories in year $x+1$ (Table 5, Fig. 3a), and pairs formed by widowed birds had lower breeding performances and broods with more variable weights after dispersal (Table 5, Fig. 3b, 3c).

Table 5. Minimal adequate GLMMs for fitness consequences of breeding dispersal for breeding pairs from two populations of thorn-tailed rayadito. Main effects or first order interactions were not tested when second order interactions were significant. Response variables are in bold.

Models by factors	Estimate	SE	Test*	P
Time of breeding x+1				
Intercept	0.84	0.11		
PairStatus	0.17	0.16	t113=1.06	0.29
Dispersal	0.02	0.17	t113=-0.75	0.45
Breeding performance x+1				
Intercept	0.87	0.07		
PairStatus	0.04	0.10	Not tested	
Dispersal	-0.05	0.10	Not tested	
Locality*PairStatus*Dispersal	-0.79	0.37	t113=-4.48	0.034
Clutch volume t+1				
Intercept	855.54	136.94		
PairStatus	-101.68	103.59	t77=-0.98	0.32
Dispersal	-61.36	94.45	t35=-0.65	0.52
Locality*PairStatus*Dispersal	-53.95	206.48	t59=-0.26	0.79
Territory quality index x+1				
Intercept	2.01	0.08		
PairStatus	-0.12	0.13	Not tested	
Dispersal	-0.14	0.13	Not tested	
Locality*PairStatus	0.35	0.18	Not tested	
PairStatus*Dispersal	-0.82	0.26	Not tested	
Locality*PairStatus*Dispersal	0.96	0.34	z114=2.77	0.005
SD of brood weight x+1				
Intercept	1.34	0.26		
PairStatus	-0.08	0.37	Not tested	
Dispersal	-0.44	0.38	Not tested	
Locality*PairStatus	1.08	0.57	Not tested	
Locality*PairStatus*Dispersal	-2.01	0.83	t101=-2.38	0.018
Nest volume t+1				
Intercept	689.54	455.64		
PairStatus	-226.69	161.85	t86=-1.40	0.165
Dispersal	-116.95	160.61	t66=-0.72	0.46
Locality*PairStatus*Dispersal	-131.10	333.60	t84=-0.39	0.69

Models for territory quality used a binomial distribution and a log link. The remainder models used a Gaussian distribution and identity link, excepting breeding performance, which used a log link. Nest box identity was included as a random factor.

[§] Parameter estimates and SE (Standard errors) were estimated relative to 'Navarino' (southern population) in variable 'Locality', 'reunited' in variable 'Pairing status', and 'none' in variable 'Dispersal'.

[‖] z statistic corresponds to the Wald-test (H_o: parameter/SE = 0).

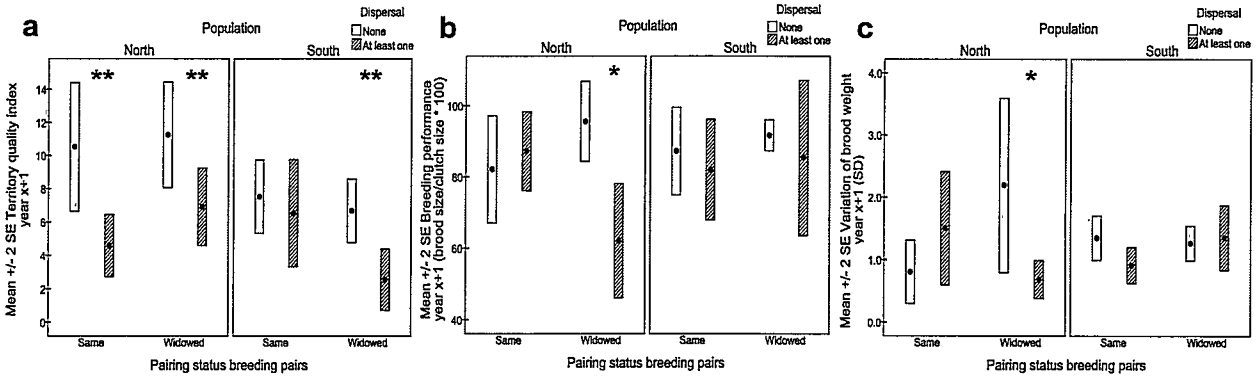

Figure 3. Reproductive consequences of breeding dispersal for breeding pairs of thorn-tailed rayadito in two populations near the northern and southern limits of its distribution. Variation of territory quality (a), breeding performance (b), and variation of brood weight (c) and their relationship with dispersal and pairing status of members of breeding pairs. Levels of significance are marked for first and/or second order interactions: * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

DISCUSSION

Context-dependent strategies of local natal dispersal

Interpopulation differences in natal dispersal strategies are expected when environmental heterogeneity exerts varying ecological, genetic and/or social pressures on dispersal (Matthysen 2012, Starrfelt and Kokko 2012). Although limited by a reduced sample size, our results suggest that in two populations of thorn-tailed rayaditos, differences in the causes and consequences of natal dispersal can be understood in light of the local environmental context. In the homogeneous and less densely occupied environment (southern population), none of the assessed factors explained variability in natal dispersal distances for either sex, even though habitat quality was expected to predict dispersal behavior. In the fragmented and densely populated environment (northern population), density-dependence and kin competition apparently affected female and male natal dispersal, respectively, but the expected influence of inbreeding avoidance was not detected. No apparent consequences of natal dispersal were evidenced for post-fledging dispersers, excepting male birds in the northern population, for which a reproductive cost in terms of paternity loss was apparent.

The lack of a relationship between natal dispersal and inbreeding avoidance was not surprising for a continuous environment like the southern locality, where random settlement after natal dispersal and no fine-scale genetic structure have been described previously (**Chapter 1**). Nonetheless, we expected this relationship to partially explain the long dispersal distances of females in the north, which frequently left their natal forest patch, presumably as a response to the spatially restricted movements of males and their tendency to form clusters of more genetically related individuals within forest fragments (**Chapter 1**). Although we did not find evidence of active inbreeding avoidance (see e.g., Szulkin and Sheldon 2008), females may already be decreasing the probability of mating with relatives by moving away from their natal sites where male offspring usually remain. In fact, a number of studies have shown that demographic processes and random dispersal may suffice to account for low levels of inbreeding in natural populations (e.g., Arcese 1989, Gibbs and Grant 1989), also hindering the detection of active avoidance mechanisms (Wheelwright and Mauck 1998).

Many studies have shown that high population densities and habitat heterogeneity could lead to increasing dispersal via intraspecific competition (Matthysen 2012). Despite males in the north are more philopatric than females (**Chapter 1**), we still expected kin competition to explain the variability in male dispersal distances, which indeed occurred. Adult males that were more genetically related to local occupants around its natal site dispersed farther to establish their first breeding territory. These results support the idea that the northern locality is a more saturated and highly competitive environment, where nesting cavity availability appears low in relation to the density of breeding birds (**Chapter 1**). Moreover, the long natal dispersal distances of females and the resulting sex-biased patterns could also be a consequence of the high levels of intraspecific competition, as would be expected for populations under crowded conditions (Gowaty 1993).

Despite density-dependence is important for dispersal decisions (Bowler and Benton 2005), we found little evidence of its potential role as a driver of natal dispersal. This was not completely unexpected in the southern locality, where a lower density of breeding birds and higher availability of forested habitats would reduce competition for breeding territories (see **Chapter 1**). Nonetheless, we observed that females in the northern population seemed to respond to density of adult neighbors in their natal patch, supporting the idea that saturated and patchy environments promote sex-specific dispersal responses (Wheelwright and Mauck 1998). Specifically, females dispersed larger distances to less densely occupied patches, presumably as a consequence of higher levels of female-female competition for breeding opportunities. Although direct evidence for this is lacking, the documented settlement patterns of post-fledging females in this population indicate this might be the case, as they gradually move away from their natal site until the first available male/vacant site is found (**Chapter 1**).

Potential costs of natal dispersal can result from the lack of familiarity with the first breeding site and/or the lack of reproductive experience of young birds (Greenwood 1980, Greenwood and Harvey 1982). Such costs should be low, or even absent, in a continuous and less populated environment, particularly if dispersal is not restricted by landscape configuration (Winkler et al. 2005), and if availability of breeding sites are higher and less variable (Payne 1991). Furthermore, costs/benefits of dispersal should not differ between sexes in socially monogamous birds with symmetrical parental roles (Clarke et al. 1997, Arlt and Pärt 2008), as is the case of thorn-tailed rayaditos (Moreno et al. 2007). However, male natal site fidelity would be enhanced in saturated and heterogeneous environments, for dispersal can increase the risk of not finding a suitable nesting site because of higher social competition (Ward and Weatherhead 2005, Forero et al. 1999), but also the likelihood of breeding failure due to unfamiliarity with the breeding territory/neighborhood (Greenwood and Harvey 1982). Our results agreed with these predictions, as no negative consequences were detected for either sex in the southern population, whereas males in the north had higher levels of EPY (paternity loss) as dispersal distance increased. This cost might represent a social restriction to natal dispersal, which in turn would promote male philopatric behavior. In addition, if dispersal distance is inversely related with male quality, as the social dominance hypothesis predict (Arcese 1989), this would also imply that females can compensate for the low quality of their social mate by incurring in more extra-pair copulations.

We did not test the effect of natal dispersal on other variables of breeding success such as clutch volume or breeding performance (clutch size/brood size), given that these factors are a consequence of the combined parental effort of both adults (Clutton-Brock 1988; see Methods). This means that variation in these factors could be accounted at the breeding pair level, but this was not possible for natal dispersal analyses, since nearly all recaptured post-fledging birds were mated with adults of unknown age and whose dispersal and social status were not certain (i.e., new captures). Mortality costs were also not tested given the impossibility to estimate apparent survival rates for post-fledging birds, but the long-term effects of dispersal on bird survival are discussed in detail in the following section.

Context-dependent strategies of local breeding dispersal

Breeding experience in birds is assumed to increase with age, as well as familiarity with a breeding area (Greenwood and Harvey 1982). The higher philopatric behavior of adults is well documented (Clarke et al. 1997), and it is explained as a 'win-stay, lose-shift' strategy (Switzer 1993), which is based on the premise that philopatry is the best choice whenever past breeding success predicts future success (Ward and Weatherhead 2005, Öst et al. 2011). Therefore, breeding dispersal is widely viewed as a costly decision that can be advantageous after a poor breeding performance (e.g., Weatherhead and Boak 1986, Calabuig et al. 2008) or after mate loss (e.g., Harvey et al. 1979, 1984, Forero et al. 1999). The frequency of breeding dispersal in populations of thorn-tailed rayadito is low and the distances travelled during such events rarely exceed 100 m long (**Chapter 1**), suggesting that the benefits of philopatry could increase for adult individuals. We found, however, that widowed females were more likely to disperse than those reunited with their previous mate, whilst males seemed to be highly faithful to their breeding site regardless of their pairing status. These results imply that drivers of breeding dispersal could vary between sexes due to differences in competition and life-history strategies, with 'mate-faithful' females competing for male availability and 'site-faithful' males competing for breeding territories (see Le Galliard et al. 2003 for a similar pattern for a lizard species).

Our results showed that the use of public information was important for breeding dispersal decisions for widowed birds from both populations. The direction of this relationship was not always consistent, but it was evident that information on conspecifics either helped avoiding dispersal towards less productive areas (i.e., females), or prompted individuals to seek for patches with more presence of adult birds (i.e., males in the northern locality). As discussed above, poor breeding performance was also expected to increase the probability of breeding dispersal, but this happened only for widowed birds. The fact that only widowed individuals seemed to respond to public information or past breeding success could be an indicative of the condition-dependent nature of dispersal decisions (Blakesley et al. 2006). While social benefits of remating may allow pairs to relocate themselves nearby their previous nesting site after breeding failure (Bai and Severinghaus 2012), widowed birds, particularly females, might be forced to move farther, and thus informed decisions prior to dispersal would have a critical value (Cote and Clobert 2007).

Breeding dispersal and/or mate loss can have opposite reproductive consequences for female and male birds (Montalvo and Potti 1992, Valcu and Kempenaers 2008), as we observed in rayaditos. Despite all the potential advantages of philopatry, dispersal could be beneficial for females due to their ability to better perceive the quality of neighboring territories in relation to males (Pärt 1995), but also because of the opportunity to mate with more experienced or socially dominant partners after leaving a breeding site ('mate choice' hypothesis; see Payne and Payne 1993). Although we did not assessed this possibility, we found that females were more prone to engage in extra-pair copulations after dispersal, suggesting this can be a strategy to increase breeding success, especially if dispersed females are not able to mate with the highest quality male nearby their new breeding site. The breeding cost carried by males (i.e., paternity loss) also point to this direction, if we assume that dispersed males are of lower quality because of their unfamiliarity with the new habitat and/or the social neighborhood (Greenwood 1980, Greenwood and Harvey 1982). More interesting is that only widowed males paid such a cost in the southern population, while in the north, paternity loss was higher for all dispersers regardless of their social status, reinforcing the idea that levels of social competition are higher in the more populated and heterogeneous environment. Reproductive consequences at the breeding pair level also hinted that dispersal is more costly in the northern population, and that the number/type of traits affected might depend on the local context. Again, breeding dispersal involved lower reproductive performance for dispersing pairs composed of widowed birds, but no adverse consequences for reunited pairs. This seems logical, as remating can provide enormous benefits like increased habitat familiarity and improved social coordination between breeding partners (Black 2001, Morrison et al. 2008).

Mortality costs of breeding dispersal have been described for a number of bird species (e.g., Daniels and Walters 2000, Pakanen et al. 2011), showing sex-differences in some instances (Pärn et al. 2009), or also co-varying with the local ecological conditions (Terraube et al. 2014). Despite we did not find sex-specific differences, we observed context-dependent effects of breeding dispersal on adult long-term survival. In the northern population, apparent survival was lower for females and males that incurred more frequently in dispersal throughout their lives, confirming that fragmented landscapes increase the risk of mortality for this forest passerine. It has been shown that habitat fragmentation negatively affects breeding success (Chalfoun et al. 2002, Tewksbury et al. 2006) and survival of several forest species (Horak and Lebreton 1998, Matthysen et al. 1999, Ruíz-Gutierrez et al. 2008), sometimes through an increase of dispersal-related mortality (Ewers and Didham 2006). Although we did not estimate post-fledging survival, it is reasonable to expect that natal dispersal would have the same effect on juvenile mortality, considering that longer distances can represent a higher predation risk.

Concluding remarks

The correspondence between predictions and results in this study supports our assumption that population-specific dispersal patterns can be explained by context-dependent costs and benefits of local natal and breeding dispersal. We are not sure to what extent the limited sample size in the southern locality reduced our power for detecting potential causes and consequences of natal dispersal in this population, but this result agreed with the random pattern of post-fledging movements and the consequent random spatial distribution of rayaditos' genotypes reported there (**Chapter 1**). Random dispersal is predicted to occur in unstructured habitats (Wotton et al. 1986), and could reflect a non-adaptive or neutral process whenever no fitness consequences are evident (see Payne 1991). In the north, fitness costs were only detected for males, as would be expected in a population where natal dispersal is female-biased (**Chapter 1**). In this locality, female natal dispersal can be a response to increased competition for available males, while variability in male dispersal distances might result from a trade-off between the social benefit of settling nearby the natal site and the associated costs of kin competition.

Breeding dispersal was costly for individuals and breeding pairs in both localities, but it appeared to be an adaptive response after a bad experience during the previous breeding season, such as mate loss or low reproductive success (Calabuig et al. 2008). Higher costs were anticipated for birds and breeding pairs inhabiting the heterogeneous and more densely populated environment (see Bensh and Hasselquist 1991, Forero et al. 1999, Ward and Weatherhead 2005), which was indeed confirmed. Results for this population also suggested that despite the higher risk of mortality, female dispersal might be promoted by intense intrasexual competition for potential mates, which ultimately could favor mate fidelity in females. Meanwhile, male dispersal would be a balance between competition and breeding/mortality costs, potentially benefiting site fidelity in males.

Although some authors have proposed that the proximate causes and consequences of dispersal may be widespread at the within-species level (Montalvo and Potti 1992), this study provides evidence of intraspecific differences in the costs and benefits of natal and breeding dispersal, showing population-specific responses to spatial environmental variation. Furthermore, we showed that differences between sexes in the fitness consequences of dispersal are particularly evident when the pairing status of individuals is considered. This illustrates the role of mate loss on conditioning breeding dispersal decisions in socially monogamous passerines, despite the relevance of social bonds in 'short-lived' species are sometimes underestimated.

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Table S1. Model selection for apparent survival (φ) and recapture rate (p) from capture-mark-recapture (CMR) data from two populations of thorn-tailed rayadito. Models' goodness of fit was assessed using values of AICc. Most adequate models are in bold.

Population	Sex	Model	AICc	Delta AICc	AICc Weights	Model Likelihood	No. Par	Deviance
North	Females	φ(t), p(.)	**193.59**	**0.00**	**0.60**	**1.00**	**4**	**187.32**
		φ(.), p(.)	195.56	1.97	0.22	0.37	2	187.10
		φ(t), p(t)	196.78	3.19	0.12	0.20	6	186.08
		φ(.), p(t)	198.84	5.25	0.04	0.07	4	185.85
		φ(t*BDE), p(.)	202.04	8.45	0.01	0.01	7	181.85
	Males	φ(t), p(.)	**171.35**	**0.00**	**0.89**	**1.00**	**4**	**162.86**
		φ(.), p(.)	177.16	5.80	0.05	0.05	2	156.79
		φ(t), p(t)	178.11	6.75	0.03	0.03	6	162.67
		φ(t*BDD), p(.)	178.58	7.23	0.02	0.03	7	163.15
		φ(t*BDE), p(.)	183.39	12.04	0.00	0.00	7	167.95
South	Females	φ(BDE), p(.)	**189.59**	**0.00**	**0.49**	**1.00**	**3**	**183.32**
		φ(.), p(.)	192.33	2.73	0.12	0.25	2	188.19
		φ(t), p(t)	192.57	2.98	0.11	0.23	6	184.11
		φ(BDD), p(.)	193.32	3.73	0.08	0.16	3	187.05
		φ(t*BDE), p(.)	202.04	12.45	0.00	0.00	7	181.85
	Males	φ(BDE), p(.)	**169.19**	**0.00**	**0.61**	**1.00**	**3**	**162.90**
		φ(BDD), p(.)	171.61	2.42	0.18	0.30	3	165.32
		φ(.), p(.)	172.32	3.13	0.13	0.21	2	168.17
		φ(t), p(t)	173.56	4.37	0.07	0.11	6	165.07
		φ(t*BDE), p(.)	177.16	7.97	0.01	0.02	7	156.79

Time-dependent variables were denoted with (t), whereas variables that were constant through time were denoted with (.). BDE = breeding dispersal events throughout the capture history for every individual; BDD = breeding dispersal distance (cumulative value) throughout the capture history for every individual. Both estimates were corrected by the total number of individual recaptures.

CAPÍTULO III

CONTEXT-DEPENDENT RELATIONSHIP BETWEEN BREEDING DISPERSAL AND PERSONALITY IN A PASSERINE BIRD: INTERPOPULATION DIFFERENCES IN EXPLORATION, AGGRESSIVENESS AND RISK TAKING BEHAVIOR

MANUSCRITO FORMATEADO PARA ENVIAR A BEHAVIORAL ECOLOGY AND SOCIOBIOLOGY

Context-dependent relationship between breeding dispersal and personality in a passerine bird: interpopulation differences in exploration, aggressiveness and risk-taking behavior

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Abstract

Studies of intraspecific variation on the relationship between personality and dispersal are necessary to understand the evolution of dispersal syndromes. Empirical studies have focused on natal dispersal, even though behavioral differences between dispersers and philopatric individuals might hold through the whole life cycle, subsequently affecting breeding dispersal propensity. Using capture-mark-recapture (CMR) data and behavioral trials in two wild populations of thorn-tailed rayadito (*Aphrastura spinicauda*), we investigated intraspecific differences in exploratory behavior, aggressiveness and risk-taking behavior, and tested for a context-dependent relationship between those traits and breeding dispersal. We compared two contrasting environments; an isolated population in Fray Jorge National Park, north-central Chile, that represented a fragmented and saturated environment; and a population from Navarino island, representing a homogeneous, less densely populated and less stressful habitat. We found that behavioral variation followed the predicted pattern, with birds from Fray Jorge being less exploratory, less aggressive and shyer than individuals from Navarino, suggesting site-specific behavioral strategies. Our results also showed that personality could predict fine-scale breeding dispersal, but this relationship would depend on the local environmental context. The absence of breeding dispersal syndromes in Navarino was expected, as the local habitat could have relaxed selective pressures on dispersal. The higher propensity to disperse of more exploratory females and more aggressive males in Fray Jorge implied that dispersal syndromes are more likely to occur when local conditions impose more restrictions to dispersal.

