RASGOS DE LA PERSONALIDAD Y SUS IMPLICANCIAS EN LA BIOLOGÍA REPRODUCTIVA DEL RAYADITO *Aphrastura spinicauda* (FURNARIIDAE).

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Dr. Hugo Torres ....

A todas las personas que se maravillan cuando observan a los animales!!!

YANINA POBLETE QUINTANILLA

Yanina es profesora de biología egresada de la Universidad Metropolitana De Ciencias de la Educación. Desde sus inicios como estudiante de pedagogía sintió un gran interés por la investigación, particularmente en el ámbito del comportamiento animal. En la búsqueda por ampliar sus conocimientos en 2010 ingresó al programa de Magister en Ecología y Biología Evolutiva en la Universidad de Chile, integrándose al laboratorio de Ecología y Evolución del Comportamiento dirigido por el Dr. Rodrigo Vásquez. Esta primera aproximación a la investigación, no solo le permitió adquirir nuevos conocimientos y experiencias asociadas al quehacer científico, sino que además contribuyó a reafirmar su compromiso con la protección de la naturaleza.

En el año 2013 Yanina se integró al Doctorado en Ecología y Biología Evolutiva donde continúo trabajando junto al Dr. Rodrigo Vásquez. En su tesis doctoral Yanina logró demostrar la naturaleza adaptativa de los rasgos de la personalidad y su relación con aspectos de la biología reproductiva del Rayadito, un ave endémica de los bosques sub-Antárticos. De esta forma su investigación sugiere que drásticos cambios en el ambiente podrían afectar profundamente a estas poblaciones, debido a que probablemente los individuos no logren ajustar su comportamiento al ritmo al cual ocurren algunos de estos cambios.

Yanina pretende seguir una línea de investigación en ecología conductual, con especial énfasis en los aspectos ecológicos y evolutivos que modulan la variabilidad intra-específica en especies silvestres.

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ÍNDICE DE MATERIAS

Lista de tablas	viii
Lista de figuras	ix
Resumen	1
Summary	3
Introducción general	5
Objetivos	15
Hipótesis	16
CAPÍTULO I: Characterizing aggressiveness as evolutionary character	33
Characterizing the relationship between aggressiveness, exploratory behavior and body size in Thorn-tailed rayadito	34
Abstract	35
Introduction	37
Methods	42
Results	48
Discussion	53
Bibliography	60
Supplementary material	76
Heritability in aggressiveness in an endemic bird of the sub-Antarctic rainforests: A study based on markers.	81
Abstract	82
Introduction	83
Methods	87
Results	92
Discussion	94

Bibliography 99

Supplementary material 111

CAPÍTULO II: Personality traits and its relation with extra-pair offspring and parental investment in a sub-Antarctic Rainforest bird 117

Abstract 119

Introduction 121

Methods 124

Results 129

Discussion 132

Bibliography 138

Supplementary material 151

CAPÍTULO III: Behavioural compatibility and its relation with parental investment and extra-pair behaviour in an endemic bird of the sub-Antarctic rainforests 152

Abstract 154

Introduction 156

Methods 160

Results 165

Discussion 166

Bibliography 171

Supplementary material 185

Discusión general 187

LISTA DE TABLAS

CAPÍTULO I: Characterizing aggressiveness as evolutionary character.

Characterizing the relationship between aggressiveness, exploratory behavior and body size in Thorn-tailed rayadito.

Table 1. Sources of variation in observable behaviors (agonistic and exploratory behaviors).

Table 2. Sources of variation and fixed-effects in approach during CIT as proxy of aggressiveness.

Table 3. Sources of variation and fixed-effects in aggressiveness.

Supplementary Material Table S1: Correlation matrix among agonistic behaviors, exploratory tendency and morphometric measurements.

Heritability in aggressiveness in an endemic bird of the sub-Antarctic Rainforests: A study based on genetic markers.

Supplementary Material Table S1. Details of 13 polymorphic microsatellite loci and one chromosome-linked marker (Ps/P) for thorn-tailed rayadito.

Supplementary Material Table S2. Correlation matrix among agonistic behaviors in thorn-tailed rayadito

Supplementary Material Table S3. Eigenvalues of correlation matrix among morphometric traits to characterize body size.

Supplementary Material Table S4. Sources of variation in observable behaviors.

CAPÍTULO III: Behavioural compatibility and its relation with parental investment and extra-pair behaviour in an endemic bird of the sub-Antarctic rainforests

Supplementary Material Table S2. Principal component analysis (PCA) to characterize aggressiveness and nest defence.

LISTA DE FIGURAS

CAPÍTULO I: Characterizing aggressiveness as evolutionary character.

Characterizing the relationship between aggressiveness, exploratory behavior and body size in Thorn-tailed rayadito.

Figure 1. Six hypothesized structural equation models explaining correlation structure among agonistic behaviors during two intrusion contexts (conspecific (CIT) and human (HIT), respectively). Model (A) proposes a scenario where each combination of observable behaviors and intrusion contexts are underpinned by an independent factor (the null model); model (B) hypothesizes a latent variable is present across all observable behaviors regardless of intrusion context; model (C) hypothesizes latent variables separated for each intrusion context; model (D) hypothesizes that those latent variables are sub-units affected by an common factor. Model (E) shows a hypothesized latent variable only at the con-specific intrusion context (CIT); and model (F) shows a hypothesized latent variable only at the human intrusion context (HIT), respectively.

Figure 2. Representation of between-individual correlations among agonistic behaviors observed in wild Thorn-tailed rayaditos. The values plotted are the individual's values to each observable behavior, across all agonistic behaviors (A), and both intrusion contexts, CIT (B) and HIT (C), respectively..

Figure 3. Parameter estimates from SEM that best support for the existence of a latent variable for aggressiveness (A) and body size (B).

Supplementary Material Figure S1. Photograph of thorn-tailed rayadito (*Aphrastura spinicauda)* taken in Navarino Island, Southern Chile. Photograph by