Significance statement Depending on the ecological and social conditions in any given population, dispersal syndromes can be quite variable, or even absent. Surprisingly, most studies testing this variation have focused on natal dispersal, although the decision of adult individuals to disperse could still be affected by phenotypic characteristics, particularly personality traits. To our knowledge, this is the first study documenting a relationship between breeding dispersal and personality, and furthermore, assessing if such association is context-dependent. We found that personality in the thorn-tailed rayadito predictably varied between contrasting environments, and that breeding dispersal syndromes were absent in an environment with no apparent restrictions to dispersal. On the contrary, breeding dispersal was related with exploratory behavior and aggressiveness in a fragmented and saturated habitat, supporting the idea that dispersal syndromes are more likely to occur when local dispersal is restricted.

Key words Breeding dispersal, dispersal syndromes, intraspecific variation, personality-dependent dispersal, thorn-tailed rayadito

Introduction

Dispersal syndromes, or the integration of dispersal with physiological, morphological, behavioral and/or life-history traits, have been documented in several animal species (Cote and Clobert 2012; Ronce and Clobert 2012). In addition, recent evidence suggests that dispersal phenotypes may be functionally and genetically integrated with personality traits (Duckworth 2012; Duckworth et al. 2015; Korsten et al. 2013), a phenomenon often referred as personality-dependent dispersal (Cote et al. 2010). Consistent inter-individual differences in personality appear to be linked with the propensity to disperse: for many species, dispersers tend to be faster explorers, bolder, more active, more aggressive and less social than philopatric individuals, although opposite trends have been reported (Clobert et al. 2009; Cote et al. 2010). Because animal personalities might constitute a set of strategies for individuals to cope with environmental stress (e.g., the fast-bold and slow-shy spectrum; Sih et al. 2004; Réale et al. 2007), it is expected that a relationship between personality and dispersal would be a complex and varying response exhibiting population-specific differences (Matthysen 2012). Dispersal syndromes have, for instance, been shown to vary depending on the ecological and social environment (Spinks et al. 2000; Verhulst et al. 1997), but the available examples are particularly restricted to the association between dispersal and morphological/physiological traits (Clobert et al. 2012). While studies of intraspecific variation in the relationship between personality and dispersal are needed to further understand the evolution of dispersal syndromes (Bonte and Saastamoinen 2012), these still remain scarce.

Although personality traits can affect individual decisions during different behavioral stages of dispersal (Cote et al. 2010), natal dispersal (i.e., the movement from the natal site to the first breeding site) decisions are more likely to be influenced by genetic and maternal effects than breeding dispersal (i.e., the movement between breeding sites during consecutive breeding seasons), given that adults have accumulated more experience and information on the distribution of resources, which subsequently affects future dispersal decisions (Bowler and Benton 2005; Pakanen et al. 2011). Furthermore, several studies in avian taxa reveal that the proximate causes of breeding dispersal are usually different from those promoting natal dispersal, being habitat quality, pairing status and past breeding success the main predictors of its occurrence (Clarke et al. 1997; Greenwood and Harvey 1982). As a result, natal dispersal has been the main focus of interest in studies of personality-dependent dispersal, even though some authors propose that behavioral differences between dispersers and philopatric individuals may hold through the whole life cycle (Cote et al. 2010). Some studies have suggested that aggressiveness or boldness could explain differences in breeding dispersal propensity between adult individuals (Valcu and Kempenaers 2008), but this remains to be tested.

In this study, we investigated interpopulation variation in personality traits in a passerine bird, and their relationship with breeding dispersal under contrasting environmental conditions. We studied two wild populations of the thorn-tailed rayadito (*Aphrastura spinicauda*), a small cavity nesting bird that breeds in temperate forests along an extensive latitudinal gradient throughout Chile and western Argentina (30° S–55° S; Remsen 2003). A long-term study on the breeding ecology of this species has shown that populations occurring at the northern and southern limits of its distributional range show important physiological (Quirici et al. 2014, 2016), behavioral (Botero-Delgadillo et al. 2017), and ecological differences (**Chapter 1, 2**). Close to the northern limit of its distribution, in Fray Jorge National Park (hereafter Fray Jorge; S30° 38', W71° 40'), a relatively isolated population of rayaditos occupy naturally fragmented forests surrounded by an extensive semiarid matrix, while in the southern limit, in Navarino

Island (hereafter Navarino: S55° 4', W67° 40'), the species inhabits relatively continuous forests and maintains gene flow with other populations (González and Wink 2010; Quirici et al. 2014; Yáñez 2013). Comparative estimates of population density (Vergara and Marquet 2007; **Chapter 1**), baseline CORT levels (Quirici et al. 2014), and telomere lengths (Quirici et al. 2016) indicate that Fray Jorge represents a more stressful and densely populated environment than Navarino, and recent evidence also suggest that both natal and breeding dispersal are more restricted and involve higher breeding and mortality costs in this locality (**Chapter 2**).

Using capture-mark-recapture (CMR) data and behavioral trials for two wild populations of rayaditos, we studied intraspecific differences in exploration, aggressiveness and risk-taking behavior, and tested for a context-dependent relationship between those traits and breeding dispersal. Based on empirical studies for birds in general and information about interpopulation differences in ecological and physiological traits of rayaditos, we make explicit predictions about expected patterns of context-dependent variation. Levels of aggression and activity have been shown to increase in high-density populations (Cote and Clobert 2012). However, artificial selection experiments in birds show that stress-hormone profiles differ between proactive (i.e., fast-bold) and reactive (i.e., slow-shy) individuals, the second having higher levels of baseline CORT levels and higher stress responses (Baugh et al. 2012; Cockrem 2007; Groothuis and Carere 2005; Øverli et al. 2007), suggesting a genetic correlation between personality and physiology. Considering that baseline CORT levels are lower in both nestlings and adult rayaditos in the continuous and less densely populated environment of southern Chile (Quirici et al. 2014), and assuming that behavioral syndromes in rayaditos are broad and consistent associations of personality traits as in other bird taxa (see Duckworth 2012; Groothuis and Carere 2005; Réale et al. 2007), we predicted (1) that birds from this population are on average, more exploratory, more aggressive and bolder than birds from north-central Chile. Current evidence for a number of species indicates that faster explorers and/or more aggressive individuals are more prone to disperse (Cote et al. 2010). Nevertheless, comparative studies show that despite saturated and competitive environments promote the differentiation between dispersers and philopatric individuals in distinct phenotypic traits, such differences might be cancelled in the absence of competition, even though dispersal still occurs (Aragon et al. 2006; Spinks et al. 2000). Given the differential ecological and social pressures on breeding dispersal between the two study populations (**Chapter 2**; see above), we predicted (2) no differences between dispersers and non-dispersers in the homogeneous and less stressful environment of southern Chile, but breeding dispersers in the northern population to be more exploratory, more aggressive and bolder than philopatric birds.

Materials and methods

Study areas

This study was part of a long-term nest-box monitoring program carried in Fray Jorge National Park, Coquimbo Region, northern Chile, and Navarino Island, Magallanes and Chilean Antarctic Region, southern Chile. Fray Jorge is a semiarid landscape dominated by matorral steppe (Luebert and Pliscoff 2006), where a fog-supported fragmented relict of Valdivian temperate forest occurs at the top of the coastal mountain range (del-Val et al. 200). Navarino, on the other hand, comprises a large and nearly continuous extent of sub-Antarctic forest and secondary growth (Rozzi and Jiménez 2014). A total of 101–157 and 171–222 nest boxes were installed between 2006 and 2015 in forest habitats of Fray Jorge and Navarino, respectively, being regularly distributed (25–35 m) and geo-referenced with 2 m measurement error (**Chapter 1**).

Breeding monitoring and capture procedure

The frequency of second clutches in rayaditos is extremely low (R. A. Vásquez, unpublished data), and the few cases recorded were not considered in this study. During each year, occupied nest boxes were monitored on a daily basis to record laying dates, hatching dates and fledging dates (see details in Moreno et al. 2005). Breeding adults were captured using nest-box traps when nestlings were 12–14 days old, and subsequently marked with numbered aluminum bands (Moreno et al. 2005; Quirici et al. 2014), and a unique combination of plastic colored bands for subsequent identification during behavioral trials (see below). During capture, birds were measured and weighted (tarsus length, wing chord and tail length, ± 0.05 mm; body mass, ± 0.1 g; see Moreno et al. 2005, 2007), and before release, a blood sample of ca. 17 μl was obtained by puncturing the brachial vein with a sterile needle (Quirici et al. 2014). Blood samples were stored on FTA™ Classic Cards (Whatman™) for molecular sexing.

Molecular sexing

Molecular sexing was necessary due to the lack of obvious sexual dimorphism in thorn-tailed rayaditos (Moreno et al. 2007). A detailed protocol is described elsewhere (see **Chapter 1**). In brief, we used a sex-specific length polymorphism in the CHD gene that can be PCR amplified with primers P2 and P8 (Griffiths et al. 1998). One primer (P8) was fluorescently labelled with 6-FAM™ (Thermo Fisher Scientific). The PCR products were mixed with formamide and a size standard (GeneScan™ 500 LIZ®), heat denatured and resolved in POP4 polymer on an ABI™ 3130 Genetic Analyzer (Thermo Fisher Scientific, Darmstadt, Germany). The size of fragments was determined with the GeneMapper 4.0 software (Applied Biosystems). The chromosomal origin of the fragment was detected by their size and appearance: the 382 bp W-chromosomal fragment CHD-W is specific for heterogametic females (ZW), and appeared together with one of the Z-chromosomal fragments that are either 357 bp (CDH-Z1) or 358 bp (CDH-Z2). Homogametic males (ZZ) can be homo- or heterozygous at the CHD locus.

Behavioral trials

Behavioral tests were carried during 2013–2015 between 0600 and 1300 h during the last two weeks of the breeding attempt of adult birds. It was not possible to record data blind because our study involved focal animals in the field. Exploratory behavior was assessed using novel environment experiments (Réale et al. 2007), following the methodology described in van Dongen et al. (2010). Trials were carried immediately after bird capture (see above), but prior to marking and processing. For these tests, we used large field-portable cages (270 cm length × 150 cm width × 150 cm height) that were installed across the study plots but not in close proximity to nest boxes (30-60 m). Cages were made of polyvinyl chloride poles and semitransparent black shading cloth, with four wooden perches diagonally arranged at regular distances (60–70 cm) along the long axis. A small holding cage (30 cm length × 25 cm width × 39 cm height) covered with a cloth was placed in a corner of each experimental cage, where birds were initially introduced for a 5 min acclimatization period, after which the cloth was removed and the door open (van Dongen et al. 2010). Experimental trials lasted for 10 min, and all events were recorded with a high definition camera placed at 5–7 m from the cage. We focused on documenting the number of movements (flights and hops) during trials, and the destination of every movement in each of the 14 possible areas to be visited by the birds, including the four perches and 10 additional surfaces (i.e., floor, walls and roof) that were defined according to the inner subdivisions of the exploration cage (see van Dongen et al. 2010). All videos were analyzed using JWatcher 1.0 (Blumstein et al. 2010). Individual exploratory behavior was quantified using two uncorrelated variables (Pearson's $r = 0.21$, $p = 0.11$): (i) movement rate (total movements/minute), used as a proxy of exploration speed; and (ii) exploratory diversity (van Dongen et al. 2010), quantified with the Brillouin's diversity index, which is more appropriate when the probability of obtaining any sample (i.e., visited surfaces) is not necessarily equal (see Krebs 1989). To calculate this index, we used the frequency of visits in each of the 14 areas and the exact time spent there by each bird.

For measuring aggressiveness, we used agonistic behavior tests (Carere et al. 2005), simulating territory intrusions by a conspecific male (simulated territory intrusion, STI; Wingfield et al. 1987). These tests were carried when nestlings were 15–16 days old, always three days after exploration experiments. Although measurement of aggression towards conspecifics might be best carried before incubation (Gowaty 1981; Wingfield et al. 1990), it was not possible to perform these tests until both members of each pair were marked with color bands. For these trials, we placed a stuffed mount of a male rayadito at 3–5 m from the nest box, and played tape-recorded songs of a male from the respective population (see details in Ippi et al. 2010, 2013) during 10 min using a sound speaker. An experimented observer recorded all behaviors using a digital audio recorder while remained hidden from view. Recordings were further analyzed in the JWatcher software, in order to quantify two uncorrelated variables (Pearson's $r = 0.42$, $p = 0.08$): (iii) the total number of movements during the trial, used as a representative of an individual's alarm activity (Ippi et al. 2013); and (iv) the total number of aggressions over the intruder, including physical aggressions (e.g., pecking the intruder), or aggressive maneuvers (e.g., flying over the intruder or hovering close to it).

Finally, risk-taking behavior was assessed by a predator presentation test (Réale et al. 2007), scoring nest defense intensity towards a human observer (see Hollander et al. 2008). Tests were performed when nestlings where 17–19 days old, three days after the STIs. These trials were carried out a few days before fledging, given that increased nest defense during the end of nestling growth in several birds makes this an appropriate time for testing this behavior (Montgomery and Weatherhead 1988). An observed stood at 1.5 m from the nest box, measuring (v) the minimum approach distance of both adults during a period of 3 min after they arrived to the nesting site. Contrary to Hollander et al. (2008), we carefully selected the observer's position during previous days to be sure that the availability of surrounding vegetation would not limit bird's approachability to the intruder. Exact distances were measured with a laser rangefinder.

Capture-recapture and breeding dispersal

We used CMR data obtained during 2012-2015 to track bird movements between consecutive breeding seasons. Although dispersal can be measured both as a continuous variable and as a binary state (e.g., Forero et al. 1999), previous analyses on breeding dispersal strategies of rayaditos showed similar results when considering linear distances (m) or the occurrence/absence of dispersal (**Chapter 2**). We thus defined dispersal status ('dispersed'/'non-dispersed') for every individual according to the linear distance moved between consecutive years in relation to a threshold value. Recaptured birds moving a distance higher than the upper limit of the 95% confidence interval (CI) of the annual mean territory diameter in each population were considered as 'dispersed', whereas individuals retaining the same nest-box or moving to adjacent nest boxes were defined as 'non-dispersed' (sensu Valcu and Kempenaers 2008). Breeding territories were modeled separately for every breeding season using Dirichlet tessellation

(Adams 2001), and annual mean territory diameters were subsequently calculated for each population. Because we contrasted bird movements with mean values computed for every year, we avoided the potential effects of the yearly variation of bird density on territory size (Valcu and Kempenaers 2008). All spatial analyses were performed in ArcGIS 9.3 (ESRI 2008).

Data analysis

Due to adult mortality and/or nest failure in some nest boxes, not all individuals were subjected to all experiments, either during a specific year or throughout the sampling period. As a result, sample sets for each behavioral test were not necessarily composed by the same individuals and/or were unbalanced, so interpopulation comparisons of behavioral traits were assessed with separated analyses. Furthermore, we removed duplicate records from the same individual, and hence, our analyses only included first captures. Although repeated measurements are essential to assess repeatability and behavioral plasticity (Dingemanse et al. 2010), we focused only on inter-individual variation at the within- and among-populations levels (Réale et al. 2007). However, exploration, aggressiveness and risk-taking behavior in rayaditos show similar values of repeatability relative to other bird species, ranging from 0.2 to 0.5, and are considered elsewhere (Poblete et al., unpublished data).

Normality was tested for all variables using Shapiro-Wilk's test. With the exception of the number of aggressions during STIs, all variables fitted the assumptions of normality (all $p >$ 0.05). Preliminary tests were carried in order to test for inter-annual variation in behavioral traits within each population. Since no temporal variation was found for any of the variables tested (see Results), we combined data from all sampled years for behavioral comparisons between populations. For this, we used two separate multivariate general linear models (Quinn and

Keough 2002) for normally distributed variables, one for variables describing exploratory behavior, and another for the alarm activity/minimum approaching distance. The number of aggressions was analyzed using generalized linear models with a Poisson error structure and a log link function (GLZ; Quinn and Keough 2002). All these models tested the main effects of locality (i.e., population of origin) and sex, and their two-way interactions.

For validating context-dependent phenotypic correlations between behavioral traits and breeding dispersal (sensu Réale et al. 2007), we analyzed recaptured individuals with known dispersal status and with data from at least one behavioral experiment carried out during the same year of recapture. We fitted generalized linear mixed models (GLMM; Bolker et al. 2008), using binomial error distributions and log link functions (Quinn and Keough 2002), performing separated analyses for exploratory behavior and aggressiveness/risk-taking. Dispersal status ('dispersed'/'non-dispersed') was included as the response variable and behavioral traits as fixed effects, while locality was introduced as interacting factor. Only year of recapture and bird age were included as random factors, since other potential random effects were accounted for by excluding duplicated samples (individual effect) and by performing separated analyses for females and males ('nest-box effect'; see Ippi et al. 2013). By separately analyzing each sex, we also prevented both members of a breeding pair to contribute twice in the analyses (Calabuig et al. 2008). All independent variables were introduced in full models, from which minimal most adequate models were selected using the corrected Akaike's Information Criterion AICc and by manually removing non-significant effects through a backward stepwise procedure (Crawley 1993). Although pairing status of adult birds is an important predictor of breeding dispersal in birds (e.g., Blakesley et al. 2006; Calabuig et al. 2008; Valcu and Kempenaers 2008), including rayaditos (**Chapter 2**), we did not considered this variable due to the extremely low number of widowed or divorced adults for which behavioral information was available (< 10 individuals for each sex for novel environment tests or agonistic behavior/predator presentation tests). Consequently, all analyses were focused on dispersed and non-dispersed birds that remated with their previous breeding partner.

All statistical tests were performed using $\alpha = 0.05$ for hypothesis testing, and were performed in R version 3.3.1 (R Core Team, 2016), using the packages lme4 (Bates et al. 2008), MASS (Venables and Ripley 2002), and MuMIn (Bartoń 2014).

Ethical note

Birds were captured and marked under the authority of Servicio Agrícola y Ganadero (SAG; permits 5193/6295) and Corporación Nacional Forestal (CONAF), Chile. Research was carried with the supervision of the Ethics Committee of the Sciences Faculty, Universidad de Chile. Birds that were subjected to novel environment experiments were gently captured with a butterfly net after the test, subsequently processed (mark and blood sample) in 3-5 minutes, and then released nearby their nest box. Subsequent visits to the nest boxes allowed us to confirm that captured adults resumed their parental duties and that fledging success was not compromised.

Results

Personality traits and annual variation

Multivariate general linear models (MGLMs) performed with normally distributed variables revealed that neither the measurements of exploratory behavior, nor the variables describing alarm activity and risk-taking behavior varied between years in Navarino (exploratory behavior: Roy's Largest Root = 0.08; $F_{3,76} = 2.05$; $p < 0.11$; alarm activity/risk-taking: Roy's Largest Root

= 0.11; $F_{3,58}$ = 1.62; $P < 0.18$) and Fray Jorge (exploratory behavior: Roy's Largest Root = 0.007; $F_{2,81}$ = 0.27; $P < 0.76$; alarm activity/risk-taking: Roy's Largest Root = 0.03; $F_{2,71}$ = 0.09; $P < 0.91$). Similarly, GLZ models indicated that there was no effect of the breeding season on the number of aggressions recorded during STIs for birds in Navarino (Wald $\chi^2 = 1.61$; $df = 1$; $p = 0.20$) and Fray Jorge (Wald $\chi^2 = 0.04$; $df = 1$; $p = 0.85$).

Interpopulation differences in behavior

The interpopulation comparison of exploratory behavior was based on 80 captured birds in Navarino (40 from each sex) and 84 in Fray Jorge (42 from each sex). Mean values of movement rates and exploration diversity per population are summarized in Table 1. According to MGLMs, exploratory behavior differed between populations (Roy's Largest Root = 0.66; $F_{2,159}$ = 52.45; $p < 0.001$), but there was no a sex-difference (Roy's Largest Root = 0.002; $F_{2,159}$ = 0.19; $p = 0.87$) nor a significant interaction between main effects (Roy's Largest Root = 0.001; $F_{2,159}$ = 0.01; $p = 0.98$). Although there was no effect of the population on movement rates, values of exploratory diversity were significantly higher in Navarino than in Fray Jorge (Table 2, Fig. 1a).

Contrasts of aggressiveness and risk-taking behavior included 74 individuals captured in Navarino (37 from each sex) and 63 in Fray Jorge (31 females and 32 males). Table 1 summarizes for each population the mean values of the number of movements during STIs, the number of aggressions towards a conspecific intruder, and the minimum approaching distance to a human observer (MADH). Results from MGLMs showed a significant interaction between population of origin and sex on two normally distributed variables, i.e., alarm activity during STIs and MADH (Population*Sex effect: Roy's Largest Root = 0.07; $F_{2,132}$ = 4.71; $p = 0.01$).

Table 1. Mean values (± standard deviation, SD) of five measures of personality traits using three distinct behavioral tests in two populations of thorn-tailed rayadito in two contrasting environments in southern (Navarino Island) and north-central (Fray Jorge National Park) Chile. See text for an explanation on differences in sample sizes for novel environment tests (Navarino, *n* = 80; Fray Jorge, *n* = 84) and agonistic behavior/predator presentation tests (Navarino, *n* = 74; Fray Jorge, *n* = 63).

Behavioral test	Personality trait[1]	Variable measured	Mean values (SD)	
			Navarino	Fray Jorge
Novel environment[1]	Exploration	Movement rate (movs/min)	24.9 (7.2)	24.2 (6.3)
		Exploration diversity (Brillouin's index)	1.7 (0.2)	1.2 (0.2)
Agonistic behavior[2]	Aggressiveness	Alarm activity (number of movements)	61.6 (36.1)	54.8 (33.1)
		Aggressions towards intruder (total)	2.8 (3.8)	1.3 (1.8)
Predator presentation[1]	Risk-taking	Minimum approach distance to human observer (m)	1.9 (1.3)	3.6 (1.9)

[1] Sensu Réale et al. (2007).

[2] Agonistic behavior tests were carried using a simulated territorial intrusion (STI; Wingfield et al. 1987) by a conspecific male (see text for details).

After the inspection of between-subject effects, however, we noticed different patterns for each variable: a significant and opposite interaction was detected for the alarm activity, with males and females being the more active sex in Navarino and Fray Jorge, respectively (Fig. 1b); MADH values only varied between localities, with birds of both sexes approaching more to the observer in Navarino (Table 2, Fig. 1c). According to the GLZ model, the number of aggressions towards a conspecific stuffed mount during STIs differed between both populations (Table 2), being higher in Navarino (Fig. 1d). Nevertheless, a significant interaction with sex was detected (Table 2), as females and males in Navarino almost equally attacked the intruder, whereas males from Fray Jorge where more aggressive than females (Fig. 1d).

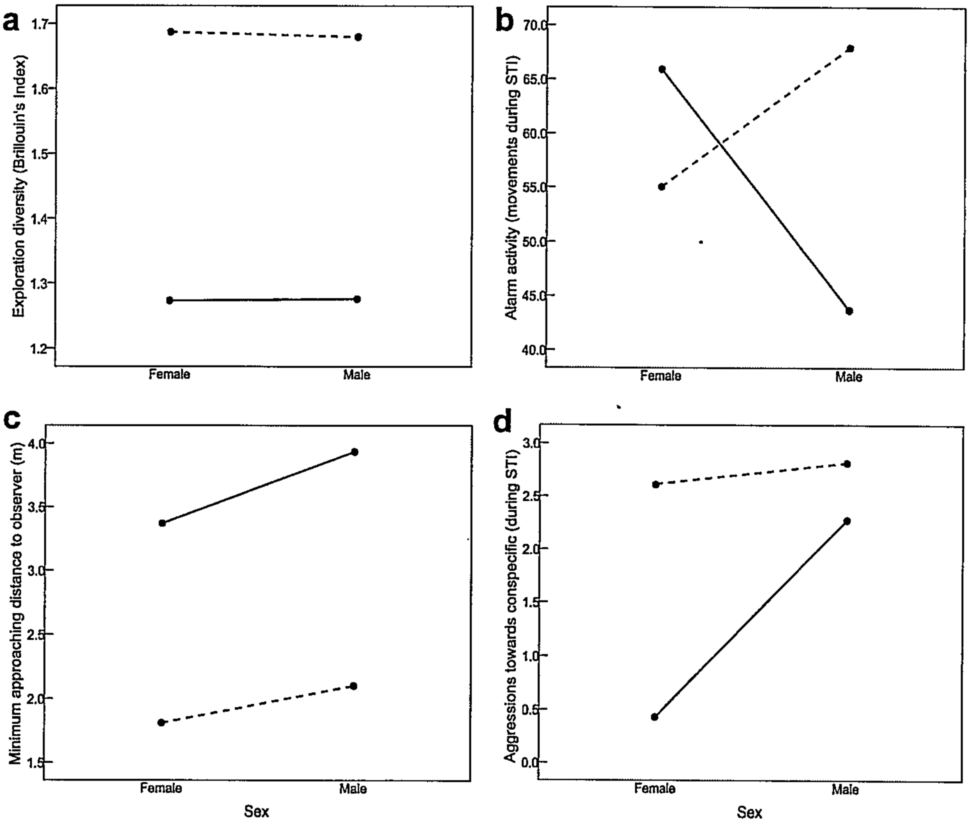

Figure 1. Interaction plots for the effects of population and sex on personality traits of thorn-tailed rayadito in two populations in southern (Navarino Island; dashed line) and north-central (Fray Jorge National Park; solid line) Chile.

Table 2. Between-subject effects of multivariate general linear models (MGLMs) for variation in personality traits between two populations of thorn-tailed rayadito in contrasting environments in southern (Navarino Island) and north-central (Fray Jorge National Park) Chile.

Personality trait	Variable measured	Explanatory terms	Estimate	SE	Test[1]	p
Exploration	Movement rate (movs/min)	Intercept	24.62	1.04		
		Population	0.56	1.48	$F_{1,160}$=0.43	0.51
		Sex	-0.76	1.47	$F_{1,160}$=0.34	0.57
		Population*Sex	0.29	2.11	$F_{1,160}$=0.02	0.89
	Exploration diversity (Brillouin's index)	Intercept	1.27	0.39		
		Population	0.41	0.05	$F_{1,160}$=101.02	< 0.001
		Sex	-0.003	0.06	$F_{1,160}$=0.003	0.95
		Population*Sex	0.01	0.08	$F_{1,160}$=0.01	0.91
Aggressiveness	Alarm activity (number of movements)	Intercept	43.70	5.42		
		Population	24.23	7.96	$F_{1,133}$=1.35	0.25
		Sex	22.21	7.67	$F_{1,133}$=0.66	0.42
		Population*Sex	-35.12	11.31	$F_{1,133}$=9.35	0.003
	Aggressions towards intruder (total)	Intercept	0.82	0.19		
		Population	0.41	0.28	z_{136}=-3.05	< 0.001
		Sex	-1.65	0.35	z_{136}=-3.05	< 0.001
		Population*Sex	1.58	0.46	z_{136}=-3.05	0.001
Risk-taking	Minimum approach distance to human observer (m)	Intercept	3.93	0.27		
		Population	-1.83	0.40	$F_{1,133}$=34.39	< 0.001
		Sex	-0.56	0.38	$F_{1,133}$=2.18	0.14
		Population*Sex	0.28	0.57	$F_{1,133}$=0.23	0.63

[1] z statistic corresponds to the Wald-test (H_o: parameter/SE = 0).

Behavioral correlates of breeding dispersal

The GLMMs used for testing the relationship between breeding dispersal and exploratory behavior included 53 recaptured birds with known dispersal status from Navarino (25 females and 28 males) and 57 from Fray Jorge (29 females and 28 males). After correcting for random effects, most adequate models for females and males showed that the relationship of exploration and breeding dispersal was dependent on the population (see Table 3). Although there was no effect of exploratory behavior on breeding dispersal status in Navarino, in Fray Jorge, dispersed females moved faster than non-dispersers during exploration trials (Fig. 2a), whereas male dispersers tended to show a more diverse exploratory behavior (marginally significant effect; see Table 3).

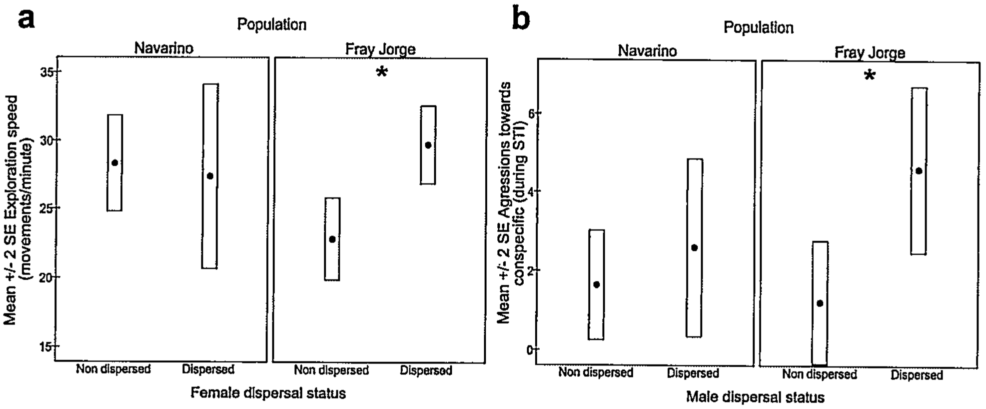

Figure 2. Relationship between behavioral traits and breeding dispersal in two populations of thorn-tailed rayadito in southern (Navarino Island) and north-central (Fray Jorge National Park) Chile. **a.** exploration speed of female birds during exploration experiments; **b.** number of aggressions towards a conspecific stuffed mount during simulated territory intrusions (STI) by males. Bars represent ± 2 standard errors (SE) around mean values. Levels of significance are marked for interactions between behavioral traits and population: * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

GLMMs for aggressiveness and risk-taking behavior included 42 recaptured breeding adults (21 from each sex) in Navarino and 49 in Fray Jorge (24 females and 25 males). The effect of aggressiveness or risk-taking on breeding dispersal behavior also interacted with the population, as no relationship between these personality traits and dispersal was detected in Navarino (Table 3). On the other hand, in Fray Jorge, aggressiveness and risk-taking behavior only predicted breeding dispersal in males (Table 3), as dispersed individuals were more aggressive towards the male conspecific intruder (stuffed mount) than non-dispersers (Fig. 2b).

Discussion

Personality traits and environmental variation

Inter-individual differences in personality traits are viewed as the result of a complex interaction between an individual's genetic make-up and environmental conditions (Dingemanse and Wolf 2013), having variable fitness consequences at the within- and between-populations levels, depending on the social and ecological context (Dingemanse and de Goede 2004; Dingemanse et al. 2003). Personality traits can be associated in a consistent fashion across populations (e.g., positive correlation of exploration and aggressiveness regardless of the local conditions) if they are more or less genetically restricted ('genetic constraint models'), but if the influence of the selective environment is more important, within and between population associations might not be necessarily identical ('adaptive divergence models'; see Dingemanse and Réale 2005). At the risk of being too simplistic, our predictions anticipated that all traits assessed in this study were positively correlated in both populations, implicitly assuming either (i) a genetic constraint and/or (ii) selective pressures favoring the same correlation of traits in both environments (see Lande 1979, 1986). Despite we did not assess behavioral correlations and repeatability in rayaditos, our results suggest that exploratory behavior, aggressiveness (number of aggressions towards conspecifics), and risk-taking consistently varied across distinct populations of this passerine bird.

Table 3. Minimal adequate GLMMs for testing phenotypic correlations between behavioral traits and breeding dispersal in two populations of thorn-tailed rayadito in contrasting environments in southern (Navarino Island) and north-central (Fray Jorge National Park) Chile. All models used individual dispersal status ('dispersed'/'non-dispersed') as the response variable. Main effects were not tested when interactions where significant. See text for sample sizes for novel environment tests and agonistic behavior/predator presentation tests.

Personality trait	Sex	Models by factors[2]	Estimate	SE	Test[1]	*P*
Exploration	Females	Intercept	-4.65	1.92		
		Movement rate	0.58	0.46	Not tested	
		Exploration diversity	2.12	1.22	Not tested	
		Movement rate*Population	0.12	0.05	z_{51}=4.04	0.04
	Males	Intercept	-1.61	1.14		
		Movement rate	0.02	0.02	Not tested	
		Exploration diversity	0.52	0.69	Not tested	
		Exploration diversity*Population	1.96	1.05	z_{53}=3.30	0.06
Aggressiveness/Risk-taking	Females	Intercept	-0.97	0.54		
		Alarm activity (STI)	0.09	0.06	z_{44}=1.94	0.16
		Minimum approaching distance	0.23	0.13	z_{44}=3.08	0.08
	Males	Intercept	-0.48	0.24		
		Aggressions (STI)	0.35	0.11	z_{43}=0.11	0.74
		Aggressions (STI)*Population	-0.16	0.07	z_{43}=4.50	0.03

[1] z statistic corresponds to the Wald-test (H_o: parameter/SE = 0)

[2] Minimal adequate models were selected according to AICc values. Full models for exploration included the effects of 'Movement rate' and 'Exploration diversity', and their interaction with 'Population'. Full models for aggressiveness/risk-taking considered the effects of 'Alarm activity (STI)', Aggressions (STI)' and 'Minimum approaching distance', and their interaction with 'Population'.

Moreover, we evidenced that these behavioral traits predictably varied between natural populations occurring under contrasting ecological and social conditions (prediction 1; but see below for a discussion of population*sex interactions). Anyway, conclusions from this data should be taken with precaution, as we did not directly test the presumable factors causing this variation (i.e., landscape heterogeneity, population saturation, levels of stress).

Differences between Navarino and Fray Jorge may not be necessarily adaptive (Dingemanse and Réale 2005), but considering the local contexts in each locality, it is reasonable to expect that the observed 'profiles' of personality could be a result of selective forces causing such variation. A more saturated, stressful, and probably more competitive environment such as Fray Jorge could impose higher ecological and social pressures on certain phenotypes, particularly fast-bold individuals. We found supporting evidence for this, as birds from Fray Jorge were less exploratory, less aggressive and shyer than individuals from Navarino. For instance, field-based experiments have shown that slow-exploring Great tits (*Parus major*) are better at coping with social defeat and can remain in highly competitive instances, suggesting that the benefits of exploratory behavior (e.g., higher foraging efficiency, consecution of high-quality territories; Dingemanse and de Goede 2004; van Overveld and Matthysen 2010) are traded off against an individual's ability to deal with social stress (Dingemanse et al. 2003). Because exploration is in general positively correlated with aggressive behavior, this also means that aggressiveness tends to be negatively associated with sociability, and hence, that factors affecting competitive and social abilities might act in opposite directions (Dingemanse and Réale 2005; Groothuis and Carere 2004; Réale et al. 2007).

The lower levels of exploratory behavior and aggressiveness in Fray Jorge can be interpreted as a population-specific strategy to deal with high population density and more frequent social interactions (**Chapter 1**), with higher levels of stress (see Quirici et al. 2014, 2016) being a physiological consequence (Cockrem et al. 2007). But why birds in Fray Jorge were shyer than in Navarino during predator presentation tests? How the local conditions in Fray Jorge might also favor risk-aversion? Landscape heterogeneity caused by forest fragmentation could be a valid answer to these questions, as adult mortality (Horak and Lebreton 1998; Matthysen et al. 1999) and nest predation rates (Chalfoun et al. 2002) in several forest birds increase under these conditions. In fact, previous studies point to local fragmentation as a factor negatively affecting rayaditos' spatial movements (Vergara et al. 2010) and breeding success (Cornelius 2008), and also increasing dispersal-related mortality in adults (**Chapter 2**). Although levels of nest defense as assessed here (see also Hollander et al. 2008) could not only be a measure of risk-taking, but also a proxy of reproductive investment of breeding rayaditos, current evidence is consistent with the idea that risk-aversion is favored in a risky environment.

There were two interesting results that are difficult to explain with information at hand, but should be briefly considered and discussed. First, although exploration diversity differed between populations, exploration speed did not. While there are several potential reasons for this, differences in repeatability between these measures of exploration is likely to be the cause (see van Dongen et al. 2010), particularly if within-individual variation is relatively high (Dingemanse and Dochtermann 2013). Another study using the same measures of exploratory behavior in the Rufous-collared Sparrow (*Zonotrichia capensis*) showed complex variation at the within- and between-population levels, but concluded that exploration diversity is a reliable indicator of true exploratory tendency of individuals in an unknown environment (van Dongen et al. 2010). Repeatability studies in populations of Rayadito currently being carried out will provide insights into this, and will help assessing how consistent personality traits are within populations (Poblete et al., unpublished data). Second, population*sex interactions, notably for alarm activity during STIs (see Fig. 1b), revealed that interpopulation differences in behavioral traits were not entirely consistent, supporting the 'adaptive divergence' point of view. Sex-differences can occur between wild populations whenever fitness consequences of personality differ in females and males, affecting the frequency of certain phenotypes in either sex as natural or sexual selection pressures vary in space and/or time (Dingemanse and Réale 2005). Although a previous study already showed that male rayaditos engage more in physical aggressions towards a conspecific male intruder (Ippi et al. in press), as we also found, average non-physical (alarm activity) aggressions was reported to be similar between sexes, contrary to our results. The fact that females were more involved in alarm activity than males in Fray Jorge results puzzling and seems counterintuitive (see Morton and Derrickson 1996), but this apparently 'passive' strategy of males seems compensated with a markedly aggressive territorial defense, as evidenced by the pronounced sex-differences in mean number of aggressions.

Breeding dispersal syndromes in Thorn-tailed Rayadito

Individual dispersal behavior, i.e., the probability of dispersal and/or dispersal distance, appears to co-vary with exploration and sociality in several taxa, usually in interaction with population density and levels of intraspecific competition (Cote and Clobert 2012; Duckworth 2012). As we mentioned earlier, studies have focused on disentangling the relationship between personality traits and natal dispersal, even though personality is suspected to influence, at least partially, the decisions of adult birds to leave a breeding territory (Valcu and Kempenaers 2008) or how far to disperse (Öst et al. 2011). Our results showed that personality traits can predict fine-scale breeding dispersal, and that this relationship depends on local conditions. This means that the optimal dispersal strategy of distinct behavioral phenotypes not only can affect an individual propensity to engage in natal dispersal (Dingemanse et al. 2003), but also in breeding dispersal.

It is worth mentioning that our results and subsequent conclusions might be relevant to birds that remated with their previous social partner, but not to individuals under distinct pairing status or social conditions. Because mate loss through mortality or divorce is as an important precursor of breeding dispersal in birds (e.g., Greenwood and Harvey 1982; Valcu and Kempenaers 2008; Ward and Weatherhead, 2005), performing analyses with individuals of differing pairing status would allow accounting for this potential source of variation. For instance, dispersal of reunited pairs would likely result from a collective decision and mutual influence, whereas widowed/divorced birds, although disperse on their own, could be 'forced' to do so after a negative experience (see Calabuig et al. 2008). The fact that fitness-related costs of breeding dispersal are more ubiquitous among widowed rayaditos (**Chapter 2**) support the idea that mate loss and/or breeding failure are more influential on adult decisions than other factors, including phenotype-mediated propensity to disperse. We do believe, however, that if personality-dependent dispersal does occur in any given population, it will affect the probability to disperse, even though it will not always lead to dispersal due to the multiple causes affecting individual decisions (see Cote et al. 2010). Further studies incorporating this aspect should be essential in order to validate the results observed in this study.

The absence of a relationship between breeding dispersal and behavioral traits in Navarino was expected (prediction 2), as the homogeneous landscape structure and the less crowded social environment in this site would not impose major restrictions to natal or breeding dispersal (**Chapter 1**). In fact, breeding dispersal, although more limited than natal dispersal (as in many other birds; Clarke et al. 1997; Greenwood and Harvey 1982), appears to be less costly there than in Fray Jorge, and has been proposed to reflect a non-adaptive process (sensu Payne 1991) given the absence of differences in fitness consequences between dispersers and philopatric individuals (**Chapter 2**). If a relaxation of local environmental pressures upon dispersal took place in this population, this could have caused a gradual decoupling of dispersal syndromes, for bearing specialized phenotypic traits aiding to overcome the costs of dispersal would have been no longer profitable for individuals experiencing such conditions (Cote and Clobert 2012; Ronce and Clobert 2012). Supporting evidence of such a process was provided by an elegant study comparing dispersal patterns in populations of common mole-rat (*Cryptomys hottentotus*) inhabiting two contrasting environments (Spinks et al. 2000). In a sub-optimal (arid) environment where colony attrition was higher, dispersers were larger and heavier than non-dispersers, but in a more optimal (mesic) habitat without social constraints on dispersal, philopatric and dispersing individuals showed no morphological differentiation.

The historical dynamics of landscape configuration and environmental conditions in Fray Jorge National Park can be the key factor to explain the apparent presence of breeding dispersal syndromes in rayaditos. The relict forest in Fray Jorge, once widely distributed, became gradually isolated by the end of the Tertiary due to climatic changes, and was restricted to its current distribution by the Quaternary (see Cornelius et al. 2000, Kelt et al. 2016). This means that the Fray Jorge population has been evolving in an isolated and increasingly fragmented environment, settling the conditions for the evolution of dispersal syndromes as a mechanism to reduce dispersal costs (Ronce and Clobert 2012). Because local natal and breeding dispersal seem unavoidable in Fray Jorge despite the fitness consequences (**Chapter 1, 2**), more exploratory habits (speed in the case of females and diversity in the case of males) could increase an individual's probability to procure territories of relative high quality after dispersal by acquiring knowledge about the distribution of key resources away from their natal/breeding area (van Overveld and Mathhysen 2010; Yasukawa 1979). The levels of aggression were only correlated to dispersal propensity in males, which make sense given the higher costs of dispersal for them compared to females in this population (**Chapter 2**). Higher levels of aggression could confer both competitive advantages to dispersers when initially establishing a breeding territory (Bonte and Saastamoinen 2012; Yasukawa 1979), and subsequent site-specific advantages related with social dominance during intrasexual encounters (see Dingemanse and de Goede 2004). As local habitat saturation and the frequency of social interactions increase through time, so would dispersal propensity of aggressive males. In fact, it has been documented that aggressive, and usually asocial, individuals tend to disperse when population densities get too high (Cote and Clobert 2012; Ronce and Clobert 2012). Finally, the fact that nest-defense was not coupled with dispersal might be due to similarities in parental effort between dispersers and non-dispersers of both sexes, or could indicate that risk-aversion have been fixed in the population, which is plausible given that female and male dispersal-induced mortality is similar (see **Chapter 2**).

Conclusions

Documenting the presence and variation of dispersal syndromes is relevant to understand the ecological and social mechanisms affecting dispersal, and ultimately, the trade-offs and constrains driving the evolution of distinct strategies within and across populations (Ronce and Clobert 2012). Here we showed context-dependent variation in personality traits and their relationship with local breeding dispersal between populations of the Thorn-tailed Rayadito with documented differences in ecological factors, social environment, and costs of dispersal. The similarities between our results and those from the interpopulation comparison carried out by Spinks (2000) support the idea that contrasting environments can generate predictable variation in dispersal syndromes.

To our knowledge, this is the first study documenting an association between breeding dispersal and personality. Moreover, we evidenced that this association was not necessarily systematic along the distributional range of a species due to context-dependent and sex-specific differences in the costs of dispersal. The observed patterns, particularly in Fray Jorge, suggest that dispersal syndromes are more likely to occur when dispersal is not restricted by local conditions (see Ronce and Clobert 2012). As stated before, the absence of a correlation between dispersal and personality in Navarino could have resulted from a relaxation of ecological and social pressures. It is also possible, however, that even in the presence of dispersal syndromes, these could only affect natal dispersal decisions. More capture-mark-recapture data will help clarify this and will allow assessing the relevance of personality on individual propensity to engage in both natal and breeding dispersal.

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DISCUSIÓN

En la mayoría de especies de aves estudiadas a la fecha, la dispersión natal es más frecuente que la dispersión reproductiva y usualmente involucra movimientos más extensos (Paradis et al. 1998). Además, en aves paseriformes socialmente monógamas, quizá el grupo más estudiado, la frecuencia de la dispersión y/o su extensión exhiben un ligero sesgo positivo hacia las hembras (Greenwood y Harvey 1982, Clarke et al. 1997, Arlt y Pärt 2008). Los patrones descritos para cada especie estudiada son con frecuencia asumidos (implícitamente) como un rasgo característico de las mismas, pese a que las descripciones disponibles se han basado solamente en una población y bajo un contexto ambiental único (véase revisión en Clarke et al. 1997). Debido a la escasez de comparaciones a nivel intra-específico (véase Payne y Payne 1993 para una excepción) y a que el contexto ambiental de los estudios realizados raramente se menciona (e.g., hábitat continuo o fragmentado; alta o baja densidad poblacional), resulta difícil inferir hasta qué punto el ambiente local es el responsable de patrones infrecuentes o que parecen atípicos en relación a la moda (Clarke et al. 1997). Por ejemplo, en algunas aves se ha registrado ausencia de sesgos sexuales en la dispersión natal (e.g., Arcese 1989) y/o reproductiva (e.g., Norment 1994), o incluso se ha observado mayor filopatría en hembras adultas respecto a los machos (e.g., Payne y Payne 1993). Más inusual es la posibilidad que la dispersión reproductiva sea más frecuente o más extensa que la dispersión natal, lo que puede ocurrir si la oferta de oportunidades para la reproducción en un determinado ambiente es muy alta (Harts et al. 2016). Estos antecedentes apoyan la relevancia de considerar la influencia del contexto ambiental en la conducta dispersiva (Matthysen 2012) y la necesidad de interpretar los patrones de dispersión en función de dicho contexto. Este trabajo muestra que al comparar la dispersión en dos poblaciones de un ave que varían en factores ambientales relevantes, es posible observar patrones y estrategias específicos que no necesariamente son generalizables para toda la especie. En consecuencia, es importante que futuros estudios incorporen más localidades para obtener una visión más detallada de la variación intra-específica en la conducta dispersiva del rayadito en el amplio gradiente ambiental que experimenta a lo largo de su distribución geográfica.

Los movimientos asociados a la dispersión en aves paseriformes no suelen ser superiores a 1 km de longitud (Paradis et al. 1998), pero los restringidos desplazamientos observados en el rayadito son típicos de aves especialistas de bosque, los cuales pueden ser bastante limitados (50-600 m), particularmente en hábitats heterogéneos (Harris y Reed 2002). Estas observaciones fueron comunes a las dos poblaciones estudiadas, lo que sugiere una habilidad limitada para desplazarse a través de paisajes fragmentados, como ya lo sugerían estudios previos sobre la ecología espacial de esta especie en otras localidades de Chile (Vergara y Marquet 2007, Vergara et al. 2010). Otra característica que podría generalizarse para la especie es la limitada extensión/ocurrencia de eventos de dispersión reproductiva en relación a la dispersión natal. La baja variabilidad en la dispersión reproductiva respecto a la dispersión natal es esperable cuando la disponibilidad de oportunidades reproductivas (o la abundancia de sitios de nidificación) es baja (Harts et al. 2016), una situación común para nidificadores secundarios de cavidades, como el rayadito, para los cuales las cavidades constituyen un recurso limitante (Newton 1998). De hecho, observaciones recientes indican que la competencia intra-específica por cavidades no sería la única presión para el rayadito, puesto que las interacciones inter-específicas con otros usuarios de cavidades pueden resultar en agresiones físicas y la mortalidad de los polluelos dentro del nido (Botero-Delgadillo et al. 2015).

La comparación inter-poblacional de diversos rasgos y patrones relacionados con la dispersión en el rayadito reveló que la variabilidad intra-específica es predecible, dependiendo de cuán contrastantes sean los contextos ambientales evaluados. La limitada evidencia disponible respecto a diferencias entre poblaciones sugiere que la variación entre individuos respecto al fenotipo dispersivo puede acentuarse en ambientes heterogéneos (Matthysen et al. 1995, Verhulst et al. 1997), densamente poblados (Wheelwright y Mauck 1998, Ward y Weatherhead 2005) o estresantes (Spinks et al. 2000), y que dicha variación podría involucrar varios rasgos (Ronce y Clobert 2012). Los resultados de este estudio no solo proporcionan evidencia a favor de esta hipótesis, sino que muestran como las diferencias en el fenotipo individual y los costos y beneficios asociados a la dispersión se interconectan con las presiones ambientales y los patrones observables en la naturaleza. A continuación se discute dicha relación en el contexto propio de cada uno de los ambientes contrastados y sus posibles causas y consecuencias.

En ambientes con una configuración del paisaje relativamente homogénea, no solo se espera un patrón aleatorio en las distancias o direcciones de la dispersión natal (Wotton et al. 1986), sino una ausencia de sesgos hacia cualquiera de los sexos (Winkler et al. 2005), sobretodo en especies monógamas, debido a que la estructura del hábitat no limitaría el movimiento de los individuos (Weatherhead y Boak 1986). Es así como los movimientos aparentemente no restringidos del rayadito y el patrón de asentamiento aleatorio posterior a la dispersión natal en ambos sexos en la isla Navarino sería explicado, al menos en parte, por la cobertura relativamente continua de bosques sub-Antárticos y zonas de crecimiento secundario en dicha localidad (Luebert y Pliscoff 2006, Rozzi y Jiménez 2014). Adicionalmente, las bajas densidades de individuos reproductivos y la aparente mayor oferta de sitios para nidificar sugerirían mayores oportunidades para reproducirse (Weatherhead y Boak, 1986), facilitando a los individuos jóvenes el establecimiento de su primer territorio reproductivo en prácticamente cualquier dirección, tal como sugieren los patrones de asentamiento observados (véase también Winkler et al. 2005). Aunque los datos de captura-marcaje-recaptura (CMR) usados para analizar la dispersión natal eran limitados en el caso de esta población, los análisis genéticos, basados en una muestra 4-5 veces mayor, también apuntaron a que el desplazamiento de los juveniles dispersantes no es distinto de un patrón aleatorio. Como sugieren los resultados, esta posible ausencia de restricciones y sesgos a la dispersión natal en Navarino estaría relacionada con los bajos costos asociados a la dispersión en ambos sexos. Un escenario donde no se evidencian consecuencias negativas sobre la adecuación biológica de los individuos (e.g., condición física o éxito reproductivo) podría haber relajado las presiones sociales y ecológicas que afectan la dispersión, por lo que los patrones y estrategias encontrados en Navarino pudiesen reflejar un proceso no adaptativo (véase Payne 1991). Aunque esto requeriría que dichas condiciones se mantuviesen durante varias generaciones (Clobert et al. 2012), la evidencia filogeográfica indica que esto es plausible. Primero, el recurrente flujo genético entre Navarino y otras poblaciones revelan que las condiciones de alta conectividad en el sur de Chile se habrían mantenido desde la conclusión del último máximo glacial (ca. 10.000 años; González y Wink 2010). Segundo, modelos basados en marcadores mitocondriales y estimaciones de diversidad genética muestran que la población de rayaditos aún se encuentra en etapa de expansión desde su llegada estimada a Navarino (Yáñez 2013), siendo probable que dicha población no haya estado expuesta aún a condiciones de saturación y estrés social.

La dispersión reproductiva en Navarino fue más limitada y menos frecuente que la dispersión natal, pero tampoco pareció afectar el éxito reproductivo y la mortalidad de aquellos individuos que incurrían en ella. Es más, solo los machos viudos percibieron mayor pérdida de paternidad tras abandonar su territorio reproductivo anterior. En el caso de los individuos que se reunieron con su pareja social anterior, los resultados muestran que su desempeño durante la temporada reproductiva posterior a la dispersión no se vio afectado, y que las decisiones relacionadas con abandonar su territorio no se correlacionan con ningún rasgo conductual individual. La ausencia de consecuencias negativas y de rasgos especializados que redujeran los eventuales costos de dispersar (i.e., síndromes dispersivos) sugieren nuevamente que las presiones selectivas actuando sobre la dispersión en Navarino son bajas. De hecho, es esperable que las diferencias fenotípicas y en costos/beneficios percibidos entre dispersantes y no dispersantes sean mínimas en ambientes relativamente homogéneos y poblaciones no saturadas (Spinks et al. 2000, Aragon et al. 2006).

Dados los bajos costos de la dispersión reproductiva en esta población, es lógico cuestionarse por qué esta es más restringida que la dispersión natal. La respuesta más probable se relacionaría con la información adquirida y la experiencia acumulada por parte de los adultos reproductivos, ya que la fidelidad a un sitio conocido por parte de un individuo puede incrementar su familiaridad con el área, y por ende, su conocimiento respecto a la distribución de recursos y la presencia de eventuales competidores y depredadores (Greenwood y Harvey 1982, Bowler y Benton 2005). Es más, dado que las cavidades para nidificar pueden llegar a ser un factor limitante (véase arriba), los beneficios de permanecer en un territorio reproductivo para los individuos o parejas podrían sobrepasar las eventuales ventajas de buscar un nuevo sitio para nidificar (Clark 1994, Harts et al. 2016), especialmente después de un intento reproductivo exitoso (*estrategia de 'ganancia-permanencia, pérdida-cambio*; *sensu* Switzer 1993).

Los resultados mostraron un marcado sesgo hacia las hembras en la dispersión natal y una contrastante estructuración genética local para cada sexo en la población de Fray Jorge, acorde con el patrón esperado en hábitats heterogéneos (Matthysen et al. 1995) y saturados (Wheelwright y Mauck 1998, Ward y Weatherhead 2005). Cerca del 95% de todos los juveniles recapturados se encontraban entre los 2-3 años de edad, indicando que tanto hembras como machos podrían estar retrasando su primer intento reproductivo debido a la escasa disponibilidad de territorios y/o parejas reproductivas en esta población saturada (Potti y Montalvo 1991). Las hembras dispersaron mayores distancias cuando la densidad de individuos reproductores en su área natal incrementó, asentándose con frecuencia en el primer territorio disponible, probablemente a causa de la competencia con otras hembras por oportunidades para reproducirse. Aunque no se detectó evidencia de un mecanismo para evitar la endogamia, el patrón de establecimiento de las hembras previo a su primera reproducción es probablemente suficiente para disminuir la probabilidad de aparearse entre parientes (véase Arcese 1989, Gibbs y Grant 1989). Por su parte, las distancias de dispersión de los machos fueron mucho menores, ya que estos establecieron sus territorios lo más cerca posible a su lugar natal, generando un patrón local de aislamiento por distancia y agrupaciones de individuos cercanamente emparentados en los fragmentos de bosque más grandes. Un menor éxito reproductivo posterior a la dispersión solo fue evidente en los machos, implicando que los costos serían mayores para estos que para las hembras, lo que a su vez coincide con el sesgo en la dispersión natal (véase Matthysen 2012, Starrfelt y Kokko 2012). Los beneficios de la filopatría para los machos podrían asociarse a una mayor familiaridad con el área (Greenwood 1980, Greenwood y Harvey 1982) o incluso a ventajas sociales, puesto que el mantenerse cerca del sitio natal con un vecindario conformado por machos emparentados podría facilitar el establecimiento de un territorio (e.g., Payne y Payne 1993), posiblemente por los menores niveles de agresión entre parientes (Brown y Brown 1993, Ekman y Griesser 2002). De cualquier modo, los resultados indicaron que la dispersión natal en los machos es frecuente, representando un posible mecanismo para reducir la competencia entre parientes (véase Starrflet y Kokko 2012).

En Fray Jorge, la dispersión reproductiva implicó un menor desempeño reproductivo para las parejas y mayores tasas de mortalidad para individuos de ambos sexos. No obstante, los costos reproductivos a nivel individual solo fueron evidentes para adultos que perdieron su pareja social anterior (i.e., viudos), particularmente los machos, lo que apoya que la dispersión tiene distintos efectos para cada sexo. Entre las hembras que enviudaron, las dispersantes percibieron mayores beneficios reproductivos que las no dispersantes, posiblemente debido a su mayor habilidad para evaluar la calidad de territorios adyacentes (Pärt 1995), dada su mayor conducta exploratoria. Otra eventual ventaja para estas aves sería la oportunidad de emparejarse con machos de mayor experiencia o calidad tras la desaparición de su pareja anterior (Payne y Payne 1993). Los machos dispersantes en cambio, independientemente de su estatus social (viudo o reunido con su pareja anterior), experimentaron un descenso en la paternidad. Estos costos podrían haber propiciado la aparición del síndrome dispersivo observado, ya que la conducta exploratoria y la agresividad de los dispersantes les conferiría una mayor capacidad para rastrear territorios de calidad (van Overveld y Mathhysen 2010) y mayores ventajas competitivas para establecerse en áreas ecológica y socialmente desconocidas (Yasukawa 1979, Bonte and Saastamoinen 2012). El hecho de que los efectos de la dispersión reproductiva hayan sido detectados solamente en adultos viudos indica que dispersar sería una respuesta a las experiencias negativas durante la temporada anterior, incluyendo la pérdida de la pareja o un bajo desempeño reproductivo (Calabuig et al. 2008).

La dinámica histórica del paisaje y las condiciones ambientales en Fray Jorge son la causa más probable de los patrones y estrategias dispersivas en esta población de rayadito. El bosque relicto, gradualmente más fragmentado y aislado durante el período Cuaternario se comporta como un archipiélago oceánico, con poblaciones de aves cerradas y una limitada disponibilidad de hábitat (Cornelius 2008). Este relativo aislamiento y la baja permeabilidad de la matriz circundante, dominada por matorral sub-xerofítico (Villagrán et al. 2004, del Val et al. 2006), no solo habría incrementado los costos asociados con la dispersión natal y reproductiva, sino que habría favorecido la diferenciación en las estrategias óptimas para cada sexo. Esto es análogo a los patrones de dispersión observados en la Petroica de las islas Chatham (*Petroica traversi*), un paseriforme nidificador secundario de cavidades socialmente monógamo, el cual es endémico a Nueva Zelanda (Heather y Robinson 2005). Las poblaciones de esta especie son cerradas y están restringidas a los bosques de dichas islas, siendo la dispersión sesgada hacia las hembras un mecanismo para evitar la endogamia, y a la vez, una posible consecuencia de los altos costos de la dispersión para los machos (Paris et al. 2016). Más interesante aún, estos autores observaron que la dispersión reproductiva fue más restringida que la dispersión natal y ocurrió principalmente en individuos que perdieron a su pareja social anterior.

Tomados en conjunto, los resultados de este estudio indican que los patrones, estrategias y síndromes dispersivos pueden variar en función del contexto ambiental y no son características necesariamente compartidas entre las poblaciones de una misma especie (contrario a Montalvo y Potti 1992), e incluso entre sexos o clases etarias dentro de una población, dado que las interacciones sociales (e.g., *hipótesis de dominancia social* e *hipótesis de restricciones sociales*; Arcese 1989, Daniels y Walters 2000) y las características del ambiente local (*hipótesis de selección del territorio*; Payne y Payne 1993) pueden afectarlos diferencialmente. En el caso del rayadito, se observó que la variación en la conducta dispersiva involucra una interacción entre las condiciones ecológicas, la estructura del paisaje, la densidad poblacional, la disponibilidad de oportunidades para la reproducción y el fenotipo individual. Otros estudios deberían evaluar la magnitud o efecto de cada uno de estos factores, con el fin de inferir si su relevancia también es dependiente del ambiente.

Este trabajo apoya la importancia de explicitar el contexto ambiental en la descripción de la conducta dispersiva y propone que al igual que otros rasgos de historia de vida, los patrones, estrategias y síndromes de dispersión de una especie o grupo de especies no deben ser asumidos como "típicos" en tanto no se evalúen sus potenciales variaciones en poblaciones expuestas a condiciones contrastantes. Los resultados de este estudio y otros citados aquí podrían sugerir que, de no variar ningún otro factor (i.e., razón de sexos, mortalidad sexo-específica, entre otros), el ampliamente documentado sesgo hacia las hembras en aves paseriformes podría ser el patrón dominante en áreas donde la transformación y fragmentación de su hábitat ha tenido lugar. Por el contrario, un sesgo leve o la ausencia de este sería un indicador de una mayor conectividad en el paisaje y/o de menores presiones demográficas, y por tanto, de poblaciones menos expuestas a factores de estrés ambiental y bajos niveles de competencia intra-específica.

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ANEXOS

ANEXO I

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Nestling Mortality as a Consequence of Interspecific Competition between Secondary Cavity Nesters in the Sub-Antarctic Forests of Chile

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ABSTRACT.—Interspecific competition among secondary cavity nesters can involve physical conflicts between individuals, which may lead to serious injuries or death. Here we report a case of aggression by a pair of Chilean Swallows (*Tachycineta meyeni*) towards a nestling of the Thorn-tailed Rayadito (*Aphrastura spinicauda*) in the sub-Antarctic forests of Chile. This aggression caused the displacement of the breeding rayaditos from an occupied nest box and it appears, nestling mortality. Since levels of aggression among cavity nesters depend on the synchrony of their breeding phenologies, further research is needed to study the prevalence of nest usurpation by Chilean Swallows and its relation to the degree of breeding synchrony with other cavity nesters inhabiting the sub-Antarctic forests. *Received 13 May 2014. Accepted 23 October 2014.*

Key words: *Aphrastura spinicauda*, interspecific aggression, nest box, nest-site competition, nestling mortality, *Tachycineta meyeni*.

Nest-site availability is a key limiting factor in bird populations, especially for secondary cavity nesters, which cannot excavate their own cavities and therefore must rely on existing holes produced by other birds, insects, or decay (Newton 1994, 1998). Circumstantial evidence shows that bird density often correlates with variations in nest-site availability (van Balen 1982, Raphael and White 1984, Zarnowitz and Manuwal 1985, Snyder et al. 1987). Furthermore, there are numerous experiments that demonstrate how manipulations of nest-site availability can limit breeding densities and/or the proportion of adults able to breed (see table 8.2 in Newton 1998).

Given their dependence on previously existing holes, secondary cavity nesters compete for nesting sites, and these competitive interactions not only occur among conspecific individuals, but also between different species (Slagsvold 1978, Minot and Perrins 1986, Gustafsson 1988). Interspecific competition for nest-sites commonly occurs as pre-emptive competition, e.g., when a bird occupies a hole for nesting and temporally removes that cavity from the available resources

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for other individuals (*sensu* Gotelli 2008). It can also occur through interference, which implies a direct social or physical interaction between competitors (Merila and Wiggins 1995). Pre-emptive competition is perhaps the most common interaction among breeding birds but the least documented (see Newton 1998). Interference competition has been documented through nest usurpation, agonistic encounters and physical conflict (Dhondt and Eyckerman 1980, Rendell and Robertson 1991), and as lethal aggression among adult birds (Merila and Wiggins 1995). Although egg mortality is commonly observed during nest usurpation (Rendell and Robertson 1991), nestling mortality has rarely been observed during observational studies or long-term monitoring studies of nest boxes (but see Gowaty 1984, Belles-Isles and Picman 1986). Here, we describe a case of nestling mortality presumably caused by interference competition between two secondary cavity nesters that inhabit the sub-Antarctic forests of southern Chile.

During November 2013, as part of a long-term study of the breeding biology of the Thorn-tailed Rayadito (*Aphrastura spinicauda*) at Isla Navarino (55° 56′ S, 67° 39′ W; see Ippi et al. 2013, Quirici et al. 2014), located in the Magallanes and Chilean Antarctic Region, we observed two Chilean Swallows (*Tachycineta meyeni*) entering an occupied nest box and attacking a 13-day-old nestling rayadito. A pair of breeding rayaditos initially occupied the nest box on 6 October 2013, and five eggs were laid between 10–18 October. All eggs hatched on 8 November 2013, and all nestlings were alive on a subsequent inspection 4 days after hatching. On 21 November 2013, we checked the nest box in order to capture, mark, and measure one breeding adult and all 13-day-old chicks, as part of the monitoring protocol (see Moreno et al. 2005). Before reaching the nest box location on this date, we repeatedly heard a squeaking nestling and loud knocks within the box, and shortly after a swallow flew out of the box and joined another individual that was flying nearby. The adult rayaditos came close to the nest box and emitted alarm calls and loud trills during 11 mins, while the swallows remained close to the nest-site, flying around and calling insistently. This behavior by the swallows continued for more than 1 hr. During two occasions during the incident, the swallows were joined by two conspecifics, allowing them to displace the breeding adults from their nest-site for more than 5 mins and enter the cavity where the rayadito brood was present. In both cases, only one swallow entered the box, while the other remained calling in flight nearby. Although breeding rayaditos are usually very aggressive towards any potential threat (see Ippi et al. 2011, 2013), both adult rayaditos stayed away from the site during these interactions and emitted infrequent and faint alarm calls. This type of 'submission' behavior has never been reported in similar contexts, and its potential causes are difficult to explain.

When we interrupted the interaction 90 mins after our arrival in order to check the nest box and band the adults and the chicks, we found only one nestling inside. There were no signs of the remaining chicks. The nestling showed recent signs of trauma to the crown and eyes, a broken wing, and a leg immobilized by the nest fibers that were tangled around it. When attempting to mark one of the adult rayaditos with a nest box trap, we incidentally captured both swallows, which did not come back to the box during the rest of the afternoon. Both swallows were identified as adults, having fully ossified skulls and flight feathers with a shape typical for adults of other swallow species (see Pyle 1997). Although there were no clear signs of breeding condition, differences in the measurements of their external rectrices and primaries led us to consider that the swallows could be a breeding pair (see Pyle 1997). The nestling rayadito was found dead the next morning, but neither the rayaditos nor the swallows occupied the vacant box during the rest of the breeding season.

Although we cannot determine what caused the disappearance of the other nestlings, the aggression towards the chick remaining inside the nest box by the swallows suggests that competition for nesting-sites may have instigated this event. We have no evidence to rule out alternative explanations for the observed behavior, but competition for other resources (e.g., food) is less probable given the differences in habitat use patterns and feeding habits between the two species (Remsen 2003, Turner 2004). The fact that the nest box remained unused after the event seems counterintuitive if competition was the cause, but infanticide as a nest-destroying behavior could act to reduce interference from competing birds, even if such aggressions are not followed by a nesting attempt by the aggressors (Belles-Isles and Picman 1986, Botero-Delgadillo and Páez 2011). The event could have been motivated by territorial defense in the swallows, since reproductive pairs exhibiting super-territoriality often defend unoccupied cavities (Verner 1977), and such a behavior has been reported in a congener (*T. bicolor*; Leffelaar and Robertson 1985).

Our observations support the notion that competition among secondary cavity nesters for nest-sites can be fierce (see Duckworth 2006) or even lethal (Gowaty 1984; Merilä and Wiggins 1995). Interspecific conflicts have been observed in long-term nest box monitoring between closely related (Löhrl 1977, Gowaty 1984) and distantly related species (Rendell and Robertson 1991, Robillard et al. 2013). In North America and Europe, swallows (Family Hirundinidae) are often involved in usurpation or agonistic encounters with other passerine birds, frequently using a mobbing-behavior strategy, where groups (more than two individuals) successfully displace other species (Brawn 1990, Rendell and Robertson 1991, Newton 1998). Although demonstrating a demographic effect between competitors is the most clear-cut evidence for competition (Newton 1998), this is difficult to detect and has been rarely found. Negative individual effects which imply that breeding success or survival of an individual has been compromised are more easily found and reliable indicators of competition (Newton 1998). Most supporting evidence of interspecific competition by interference is based on individual effects, and the degree to which these effects extend to a population still requires further study.

The frequency and level of aggression between competitors are related to the degree of synchrony in their breeding phenologies (Slagsvold 1978; Gowaty 1981). The population of Chilean Swallows at Isla Navarino is composed of migrants that breed during the Austral summer and their arrival coincides with the latter half of the breeding season of Thorn-tailed Rayaditos (Remsen 2003, Turner 2004). At this time of year, most cavities are already occupied by rayaditos and other cavity-nesters. Therefore, a late start to the breeding season of rayaditos or an early arrival by swallows at Isla Navarino could increase the probability of confrontations for cavities or nest boxes. Future studies should consider the relationship between the breeding synchrony among cavity nesters and the prevalence of nest usurping by swallows in sub-Antarctic forests.

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ANEXO II

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RESEARCH ARTICLE

Interpopulation variation in nest architecture in a secondary cavity-nesting bird suggests site-specific strategies to cope with heat loss and humidity

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ABSTRACT

Nest morphology can affect the breeding success of birds. Thus, birds inhabiting different environments may experience divergent selection for nest structure and composition that results in intraspecific geographic variation in nest architecture. We describe interpopulation differences in nest architecture among Thorn-tailed Rayaditos (*Aphrastura spinicauda*) in 2 contrasting environments near the species' distribution limits: a temperate and very humid environment in north-central Chile (the forest relicts of Fray Jorge National Park; 30°38′S, 71°40′W) and a cold and windy sub-Antarctic environment in the south of Chile (Isla Navarino; 55°4′S, 67°40′W). We collected a total of 62 nests from Fray Jorge and 61 nests from Navarino in 2013 and 2014, measured their dimensions, and quantified their constitutive materials. We tested the nests' thermal properties (simulating heat loss by convection and conduction) and hygroscopic features (water absorption and water loss capacity) and used general linear models to (1) compare these properties between populations and (2) test for a relationship between nest morphology and function. Nests from the northern population exhibited lower rates of heat loss by convection because they were larger and had a lower ratio of surface area to volume; these nests also absorbed less water, probably because of their greater content of plant-derived materials. In the southern population, nests were more compact and better insulated with feathers and hairs, with lower rates of heat loss by conduction. By separately analyzing the roles of convection, conduction, and humidity, our results suggest that potential trade-offs (insulation–humidity) could be differently affecting the nest-building behavior of these populations. Therefore, Thorn-tailed Rayaditos may be using site-specific strategies to cope with the local climate in contrasting environments.

Keywords: *Aphrastura spinicauda*, Chile, Furnariidae, intraspecific variation, nest composition, nest structure

Variación inter-poblacional en la arquitectura de nidos sugiere diferentes estrategias para lidiar con la pérdida de calor y la humedad en un ave nidificadora de cavidades

RESUMEN

La morfología del nido puede afectar el éxito reproductivo de las aves. Por ende, especies que habitan distintos ambientes podrían experimentar presiones selectivas divergentes sobre la estructura y composición del nido que resultaría en diferencias intra-específicas. Describimos las variaciones inter-poblacionales en arquitectura de nidos del *Aphrastura spinicauda* en dos ambientes contrastantes cerca de los límites de su distribución, un ambiente templado y muy húmedo en el centro-norte de Chile (el bosque relicto del Parque Nacional Fray Jorge; 30°38′S, 71°40′W) y un ambiente sub-antártico frío y ventoso en el sur de Chile (Isla Navarino; 55°4′S, 67°40′W). Colectamos 62 nidos en Fray Jorge y 61 nidos en Navarino durante 2013 y 2014, midiendo sus dimensiones y cuantificando sus materiales constituyentes. Determinamos sus propiedades térmicas (simulando la pérdida de calor por convección y conducción) e higroscópicas (absorción de agua y tiempo de secado), y mediante modelos lineales generales buscamos (i) contrastar dichas características entre nidos de ambas poblaciones y (ii) determinar la relación funcional entre la morfología y las propiedades térmicas/higroscópicas de los nidos. Los nidos del norte exhibieron menores tasas de pérdida de calor por convección debido a su mayor tamaño y su menor relación área superficial-volumen, absorbiendo además menos agua posiblemente por el alto contenido de material vegetal. En el sur, los nidos fueron compactos y estuvieron mejor aislados con plumas y pelos, exhibiendo menores tasas de pérdida de calor por conducción. El análisis separado de los efectos de la convección, conducción y humedad sugiere que posibles compromisos (absorción de agua–aislamiento) podrían afectar diferencialmente la conducta de construcción de nidos de estas poblaciones. Por ende, los rayaditos podrían estar usando estrategias específicas para lidiar con el clima local en ambientes contrastantes.

Palabras clave: Aphrastura spinicauda, Chile, composición de nidos, diferencias intra-específicas, estructura de nidos, Furnariidae

INTRODUCTION

Nest structure and composition play a pivotal role in the breeding cycle of birds (Collias and Collias 1984, Hansell 2000). Therefore, nests are predicted to vary adaptively in response to contrasting ecological pressures associated with breeding in distinct environments (Collias and Collias 1964, Barber 2013, Mainwaring et al. 2014). The design and constitutive materials of a nest can influence predation risk for both adults and nestlings (Kreisinger and Albrecht 2008, Mayer et al. 2009, Bailey et al. 2015), the timing of egg laying (O'Connor 1978), the energetic costs of incubation and brooding (Drent 1975, Lombardo et al. 1995, Reid et al. 2000, Windsor et al. 2013), nestling thermoregulation (Møller 1991, McGowan et al. 2004, Mainwaring and Hartley 2008), and the risks of hypothermia and hyperthermia (Mertens 1977a, 1977b). Given that spatiotemporal variation of environmental factors at the time of reproduction is ubiquitous, birds occupying different habitats will often experience contrasting challenges during nest construction, such as availability of building materials, predation pressure, and local climatic regime (Hansell 2000). The relationship between nest morphology and environmental variation has been documented in several species. For example, birds' nests tend to be larger and better insulated in colder environments (Horváth 1964, Collias and Collias 1971, Heenan et al. 2015). Although intraspecific differences in nest architecture are also expected to follow this pattern, published works testing this remain relatively scarce (e.g., Schaefer 1976, 1980, Kern 1984, Briskie 1995, Rohwer and Law 2010, Crossman et al. 2011, Mainwaring et al. 2012, Rohwer et al. 2015).

Studies on intraspecific differences in nest morphology have shown that the nest properties of heat retention and water loss capacity, which are determined by the composition of nest materials, may differ according to climatic conditions (Mainwaring et al. 2014). For instance, populations breeding in colder environments can increase heat retention by building larger nests (Kern and van Riper 1984, Briskie 1995), using thicker and less porous nest walls (Crossman et al. 2011), or adding more feathers and/or hairs as cup-lining material (Møller 1984, Mainwaring et al. 2012). Nest structure can also differ because of local precipitation and humidity, given that bulkier nests can absorb more water and take more time to dry, which is likely disadvantageous in humid environments (Rohwer and Law 2010). Despite these findings, other studies have shown that behavioral traits other than nest structure may respond to climate regimes (e.g., nest location; Kern 1984, Kern et al. 1993), suggesting that variation in nesting habits can be species specific or even context dependent. Further research is thus required for a better understanding of geographic variation in nest structure within species and its causal relationship with environmental factors. Unfortunately, information is still scarce and biased toward species from the Northern Hemisphere (see Mainwaring et al. 2014). Here, we address this data gap by describing interpopulation differences in nest architecture of the Thorn-tailed Rayadito (*Aphrastura spinicauda*), a secondary cavity-nesting bird that inhabits the temperate forests of southern South America.

The Thorn-tailed Rayadito is a small, insectivorous furnariid that breeds from late September to early February along an extensive latitudinal gradient (about 30–55°S) in Chile and Argentina (Hellmayr 1932, Remsen 2003). We have studied populations located at the species' latitudinal range limits for 8 consecutive years in order to compare breeding and behavioral patterns in contrasting environments (e.g., Ippi et al. 2011, 2013, Quirici et al. 2014). Because behavioral traits may diverge at species' range limits (e.g., King et al. 1964, Muul 1974, Rohwer et al. 2015), comparing geographically distant populations provides insight into how populations of widely distributed species may adapt (or not) to distinct ecological conditions (Mainwaring et al. 2014). By comparing the nests of Thorn-tailed Rayaditos in 2 populations located at the northern and southern limits of its distribution, the present study aimed to (1) quantify differences in structure, composition, and thermal–hygroscopic properties of nests exposed to contrasting environments; and (2) determine whether any such differences are correlated with local climatic conditions. Comparisons were based on nests from 2 breeding seasons at the northern and southern range limits: Fray Jorge National Park (hereafter 'Fray Jorge'; 30.63°S, 71.66°W) in the Coquimbo Region and Isla Navarino (hereafter 'Navarino'; 55.06°S, 67.66°W) in the Magallanes and Chilean Antarctic Region (Figure 1).

The Fray Jorge population breeds in fog-shrouded remnants of Valdivian temperate rainforest (see Quirici et al. 2014, Kelt et al. 2016). Despite being immersed in a matrix of sub-xerophytic matorral (i.e. a semiarid steppe; see Luebert and Pliscoff 2006), these remnants are located in coastal hills that exhibit a very humid and cool microclimate (Villagrán et al. 2004, del-Val et al. 2006), with a temperature range of 6–20°C during the species' breeding season (source: CEAZA; see below). By contrast, the Navarino population breeds in sub-Antarctic forests,

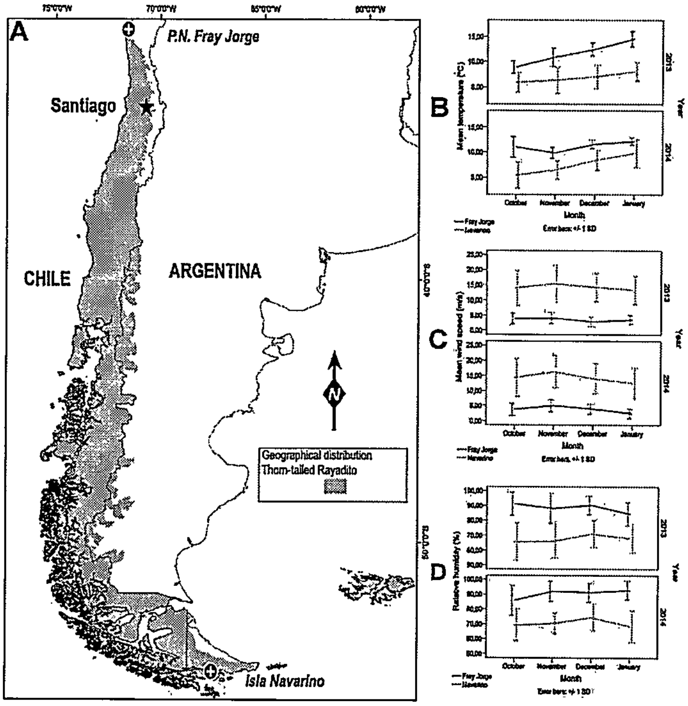

FIGURE 1. (A) Study populations of Thorn-tailed Rayaditos in the northern (Fray Jorge National Park) and southern (Isla Navarino) limits of the species' distributional range in Chile. Meteorological variables that differed between localities during the breeding season included (B) mean temperature, (C) wind speed, and (D) relative humidity.

which are less humid and are exposed to stronger winds and lower temperatures (range: –2 to 15°C; http://www.meteochile.goc.cl/). Given described patterns of local adaptation of nest morphology in birds (see Møller 1984, Mainwaring et al. 2014), we expected (1) that nest structure and composition would vary predictably between the 2 populations, with nests from Navarino being larger and containing more insulating material; (2) that differences in nest architecture between populations would be consistent during different breeding seasons; (3) that nest thermal–hygroscopic properties would differ between localities and reflect distinct strategies for coping with the local climate, with nests from the wetter and warmer Fray Jorge absorbing less water and drying faster, and nests from the colder and windier Navarino retaining heat more efficiently; and (4) that variation in nest architecture would be functionally related to variation in their thermal–hygroscopic properties.

METHODS

Nest Collection

Nests of Thorn-tailed Rayaditos were collected after the breeding seasons of 2013 and 2014 from nest boxes installed in the 2 study populations (Figure 1). We collected a total of 62 nests from Fray Jorge and 61 nests from Navarino from which we documented successful fledging. Nests were removed from nest boxes and collected during the month following the end of the breeding season in each year. Nests were measured, immediately placed in sealed plastic bags, and then transported to Universidad de Chile, where they were kept at –20°C (see Britt and Deeming 2011, Mainwaring et al. 2012).

Meteorological Data

We obtained meteorological data for both localities from the Meteorological Station Network of the Centro de Estudios Avanzados en Zonas Aridas (CEAZA, 2012:

http://www.ceaza.cl) and the Online Meteorological Stations database of the Dirección Meteorológica de Chile (http://www.meteochile.gob.cl). Meteorological stations at the 2 study sites were <200 m away from the nest-box plots. Given the extent of Thorn-tailed Rayaditos' breeding season, we downloaded raw daily data for October–January in each year. We then estimated and compared the monthly averages (± SD) of temperature, wind speed, and relative humidity (see below).

Nest Architecture

Our study of nest architecture involved (1) a quantification of nest structure based on external and internal dimensions and (2) a quantitative description of nest composition and the relative importance of constitutive materials. We took 6 different structural measurements: nest length, nest width, nest depth (i.e. from top of nest to bottom of box) in each of its 4 sides, inner cup diameters (maximum and minimum), inner cup depth, and nest dry weight. The first 5 measurements were made immediately before nest collection, using digital calipers (±0.01 mm). Although there was no variation in nest length and width because of the standardized size of all nest boxes from both localities (32 × 18 × 15 cm), these dimensions were required for additional measures (see below). Nests were weighed twice in the laboratory using a high-precision digital scale (±0.01 g). The first measurement was conducted after drying nests in a heating–drying oven for 60 hr at 70°C and before performing the thermal–hygroscopic tests (see below). Nests were redried (under equal conditions) after these tests, and then weighed for the subsequent compositional analysis. Because nests could potentially lose some material during thermal–hygroscopic tests, we used the first measurement of weight for descriptive and comparative purposes and the second to estimate the relative contribution of nest layers and constitutive materials.

We used the external and internal measurements to calculate the estimated nest cup volume and the estimated total nest volume. Assuming that the nest cup was one-half of an ellipsoid (see Lombardo 1994), nest cup volume (cm^3) was calculated as follows:

$$\text{nest cup volume} = \frac{\left[\left(\frac{4}{3}\right) \times (\pi r^2 d)\right]}{2}$$

where r is the largest radius of the top of the nest cup (major diameter/2) and d is cup depth. After estimating cup volume, we calculated total nest volume (cm^3; see Lombardo 1994, McGowan et al. 2004):

$$\text{total nest volume} = (l \times w \times d) - \text{nest cup volume}$$

where l, w, and d correspond to nest length, width, and depth, respectively.

We conducted compositional analysis after performing thermal–hygroscopic tests. Nests were divided into 2 discernible layers (*sensu* Hansell 2000): the structural layer (i.e. the base) and the internal lining. Each part was weighed to calculate its relative contribution to total nest weight and then was separated into its constituent building materials (Mainwaring and Hartley 2008, Mainwaring et al. 2012). We used 5 straightforward categories to define nest components: woody items (pieces of branches and sticks), plant fibers (roots), dry grass, animal insulating material (feathers and hairs), and miscellaneous (plastic fibers, seeds, pebbles).

Nest Thermal Properties and Water Absorption

Because there were no significant effects of the breeding season (i.e. year: 2013–2014) on the structural and compositional variation of nests (see below), we treated all nests from the same locality as one sample set, regardless of the year of construction and subsequent use. We randomly picked 36 nests from each population to determine their rates of heat loss by convection (e.g., heat loss by contact with cold air) and conduction (e.g., heat loss by contact with a cold surface). The remaining 51 nests (26 and 25 from Fray Jorge and Navarino, respectively) were used to evaluate their water absorption–loss capacity (i.e. hygroscopic properties). Tests were performed during the second half of 2015, once all nests from 2013–2014 were collected.

For thermal analysis, dried nests were first tested for heat loss by convection and subsequently tested for heat loss by conduction. Nests were placed in controlled conditions at 25°C for 12 hr, after which 2 iButtons (Maxim Integrated: DS1921G-F5) were installed in each nest to quantify temperature, one in the cup lining and the other at the side of the nest as a control (Mainwaring et al. 2012). The iButtons were previously programmed using OneWireViewer 03.17.44 software (http://www.maximintegrated.com), with a 15 min delay and the maximum sample rate (1 min). Both tests started by placing nests again at 25°C for 30 min after the delay period, in order to set iButtons to the initial conditions. For the convection test, nests were placed in a temperature-controlled compartment at 5°C for 1 hr, putting each nest inside a thin blotting-paper envelope and held in horizontal position over sheets of 600 g Kraft paper to avoid contact with the compartment's cold surface; this test aimed to simulate heat loss by contact with cold air inside the cavity (i.e. nest box). For the conduction test, nests were placed inside nest boxes that were previously cooled at 5°C for 1 hr and placed in a room at 25°C for 1 hr; in this test, nests were in permanent contact with the cooled surfaces of nest boxes (sides and bottom).

We obtained 60 recordings of temperature per nest from both tests, which were fitted to a cubic model using nonlinear regressions. Although cubic regression uses more parameters than other nonlinear models, we selected it over other methods (i.e. logarithmic, power, quadratic) because it always fit the data best (based on higher r^2 and F values; all $P < 0.001$) and better described temperature changes inside the nest cups. We used cubic regressions to calculate 2 rates of heat loss (at the first and last quarters of the test) and the equilibrium temperature (the asymptote). We also calculated the Δ_5 value from the raw data, which corresponded to the temperature differential between the initial conditions and 5 min after starting the tests. We chose 5 min because the results of prior studies suggested that this is likely to be the period of maximum heat loss when nests are exposed to cold temperatures (see Rohwer and Law 2010).

Hygroscopic properties were tested by submerging nests in water for 2 min and then taking repeated measurements of their weight over time (Rohwer and Law 2010). To estimate water absorption, we weighed nests immediately after submersion to obtain their saturated weight. We calculated the gained weight for each nest by subtracting its dry mass from its saturated mass (Rohwer and Law 2010) and subsequently calculated the nest's gain ratio (saturated mass/dry mass; i.e. magnitude of the nest's weight increase). We quantified water loss by calculating the weight loss percentage (i.e. percent loss of the saturated weight) over an 8 hr period, weighing nests every 15 min during the first hour after saturation, and then every hour for the remaining time. Because weight measurements barely changed during the last 5 hr, we considered only the first and last estimates of weight loss percentage and used these measurements as proxies of water loss capacity over short (15 min) and long (8 hr) periods after exposure to water. All hygroscopic tests were done under controlled conditions at 25°C and constant humidity.

Statistical Analyses

Statistical analyses were performed in R 2.15.2 (R Development Core Team 2012), using $\alpha = 0.05$ for hypothesis testing. We first tested all variables for normality using the Shapiro-Wilks test. None of the meteorological variables fitted the assumptions of normality, so we transformed variables using square root (daily temperature, wind speed) and log (percent humidity) transformations. Variables describing nest structure (mean nest depth, nest volume, mean inner cup diameter, cup volume, nest dry weight) were all normally distributed (all $P > 0.05$). We used the original descriptions of nest composition (percent contribution of structural layer, percent internal lining, percent woody items, percent plant fibers, percent dry grass, percent animal insulating material, percent miscellaneous) in a principal component analysis (PCA) to reduce dimensionality (correlation matrix; Digby and Kempton 1987), generating new variables from the regression factor scores of the first 3 components because they explained 80% of the total variance (see below). These 3 new variables were normally distributed (all $P > 0.05$). Finally, all but 2 variables from the thermal and hygroscopic analyses were normally distributed (all $P > 0.05$); equilibrium temperature (convection–conduction tests) and weight loss percentage after 8 hr were log transformed.

We used general linear models (Quinn and Keough 2002) for all comparative analyses between nests from Fray Jorge and Navarino. We first performed 3 separate two-way analyses of variance (ANOVA) to test whether daily temperature, wind speed, and percent humidity differed between localities (main effects) and between localities across years (interactions). Subsequently, we conducted 2 multivariate analyses of variance (MANOVA) to test the effects of locality and breeding season on nest structure and composition, respectively, and also to determine whether there were significant interactions between independent variables. We also included clutch size in these analyses to account for its potential influence on nest morphology, but given that levels of this variable barely overlapped between the two populations (Fray Jorge, mode =3 eggs, range: 2–4; Navarino, mode=5 eggs, range: 4–8), we analyzed it as a nested factor within locality (Quinn and Keough 2002). Because there were no effects of breeding season on nest features, or significant interactions among independent variables (see below), nests from the same locality were randomly divided for the thermal and hygroscopic analyses (see above).

We therefore performed separate two-tailed t-tests to compare thermal and hygroscopic properties between nests from Fray Jorge and Navarino. We used multiple linear regressions to test the effects of architecture on nest thermal–hygroscopic properties, with the structural–compositional descriptors as independent variables. For those analyses, nests from both populations were combined and analyzed as a single dataset, because we wanted to test for functional relationships regardless of their origin. However, in order to capture as much variation as possible, we considered only those variables that showed significant interpopulation differences in the comparative analyses of nest structure, composition, and thermal–hygroscopic properties (see ~~below~~). Three methods of variable entry and removal were initially used ("stepwise," "enter," and "remove"), using each model's adjusted r^2, standard error (SE) of the estimate, and F and P values for the regression as selecting criteria (Quinn and Keough 2002). The stepwise method always performed better and was therefore selected for all regressions (data not shown). The probability (P value) of F was used as the stepping-method criterion, setting the values for variable entry and removal at 0.05 and 0.10, respectively.

TABLE 1. Structural dimensions of Thorn-tailed Rayadito nests (means ± SD) from 2 populations near the species' northernmost (Fray Jorge National Park; $n = 62$) and southernmost (Isla Navarino; $n = 61$) distributional range limits in Chile. Nests were collected in 2013 and 2014.

	Locality	
Structural measurements	Fray Jorge ($n = 62$)	Navarino ($n = 61$)
Nest mean depth (mm) [a]	60.11 ± 11.49	51.22 ± 10.31
Cup diameter (mm) [b]	70.56 ± 6.64	82.18 ± 9.79
Nest volume (cm^3)	720.51 ± 226.95	506.21 ± 199.83
Cup volume (cm^3)	306.85 ± 98.43	447.43 ± 136.71
Nest dry weight (g)	40.15 ± 12.17	36.31 ± 12.73

[a] A mean value was used for each nest from measurements taken on the 4 sides.
[b] Only maximum diameter is reported.

RESULTS

Climatic Patterns

Navarino was significantly colder (Navarino, 7.3 ± 2.6°C; Fray Jorge, 11.4 ± 2.2°C; $F_{1,441} = 320.1$, $P < 0.001$), windier (Navarino, 14.3 ± 5.4 m s^{-1}; Fray Jorge, 3.8 ± 1.9 m s^{-1}; $F_{1,428} = 735.9$, $P < 0.001$), and less humid (Navarino, 69.2 ± 10.3%; Fray Jorge, 90.1 ± 8.4%; $F_{1,449} = 516.9$, $P < 0.001$) than Fray Jorge during the Thorn-tailed Rayadito's breeding season (Figure 1). These differences between localities were consistent during 2013 and 2014, with no significant interactions between meteorological variables and year (temperature, $F_{1,441} = 2.8$, $P = 0.09$; wind, $F_{1,428} = 0.4$, $P = 0.51$; humidity, $F_{1,449} = 0.7$, $P = 0.39$). Monthly average temperatures tended to increase toward the end of the breeding season in both sites, whereas the monthly average of wind speed reached its maximum during November before decreasing for the next couple of months (Figure 1). There was no clear pattern in the monthly averages of humidity (Figure 1).

Nest Structure and Composition

We used the first 3 components from a PCA of all the original descriptors of nest composition to generate new variables for analysis (see Appendix Table 4). The PCA eigenvectors showed that the first principal component (PC1) represented the variation in the relative weight of the structural layer (i.e. nest base) vs. the internal lining; PC2 was related to the composition of the internal lining and the relative amount of insulating materials; PC3 represented the variation among constitutive materials in the structural layer (Appendix Table 4).

Although nest dry mass did not vary between localities, the remaining measurements of nest dimensions showed significant differences: on average, nests from Fray Jorge were deeper and larger (i.e. greater volume), whereas Navarino's had wider and larger nest cups (Tables 1 and 2A). According to the first MANOVA, nest structure was significantly different between Fray Jorge and Navarino (Roy's largest root = 0.51; $F_{5,106} = 10.8$, $P < 0.001$); but there was neither an effect of the breeding season (year: 2013–2014; Roy's largest root = 0.11, $F_{5,106} = 0.97$, $P = 0.44$) nor a significant interaction between these 2 variables (Roy's largest root = 0.10, $F_{5,106} = 2.10$, $P = 0.07$). Although the analysis suggested a positive effect of clutch size on nest structure within each population (Roy's largest root = 0.11, $F_{5,110} = 2.43$, $P = 0.04$), only cup volume was significantly affected (Table 2A). There was no interaction between clutch size and the breeding season (Roy's largest root = 0.83, $F_{5,108} = 1.79$, $P = 0.12$).

The second MANOVA showed that nest composition differed between the 2 localities (Roy's largest root = 0.64, $F_{3,108} = 22.9$, $P < 0.001$), but there was no effect of the breeding season (Roy's largest root = 0.07, $F_{3,108} = 0.27$; $P = 0.85$) nor a significant interaction between independent variables (Roy's largest root = 0.09, $F_{3,108} = 0.32$, $P = 0.81$). Only the composition of the internal lining differed between localities (PC2 in Table 2B; Figure 2): Navarino nests were more covered with animal insulating material, particularly feathers from other birds, than Fray Jorge nests. There were no differences in the relative weights of the nest structural layer and the internal lining (PC1 in Table 2B; Figure 2) or in the composition of the structural layer (PC3 in Table 2B), even though certain building materials appeared to be more or less used in each locality (e.g., sticks and pieces of branches in Fray Jorge vs. dry grass in Navarino; see Figure 2). The analysis also showed no effect of clutch size on nest composition (Roy's largest root = 0.13, $F_{5,110} = 0.48$, $P = 0.79$) nor a significant interaction between this variable and the breeding season (Roy's largest root = 0.05, $F_{3,110} = 1.87$, $P = 0.14$).

Nest Thermal and Hygroscopic Properties

Results from the convection test showed that nests from Navarino reached lower temperatures during the first 5 min of the test (t-test: $t_{71} = -3.7$, $P < 0.001$), tended to lose heat at higher rates (t-test: $t_{71} = -2.0$, $P = 0.049$); and had lower equilibrium temperatures (t-test: $t_{71} = 2.9$, $P = 0.004$) compared to nests from Fray Jorge (for mean values, see Table 3A). However, results from the conduction test showed the opposite: Fray Jorge nests reached lower temperatures during the first 5 min of the test (t-test: $t_{71} = 8.9$, $P < 0.001$), exhibited higher rates of heat loss (t-test: $t_{71} = 2.8$, $P = 0.006$), and showed lower equilibrium temperatures (t-test: $t_{71} = -2.0$, $P = 0.049$) (for mean values, see Table 3B). The second rate of heat loss did not show significant variations in either of the tests (convection, t-test: $t_{71} = -0.3$, $P = 0.69$; conduction, t-test: $t_{71} = 1.1$, $P = 0.27$).

TABLE 2. Results from general linear models testing differences in nest architecture between 2 populations of Thorn-tailed Rayaditos near the species' northernmost (Fray Jorge National Park) and southernmost (Isla Navarino) distributional range in Chile: (A) summary for tests performed on measurements describing nest structure; (B) principal components accounting for variation in nest composition.

Source	Variable	MS[a]	F[b]	P
(A) Structural analysis				
Population	Nest volume	429,554.5	9.37	**0.003**
	Cup volume	215,812.6	17.4	**0.000**
	Dry weight	3.177	0.02	0.877
Clutch size (population)	Nest volume	49,878.4	1.08	0.374
	Cup volume	39,432.1	3.17	**0.010**
	Dry weight	79.5	0.60	0.698
(B) Compositional analysis				
Population	PC1	2.4	0.12	0.729
	PC2	26.2	158.40	**0.000**
	PC3	1.4	0.31	0.584
Clutch size (population)	PC1	1.1	1.16	0.331
	PC2	0.7	1.77	0.125
	PC3	1.1	0.99	0.425

[a] MS = mean squares estimated from Type III sum of squares.

[b] F value estimated with 1,110 and 5,110 degrees of freedom for the variables population and clutch size (population), respectively. Significant P values ($\alpha = 0.05$) are in bold.

[c] PC1: variation in the relative weight of the structural layer (i.e. nest base) vs. the internal lining; PC2: composition of the internal lining and the relative amount of insulating materials; PC3: variation among constitutive materials in the structural layer.

Tests for measuring hygroscopic properties revealed that nests from Navarino gained more weight (gain ratio) than nests from Fray Jorge (t-test: $t_{47} = -3.8$, $P < 0.001$) and also exhibited lower weight loss percentage values during the first 15 min after saturation (t-test: $t_{47} = 2.1$, $P = 0.041$) (for mean values, see Table 3C). There were no differences between the weight loss percentage values after 8 hr following saturation (t-test: $t_{47} = 1.7$, $P = 0.097$).

Relationship between Architecture and Thermal–Hygroscopic Properties

Only nest volume, cup volume, and PC2 (see above) were used as predictor variables for multiple regression analyses. Two multiple regressions were performed for each of the functional tests, using 2 dependent variables: the Δ_5 value and the equilibrium temperature for convection–conduction, and the gain ratio and weight loss percentage for water absorption and water loss. Given that the Δ_5 value and the rate of heat loss (rate 1) were highly correlated in the convection–conduction datasets (Pearson $r = 0.84$, $P < 0.001$; Pearson $r = 0.69$, $P < 0.001$), we did not include the rate of heat loss for the regressions, because the Δ_5 value showed greater variation between localities.

Nest architecture was a significant predictor of nest heat loss by convection. The Δ_5 value ($R = 0.45$, $F_{1,71} = 17.5$, $P < 0.001$) and the equilibrium temperature ($R = 0.34$, $F_{1,71} = 9.1$, $P = 0.004$) both exhibited a functional relation with the structural and/or compositional descriptors (Appendix Table 5). Nest volume was the variable that best explained variation in the Δ_5 value, whereas cup volume was the best predictor of equilibrium temperature (Appendix Table 5 and Figure 3). There was neither autocorrelation between data points (Δ_5 value: Durbin-Watson's $d = 1.96$; equilibrium temperature: Durbin-Watson's $d = 1.98$) nor collinearity among the predictor variables (Δ_5 value: all condition index < 1.94; equilibrium temperature: all condition index < 4.99).

Nest heat loss by conduction also showed a functional relationship with nest architecture. However, in this case the Δ_5 value ($R = 0.61$, $F_{1,71} = 26.6$, $P < 0.001$) and the equilibrium temperature ($R = 0.46$, $F_{1,71} = 12.6$, $P = 0.001$) were related to nest composition but not to nest structure (Appendix Table 5). The PC2 variable (i.e. composition of the internal lining and the amount of animal insulating material) was the best predictor of both the Δ_5 value and the equilibrium temperature (Appendix Table 5 and Figure 3). As in the previous analyses, there was neither autocorrelation (Δ_5 value: Durbin-Watson's $d = 1.64$; equilibrium temperature: Durbin-Watson's $d = 1.71$) nor collinearity among the predictor variables (Δ_5 value: all condition index < 1.03; equilibrium temperature: all condition index < 5.36).

Variation in hygroscopic properties was also related to nest architecture. Nest weight gain ratio ($R = 0.5$, $F_{1,47} = 15.3$, $P < 0.001$) and weight loss percentage after 15 min ($R = 0.31$, $F_{1,47} = 4.8$, $P = 0.03$) were explained by the composition of nests, but not by their structure. The PC2 variable was thus the variable that best predicted water absorption and water loss capacity (Appendix Table 5 and Figure 3). No autocorrelation (gain ratio: Durbin-Watson's

TABLE 3. Parameters used for testing the thermal and hygroscopic properties of Thorn-tailed Rayadito nests from a northern (Fray Jorge National Park) and a southern (Isla Navarino) population in Chile. Thermal tests included simulations of the effects of heat loss by (A) convection and (B) conduction. (C) Hygroscopic tests assessed the water absorption and water loss capacity. Values are means ± SD.

(A) Convection test

Variable	Locality	
	Fray Jorge ($n = 36$)	Navarino ($n = 36$)
Δ_5 value (°C) [a]	1.84 ± 0.73	2.98 ± 1.12
Rate of heat loss 1 [b]	0.76 ± 0.20	0.98 ± 0.31
Rate of heat loss 2 [b]	0.01 ± 0.03	0.01 ± 0.01
Equilibrium temperature (°C) [b]	8.12 ± 1.17	6.98 ± 2.01

(B) Conduction test

Variable	Locality	
	Fray Jorge ($n = 36$)	Navarino ($n = 36$)
Δ_5 value (°C) [a]	3.46 ± 0.94	1.29 ± 0.69
Rate of heat loss 1 [b]	1.06 ± 0.27	0.88 ± 0.16
Rate of heat loss 2 [b]	0.02 ± 0.02	0.02 ± 0.01
Equilibrium temperature (°C) [b]	16.64 ± 2.02	18.53 ± 1.23

(C) Hygroscopic test

Variable	Locality	
	Fray Jorge ($n = 26$)	Navarino ($n = 25$)
Nest gained ratio [b]	2.04 ± 0.85	3.29 ± 0.97
Percent weight loss (15 min)	36.96 ± 15.83	29.75 ± 7.66
Percent weight loss (8 hr)	51.35 ± 16.79	43.77 ± 14.38

[a] Δ_5 = temperature differential between the initial conditions and 5 min after starting the tests.

[b] Values obtained from nonlinear regression models adjusted for temperature variation during the tests. Equilibrium temperature represents the asymptote obtained from the models.

$d = 1.57$; weight loss: Durbin-Watson's $d = 2.03$) or collinearity (gain ratio: all condition index < 1.03; weight loss: all condition index < 1.04) was detected.

DISCUSSION

Variation in nest morphology is predicted to occur when environmental conditions vary temporally and/or spatially (Mainwaring et al. 2014) as birds try to regulate the nest's microclimate for optimal nestling development by adaptively modifying its structure and/or composition (Collias and Collias 1984, Webb 1987, Hansell 2000, Deeming 2002). We found that thermal and hygroscopic properties of nests in the Thorn-tailed Rayadito varied predictably between 2 populations and were related to variation in nest morphology. Furthermore, we found this variation to be consistent in both populations during 2 breeding seasons. Contrary to our expectations, however, nests at the northern part of the species' distribution (Fray Jorge) were larger and seemed to be less affected by heat loss by convection. This finding suggests that Thorn-tailed Rayaditos could be using distinct strategies to cope with the local climate (e.g., ambient temperature) in contrasting environments, especially if there are site-specific selective pressures favoring certain types of nest structure or composition (see Hilton et al. 2004).

Differences in Nest Structure and Composition

As predicted, the variation between populations in nest architecture traits that may have functional relevance was consistent throughout time, and this could be viewed as a result of adaptive divergence (see Rohwer and Law 2010, Mainwaring et al. 2012). Nests from Fray Jorge were larger and had deeper and narrower cups than those from Navarino during 2 consecutive breeding seasons (2013 and 2014). Surprisingly, however, data on nest dry weight overlapped extensively and, thus, revealed no differences between both localities, even though Fray Jorge nests were, on average, 4 g heavier. Although nest dry weight is sometimes used as a reliable proxy for nest size (Mainwaring and Hartley 2008, Dubiec and Mazgajski 2013), it is more likely affected by subtle changes in nest composition than other measurements (e.g., nest volume), producing higher within-population variability. Regarding nest composition, we observed qualitative differences in nest appearance and the relative use of some building materials (Figure 2), but we found significant variation only in the composition of the internal lining and the use of insulating materials. During both years, internal linings from Fray Jorge nests were mainly composed of plant fibers, roots, and small sticks, whereas Navarino nests had a larger amount of feathers and hairs, with a lower quantity of plant materials.

Functional Properties and the Role of Nest Morphology

Variation in nest morphology usually corresponds with predictable differences in thermal and hygroscopic properties of nests (Rohwer and Law 2010, Mainwaring et al. 2012). We expected nests from Fray Jorge to absorb less water and dry faster, and nests from Navarino to retain heat more efficiently, but the observed results were not always consistent with these predictions. Nests from Fray Jorge lost heat at a lower rate than Navarino nests when exposed to cold air (i.e. heat loss by convection), counter to our initial expectations. However, when putting these results in the environmental context, they suggest, along with the other results, that Thorn-tailed Rayaditos' nests reflect distinct strategies for dealing with the environmental challenges present in each locality.

Although Fray Jorge is located at a subtropical latitude, weather conditions in the coastal forest remnants at this site during the beginning of the breeding season are similar to those in other temperate humid forests in the Southern

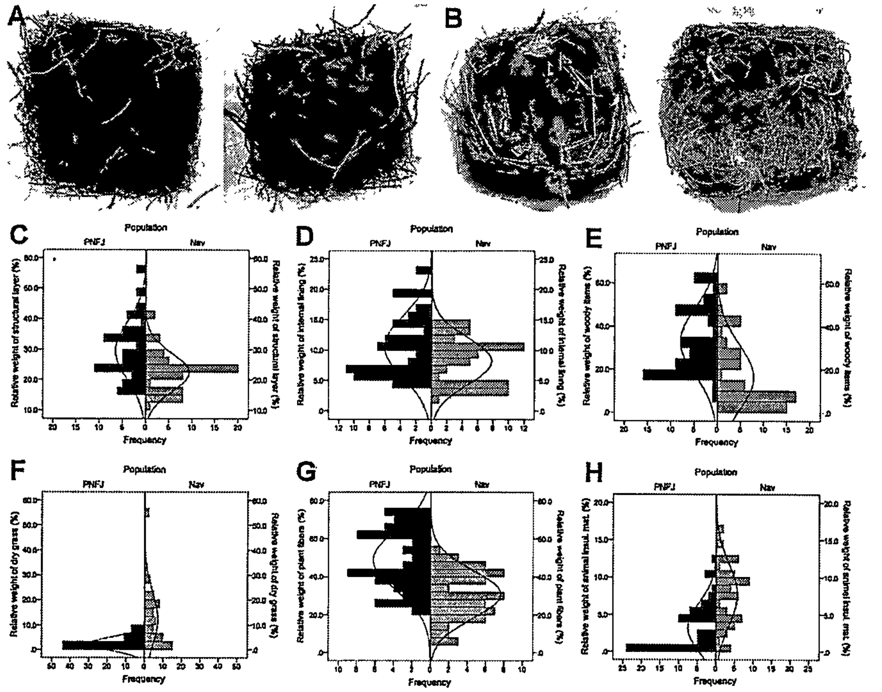

FIGURE 2. Composition of Thorn-tailed Rayadito nests from (**A**) Fray Jorge National Park and (**B**) Isla Navarino, Chile. We quantified the relative contributions of (**C**) the structural layer and (**D**) the internal lining to total nest weight. We also estimated the relative contributions of constitutive components classified as (**E**) woody parts, (**F**) dry grass, (**G**) plant fibers and roots, and (**H**) animal insulating material such as feathers and hairs.

Hemisphere during the first weeks of October (relative humidity usually >80%, with temperatures of 5–7°C; CEAZA). The constant presence of sea fog over the coastal hills of Fray Jorge results in high levels of horizontal precipitation inside forest remnants, with water constantly running down through the tree trunks or dropping down directly (Villagrán et al. 2004; del-Val et al. 2006). This means that the Thorn-tailed Rayaditos of Fray Jorge will often have to use cold and humid cavities and wet materials for nest construction. A possible way to deal with this challenge is to build a well-insulated and nonhygroscopic structure; this presumes a trade-off between nest insulation and hygroscopic properties, given that fluffy materials such as feathers or animal hairs, though providing good thermal insulation (see Møller 1991, Lombardo et al. 1995, McGowan et al. 2004, Schöll and Hille 2014), tend to absorb more water (Hilton et al. 2004, Rohwer and Law 2010, Deeming 2011). As we observed in the hygroscopic tests, Fray Jorge nests absorbed less water than Navarino nests, and this difference was likely related to less use of animal insulating materials, particularly feathers (Figure 3), which may be explained by differences in resource availability between locations, or it may be a result of the insulation–humidity trade-off (see Hilton et al. 2004). Whatever the cause, plant fibers and roots were more likely to be used in the humid environment of Fray Jorge.

How do birds at Fray Jorge deal with low temperatures if using large amounts of animal insulating materials is not the most suitable way to do so? Increasing nest size can be an alternative, and this may explain why Fray Jorge nests were larger, and lost heat at a lower rate in the convection test, compared to Navarino nests (see Table 3). Aside from using feathers for the nest's internal lining, birds can increase insulation by modifying the nest structure (see Mainwaring et al. 2014). Wider and less porous nest walls

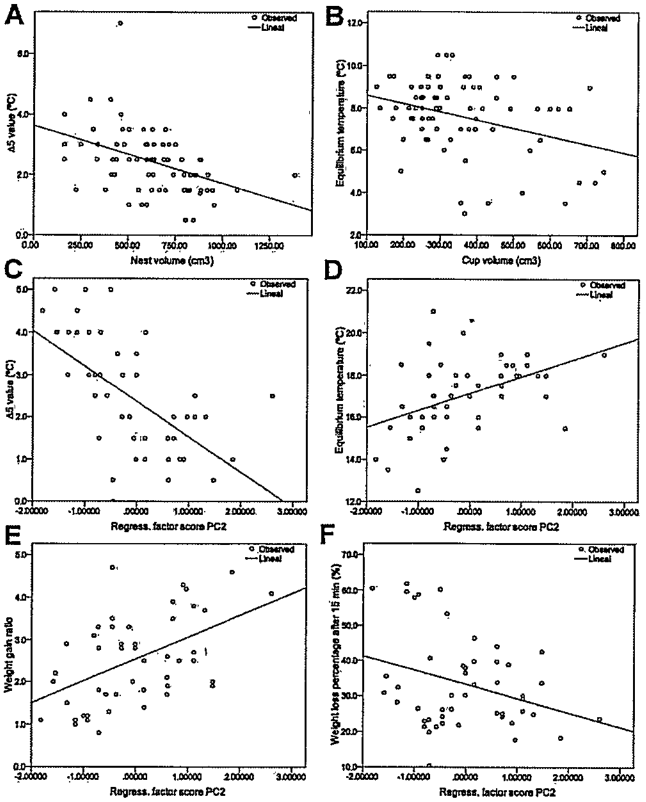

FIGURE 3. Multiple regression models testing the functional relationship between nest architecture and thermal–hygroscopic properties in Thorn-tailed Rayaditos in Fray Jorge National Park and Isla Navarino, Chile. Dependent variables for regression models were obtained from (**A, B**) a test simulating the effects of heat loss by convection; (**C, D**) a test simulating heat loss by conduction; and a test measuring (**E**) water absorption and (**F**) water loss capacity. All interactions shown here were statistically significant. Values for regression factor score PC2 are from a principal component analysis representing the composition of the nest internal lining and the relative amount of insulating materials (see text and Table 2).

have lower thermal conductivity (Kern 1984), and larger nests can retain more heat than smaller structures (White et al. 1975, Skowron and Kern 1980, Liljesthröm et al. 2009; but see Szentirmai et al. 2005). Additionally, nests with deeper and/or narrower cups can better protect the eggs and nestlings than nests with shallower and wider cups (Windsor et al. 2013).

Extremely low temperatures and strong winds are the main pressures that Thorn-tailed Rayaditos experience in Navarino during the breeding season (Figure 1), and this probably explains why they build highly insulated nests. The high abundance of feathers and the lower relative humidity would allow birds to use more hygroscopic materials for the nest lining (see Hilton et al. 2004), which in turn would reduce heat loss by conduction (Figure 3). The first 2 mo of the breeding season in Navarino can present a challenge to Thorn-tailed Rayaditos, because October and November are very windy, and temperatures frequently drop below 3°C during the first hours of daylight (http://www.meteochile.gob.cl). Nest-box walls and probably cavities' inner surfaces were very cold during the mornings, so nests could easily lose heat through contact with these surfaces (E. Botero-Delgadillo personal observation). Unless birds were not using large amounts of feathers and hairs, nests would be losing heat at faster rates because of their greater surface area and shallower and wider cups compared to nests from Fray Jorge (Table 1).

The shallower and wider cups of Navarino nests compared to Fray Jorge nests seem to suggest, counterintuitively, that birds from the colder environment made wider cups, hence making the eggs and/or the nestlings more vulnerable to the effects of heat loss via convection. Differences in clutch size may be the most parsimonious explanation for the observed difference in cups, given that Thorn-tailed Rayaditos from Navarino laid, on average, 2 more eggs (see above). Even though we used clutch size as a nested factor in the analysis of nest structure, the results indicated that the cup volume was positively affected by clutch size in both populations. Because we found no differences between cup measurements before hatching and after fledging in a selected sample taken from the nests dataset (E. Botero-Delgadillo personal observation), we can confirm that cup measurements were not significantly altered during the breeding attempt. This means that cup shape may be adjusted before egg laying, depending on clutch size (Soler et al. 1998a, 1998b), and that brood thermoregulation could compensate for the wider and shallower cups in the Navarino nests. It has been shown that larger broods provide insulation and allow nestlings to thermoregulate better (see Dunn 1976, 1979), so it is conceivable that adult birds from Navarino would not need to incur the extra costs of gathering more material for the nest and shaping a more elaborate and/or deeper cup (see Mainwaring et al. 2014). A better perspective on this could be attained by comparing heat loss rates during standardized periods between nest boxes with manipulated clutch sizes.

Concluding Remarks

Following previous studies, we tried to simulate the effects of weather conditions on the nests of a cavity-nesting bird (e.g., Mainwaring et al. 2012). In addition, we analyzed the roles of convection, conduction, and humidity separately, which indicated that potential trade-offs (insulation–humidity) could be differently affecting the nest-building behavior of 2 populations that occur near the limits of the study species' distribution. We are aware that including more populations in further studies will be essential to understanding how nest morphology varies throughout the latitudinal range occupied by Thorn-tailed Rayaditos, as well as to evaluating how nesting behavior is affected by local variations in the availability of nesting materials and biotic interactions. For instance, assessing the role of social and interspecific interactions in Thorn-tailed Rayadito nest construction can help determine to what extent climatic regimes are affecting nest morphology, and whether biotic and abiotic factors are exerting agonistic selective pressures (Rohwer et al. 2015). Unlike in open-nesting birds, the influence of competition or predation on differences in nest design is likely negligible in cavity-nesting birds, compared to the effects of climate; hence, future work could also focus on the effects of extreme weather conditions, in order to predict how bird populations would respond to the marked environmental variation potentially triggered by climate change (Møller et al. 2010).

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APPENDIX

APPENDIX TABLE 4. Principal component analysis of variables describing the composition of Thorn-tailed Rayadito nests in Fray Jorge National Park and Isla Navarino, Chile. All descriptors accounted for the relative contribution of each nest layer or building material to total nest weight.

	Component loadings		
Eigenvectors	PC1	PC2	PC3
Relative weight structural layer	0.95	−0.14	0.13
Relative weight internal lining	−0.93	0.18	−0.14
Relative weight dry grass	0.29	0.44	0.69
Relative weight plant fibers	−0.58	−0.79	0.24
Relative weight woody items	0.47	−0.45	−0.64
Relative weight animal insulation	−0.16	0.78	−0.26
Relative weight miscellaneous	0.18	0.17	0.51

APPENDIX TABLE 5. Multiple regression coefficients (± SE) testing the functional relationship of architecture and thermal-hygroscopic properties of Thorn-tailed Rayadito nests in Fray Jorge National Park and Isla Navarino, Chile. Values of Δ_5 and equilibrium temperature obtained during (A) the convection test and (B) the conduction test were used as dependent variables. Values for the weight gain ratio and weight loss percentage after 15 min obtained during (C) the hygroscopic test were used as dependent variables.

Variable	Regression coefficient *B*	Standardized *B*	*t*	*P*
(A) Convection test				
Independent variables for analysis on Δ5 value[a]				
Nest volume	−0.02 ± 0.00	−0.44	−4.18	0.000
Independent variables for analysis on equilibrium temperature[b]				
Cup volume	−0.04 ± 0.01	−0.36	−3.04	0.004
(B) Conduction test				
Independent variables for analysis on Δ5 value[d]				
PC2[c]	−0.84 ± 0.16	−0.61	−5.16	0.000
Independent variables for analysis on equilibrium temperature[d]				
PC2[c]	0.81 ± 0.23	0.46	3.55	0.001
(C) Hygroscopic properties				
Independent variables for analysis on gain ratio[d]				
PC2[c]	0.52 ± 0.13	0.49	3.92	0.000
Independent variables for analysis on percent weight loss[d]				
PC2[c]	−4.00 ± 1.82	−0.31	−2.20	0.030

[a] Nonsignificant variables were excluded from the models and are not shown (cup volume and PC2).
[b] Nonsignificant variables were excluded from the models and are not shown (nest volume and PC2).
[c] Nonsignificant variables were excluded from the models and are not shown (nest and cup volumes).
[d] PC2: composition of the internal lining and the relative amount of insulating materials.

ANEXO III

Emu - Austral Ornithology

Effects of temperature and time constraints on the seasonal variation in nest morphology of the Thorn-tailed Rayadito (Aphrastura spinicauda)

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Effects of temperature and time constraints on the seasonal variation in nest morphology of the Thorn-tailed Rayadito (*Aphrastura spinicauda*)

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Running title: Seasonal variation of avian nests morphology

Abstract

Environmental adjustment is the most invoked explanation for intra-seasonal variation in bird nest morphology. However, time constraints may also be important, coming as a trade-off between the costs of nest building and the requirement to coincide a breeding attempt with maximal food supply. We describe the seasonal variation in nest morphology of the Thorn-tailed rayadito (*Aphrastura spinicauda*) in a sub-Antarctic population in southern Chile, and investigate its relation with the seasonal fluctuation of ambient temperature (an 'environmental adjustment' hypothesis) and time constraints (an 'optimal time frame' hypothesis). As the breeding season progressed, rayaditos spent fewer days building their nests, built smaller nests, and using less animal-derived insulating material. After statistically removing the effects of daily temperatures on nest building periods and nest morphological measurements, we observed no seasonal trend in the amount of insulating material used, supporting an 'environmental adjustment' explanation. However, the nest building periods, nest depth and nest dry weight still showed a seasonal trend, favouring an 'optimal time frame' hypothesis. Our study shows that both temperature fluctuations and time constraints can affect different components of the nesting ecology of birds, and that nest morphology is the consequence of distinct non-mutually exclusive forces.

Additional keywords. Nest composition, nest structure, intra-seasonal variation, southern Chile, sub-Antarctic forests.

Introduction

As environmental conditions change during the course of a breeding season, birds' parental behaviours can help maintain an optimal microclimate inside the nest for offspring development (*e.g.* increased bouts of incubation and brooding; see Webb 1987, DuRant *et al.* 2013). Given the costs of such behaviours (Reid *et al.* 2000; Deeming 2011), structural modifications of the nest can help the parents face the prevailing conditions while saving energy (Mainwaring and Hartley 2013). In fact, recent studies propose that birds can gauge environmental conditions and consequently modify the nest thermal properties by adjusting nest morphology (Mainwaring *et al.* 2014). Hence, early breeders who may face low ambient temperatures in temperate latitudes would add more insulating material to their nests, while late breeders would reduce its use as ambient temperatures increase throughout the breeding season (Bulit and Massoni 2004; McGowan *et al.* 2004; Mainwaring and Hartley 2008; Liljeström *et al.* 2009; Britt and Deeming 2011; Deeming *et al.* 2012).

Although environmental adjustment is the most invoked explanation for seasonal variation in nest morphology, there are also other possible causes that have received less attention, such as time constraints (Mainwaring *et al.* 2014). These constraints come in the form of a trade-off between the costs incurred during nest building and the requirement to coincide a breeding attempt with the period of maximal food supply (Lens *et al.* 1994), thus late breeders still could synchronize the time of nestling growth with a peak of food availability by reducing the nest building period (Mainwaring and Hartley 2013; Mainwaring *et al.* 2014). A seasonal decrease in the time used for nest building or a reduced nest size could be indicators of time constraints, but supporting evidence is still lacking (*e.g.* Mainwaring and Hartley 2008).

This study focuses on a secondary cavity-nesting furnariid, the Thorn-tailed Rayadito (*Aphrastura spinicauda*), in order to describe the seasonal variation in nest morphology during its breeding season in a sub-Antarctic population in southern Chile. We aimed to assess the temporal differences in nest building periods and nest architecture, and their relationship with the seasonal fluctuation of ambient temperature (an 'environmental adjustment' hypothesis; see Mainwaring *et al.* 2014) and time constraints (an 'optimal time frame' hypothesis; see Mainwaring and Hartley 2008). If climate is the main causal of nest variation, we predicted (i) a decrease in nest size and a reduced use of insulating materials towards the end of the breeding season, but (ii) no seasonal trend in these variables once the effects of daily temperatures on nest morphology were statistically removed. In contrast, if time constraints are more relevant, we predicted (i) a decrease in nest building periods and nest size as the breeding season progresses, and (ii) the maintenance of such trend after correcting for the effects of temperature variation.

Materials and methods

Study area and meteorological data

This study was carried during September-December 2013 on isla Navarino (55°4' S, 67°40' W), located in the Magallanes y Antártica Chilena Region, southern Chile (Fig. 1A). This locality is part of the southern distributional range of the Thorn-tailed Rayadito, where its breeding season usually extends from October through January (Remsen 2003; Quirici *et al.* 2014). Despite daily fluctuations of temperature during this period, monthly mean temperature tends to increase towards the end of the year (Fig. 1B, 1C). Meteorological data used for description and subsequent analyses where obtained from the "Guardia Marina Zañartu" meteorological station (http://www.meteochile.goc.cl/), located in the study area.

Nest collection and measuring

Nests boxes were installed in Navarino in 2005 as part of a long-term study on the breeding ecology of rayaditos (*e.g.* Moreno *et al.* 2007; Quirici *et al.* 2014). Rayaditos occupied 38 out of 201 nest boxes that were offered during 2013, from which we could monitor 36 throughout the entire breeding season. Nest boxes were checked every day until nest building was initiated. Thereafter, boxes were monitored every other day until egg laying (see Moreno *et al.* 2005). Nest building periods were estimated as the number of days between the start of nest construction and the beginning of egg laying (Mainwaring and Hartley 2008). Subsequent monitoring was part of another study.

Nests were collected from nest boxes a month after the end of the breeding season. During nest collection, we measured the nest depth (*i.e.* from top of the nest to bottom of the box) in each of its four sides and the inner cup depth with a digital caliper (0.01 mm). External diameters were not measured because of the standardized measurements of nest boxes (320 × 180 × 150 mm). Nests were then sealed in plastic bags and carried to the laboratory, where they were kept at -20°C (see Mainwaring *et al.* 2012). After being dried in a heating oven for 60 h at 70°C, nests were weighed using a digital scale (0.01 g), and successively separated into their two constitutive layers: the nest base, or structural layer, and the internal lining (*sensu* Hansell 2000). Both parts were weighted in order to estimate their relative contribution to the nests total dry weight (percentage weight). We finally separated all the plant- (roots and plant fibers) and animal-derived insulating material (feathers and hairs) from the internal lining to quantify their relative weight.

Data analyses.

Eight variables were considered for testing the seasonal trends in the nesting ecology of rayaditos: (i) nest building period; (ii) nest depth, (iii) nest cup depth, and (iv) nest dry weight, taken as measurements of nest structure and nest size; and the relative weights of (v) the structural layer, (vi) internal lining, (vii) plant insulating materials, and (viii) animal insulating materials, used as descriptors of nest composition and nest insulating capacity (Collias and Collias 1984; Hansell 2000; Mainwaring *et al.* 2014). Descriptive values for these variables are presented as mean ± standard deviation.

Our analyses were divided in three sequential approaches: (i) determining if there was a seasonal trend in nest building periods, nest structure, and nest composition; (ii) assessing if these traits were also affected by the temporal variation in temperature, and if such, remove those effects; and (iii) testing again for seasonal trends after removing the effects of ambient temperature. The eight measurements described earlier were used as dependent variables for all analyses. We used $\alpha = 0.05$ for hypothesis testing and all statistical tests were performed in the R 2.15.2 software (R Development Core Team 2012). Shapiro-Wilk's tests confirmed normality for all dependent variables (all tests; $P > 0.05$). We first performed linear regressions for determining the seasonal trend in the response variables, using the nest building start date as the predictor variable. Building start dates were defined for each nest as the number of days after the first nest of the population began to be built. Linear regression models were subsequently used for assessing the effects of temperature variation on those variables that previously showed a seasonal trend, taking the daily mean temperature as the predictor variable. Temperature values were defined as the mean temperature recorded during each nest building start day. Finally, residuals from these analyses were used for testing if seasonal trends remained after removing the effects of temperature, regressing the residuals against building start dates.

Results

There was a range of 48 days between the dates when the first (September 29) and last (November 15) breeding pairs of rayaditos started nest building. Building starting dates for ~58% of all nests ($n = 36$) occurred during the first half of the breeding season, and the average building period for those 'early' nests was 16.7 ± 4.1 days. For the nests that start being built after the mid-part of the breeding season, the average building period was 11.6 ± 2.3. External measurements also varied between nests built before and after the mid-part of the breeding season, with 'late' nests being smaller (Table 1). With the exception of the amount of animal-derived insulating material added to the nest, variables of nest composition did not show marked differences (Table 1).

Linear regression models shown a non-significant trend towards a seasonal decline in nest building periods ($r^2 = 0.54$, $F_{1,34} = 39.88$, $P < 0.001$), and a significant decrease of nest depth ($r^2 = 0.35$, $F_{1,34} = 18.57$, $P < 0.001$), nest dry weight ($r^2 = 0.27$, $F_{1,34} = 11.06$, $P = 0.002$), and relative weight of animal-derived insulating materials ($r^2 = 0.22$, $F_{1,34} = 5.86$, $P = 0.021$) (Fig. 2). However, we detected no temporal variation in the other four variables assessed: nest cup depth ($r^2 = 0.11$, $F_{1,34} = 3.98$, $P = 0.054$); relative weight of the structural layer ($r^2 = 0.02$, $F_{1,34} = 1.03$, $P = 0.317$); relative weight of the internal lining ($r^2 = 0.02$, $F_{1,34} = 0.68$, $P = 0.415$); and relative weight of plant-derived insulation ($r^2 = 0.01$, $F_{1,34} = 0.15$, $P = 0.703$).

We used the variables that showed a seasonal trend to test and remove the independent effect of the temporal increase of ambient temperature. With the exception of nest building period ($r^2 = 0.06$, $F_{1,34} = 2.16$, $P = 0.150$), variation in nest depth ($r^2 = 0.13$, $F_{1,34} = 4.91$, $P = 0.034$), nest dry weight (r^2 = 0.13, $F_{1,34}$ = 5.26, P = 0.028) and relative weight of insulating materials (r^2 = 0.20, $F_{1,34}$ = 6.48, P = 0.015) were partially explained by temperature increases. Once we removed the effect of temperature, linear regressions still showed a seasonal decrease in nest building period (r^2 = 0.40, $F_{1,34}$ = 22.47, $P < 0.001$), nest depth (r^2 = 0.20, $F_{1,34}$ = 8.39, P = 0.007), and nest dry weight (r^2 = 0.13, $F_{1,34}$ = 4.29, P = 0.046), but not in the relative weight of animal-derived insulating materials (r^2 = 0.06, $F_{1,34}$ = 2.48, P = 0.124) (Fig. 3).

Discussion

Our results showed that in this population, nest building periods and nest structure/composition changed throughout the breeding season. Although not all measurements of nest architecture varied temporally, we observed that as the breeding season progressed, rayaditos spent fewer days building their nests, built smaller nests, and used lesser amounts of animal-derived insulating material.

The observed decrease in nest size and the use of insulating material were related to the increase of temperatures towards the end of the year, as expected under an 'environmental adjustment' explanation. However, only the amount of insulating material was completely explained by temperature increase (Fig. 3), implying that birds may adjust their nest to the prevailing conditions by only changing its composition, and that apparently co-varying changes in nest size are not a necessary consequence of the variation in environmental temperature. In fact, studies on intra-seasonal variation of nest morphology show that nest composition, but not nest dimensions, are related with the seasonal trends of ambient temperature (*e.g.* Blue Tit *Cyanistes caeruleus*; Mainwaring and Hartley 2008), even though nest size and structure can have important consequences on the insulation quality of nests

(White *et al.* 1975; Liljesthröm *et al.* 2009). Hence, our results support the idea that birds can assess the environmental conditions and adjust the frequency of use of some building materials (Bulit and Massoni 2004; Mainwaring and Hartley 2008; Liljesthröm *et al.* 2009; Britt and Deeming 2011), possibly regulating nest microclimate for an optimal development of embryos and chicks (Webb 1987; Lombardo *et al.* 1995).

Variation in nest building periods was totally explained by the nest building start date, which agreed with the predictions of an 'optimal time frame' explanation. Nest depth and dry weight were partially explained by temperature increase, but after removing such effect, we still detected a seasonal decline in both variables, further supporting the idea that time constraints can affect nest building behaviour and nest structure. Although some studies have failed to provide evidence of the potential relevance of time constraints (*e.g.* McGowan *et al.* 2004), others suggest it can cause birds to accelerate nest building, although this not necessarily will involve changes in nest structure (Mainwaring and Hartley 2008). Our results, however, point to a seasonal trend in nest building that has consequences in nest size for thorn-tailed rayaditos. Furthermore, a previous study carried out in Isla Grande de Chiloé, southern Chile, provided evidence on how other reproductive traits of rayaditos show a seasonal trend that could be a consequence of time constraints (see Moreno *et al.* 2005). The authors not only observed that the period between laying of the first egg and hatching of the brood was negatively related to laying date, but also that the duration of the nestling period was negatively associated with hatching date, indicating that either laying intervals were shortened or embryonic developmental rate increased over the course of the season.

Contrary to the 'environmental adjustment' explanation, a problem regarding an 'optimal time frame' hypothesis lies in the difficulties to remove other confounding factors, such as the availability of nesting materials or the differences in age and phenotypic quality between the breeding adults (see Mainwaring *et al.* 2014, Guillete *et al.* 2016). Future studies should account for the potential effects of nesting material availability, and also for the effect of intra-individual variation on differences in nest architecture.

Despite the fact that our data did not account for some potential confounding factors, this study has shown that both environmental adjustment and time constraints can influence the nest building behaviour of this cavity-nesting bird, and consequently, the design of the nest structure (Mainwaring and Hartley 2008). We also showed that diverse factors can affect different components of the nesting ecology of birds, and that the final product, *i.e.* the nest, can be the consequence of several non-mutually exclusive forces (Mainwaring and Hartley 2008). Given the need to provide a regulated environment for the development of their brood, breeding birds accordingly change the type and amount of insulating material as temperatures gradually increase throughout the breeding season (McGowan *et al.* 2004). On the other hand, the time invested in nest building and the dimensions of the resulting structure can be the consequence of birds synchronizing the most critical stages of its breeding attempt with peaks of resource availability (Mainwaring and Hartley 2013).

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Figure captions

Fig. 1. Location of the study area and values of daily/monthly temperature during the breeding season of 2013 of the Thorn-tailed rayadito. (A) A total of 201 nest boxes were offered to a southern population of rayaditos at isla Navarino, southern Chile; (B) Fluctuation of daily temperature during October and November 2013; (C) Increasing trend of monthly mean temperatures during 2013.

Fig. 2. Linear regression models showing significant seasonal trends in the nest building behaviour and nest morphology of the Thorn-tailed rayadito. (A) Mean nest depth values regressed against nest building start dates for the breeding season of 2013 ($y = -0.45 * x + 60.24$); (B) Values of nest dry weight against building start dates ($y = -0.26 * x + 36.47$); (C) Duration of nest building period against building start dates ($y = -0.21 * x + 19.23$); (D) Relative amount of animal-derived insulating material in the nest internal lining against building start dates ($y = -0.10 * x + 10.25$).

Fig. 3. Linear regression models showing significant seasonal trends in the nest building behaviour and nest morphology of the Thorn-tailed rayadito, after removing the potential effects of temperature increase during the breeding season (using linear regression). (A) Standardized (STD) residuals of mean nest depth regressed against nest building start dates for the breeding season of 2013 ($y = -0.03 * x + 0.65$); (B) Standardized residuals of nest dry weight against building start dates ($y = -0.02 * x + 0.49$); (C) Standardized residuals of nest building period against building start dates ($y = -0.04 * x + 0.92$); (D) Standardized residuals of relative amount of animal-derived insulating material in the nest internal lining against building start dates ($y = -0.02 * x + 0.38$).

Table 1. External measurements describing the variation in structure and composition of Thorn-tailed Rayadito nests.

For descriptive purposes, nests were grouped as 'early' and 'late' nests depending on the building start date (before/after the mid-part of the breeding season: October 25). Data shown are mean ± SD.

Structural/Compositional variables	Early nests (n = 21)	Late nests (n = 15)
Nest depth (mm)	55.17 (10.06)	44.66 (8.58)
Cup depth (mm)	35.31 (6.51)	29.28 (9.97)
Dry weight (g)	33.13 (8.02)	26.94 (6.78)
Relat. weight structural layer (%)	72.23 (10.28)	72.73 (7.42)
Relat. weight internal lining (%)	27.77 (10.28)	27.27 (7.42)
Relat. weight plant insulating material (%)	25.91 (4.11)	25.82 (4.07)
Relat. weight animal insulating material (%)	8.90 (4.54)	6.77 (2.49)

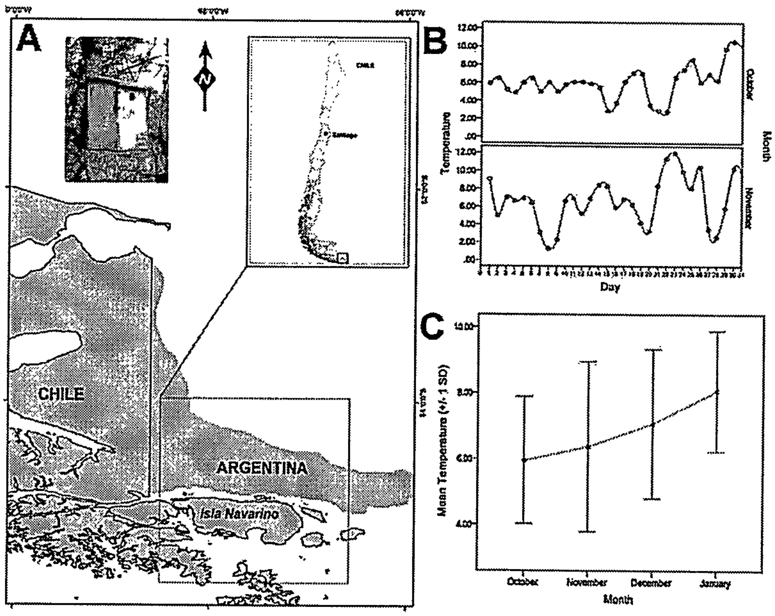

Fig. 1. Location of the study area and values of daily/monthly temperature during the breeding season of 2013 of the Thorn-tailed rayadito. (A) A total of 201 nest boxes were offered to a southern population of rayaditos at Isla Navarino, southern Chile; (B) Fluctuation of daily temperature during October and November 2013; (C) Increasing trend of monthly mean temperatures during 2013.
Fig. 1
70x54mm (300 x 300 DPI)

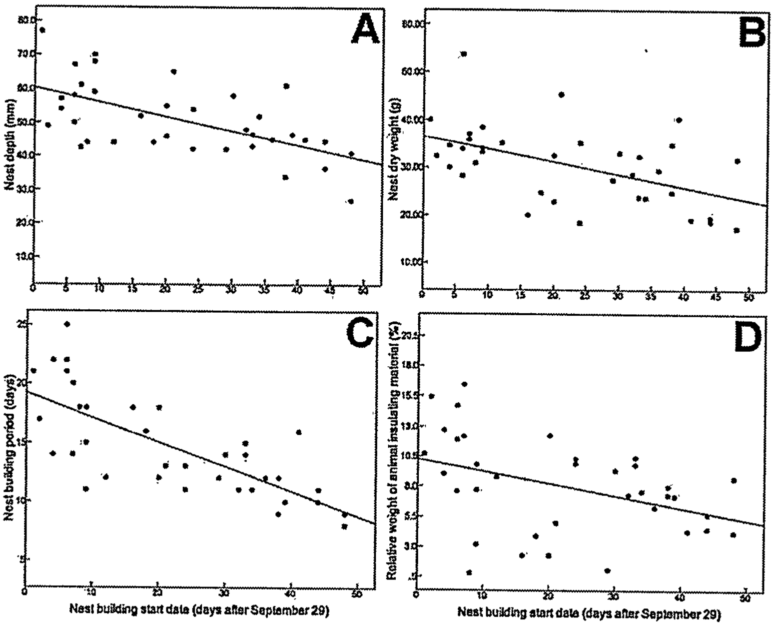

Fig. 2. Linear regression models showing significant seasonal trends in the nest building behaviour and nest morphology of the Thorn-tailed rayadito. (A) Mean nest depth values regressed against nest building start dates for the breeding season of 2013 (y = -0.45 * x + 60.24); (B) Values of nest dry weight against building start dates (y = -0.26 * x + 36.47); (C) Duration of nest building period against building start dates (y = -0.21 * x + 19.23); (D) Relative amount of animal-derived insulating material in the nest internal lining against building start dates (y = -0.10 * x + 10.25).

Fig. 2

64x52mm (300 x 300 DPI)

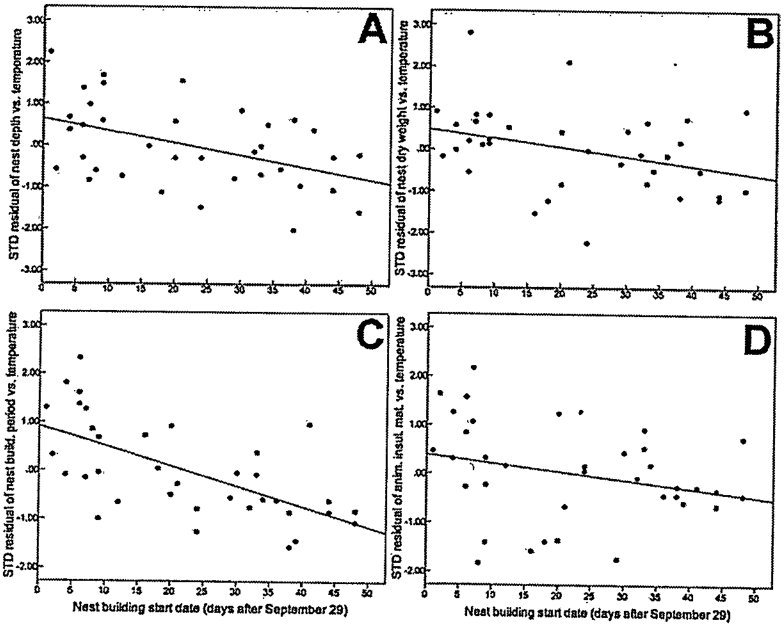

Fig. 3. Linear regression models showing significant seasonal trends in the nest building behaviour and nest morphology of the Thorn-tailed rayadito, after removing the potential effects of temperature increase during the breeding season (using linear regression). (A) Standardized (STD) residuals of mean nest depth regressed against nest building start dates for the breeding season of 2013 ($y = -0.03 * x + 0.65$); (B) Standardized residuals of nest dry weight against building start dates ($y = -0.02 * x + 0.49$); (C) Standardized residuals of nest building period against building start dates ($y = -0.04 * x + 0.92$); (D) Standardized residuals of relative amount of animal-derived insulating material in the nest internal lining against building start dates ($y = -0.02 * x + 0.38$).

Fig. 3

64x52mm (300 x 300 DPI)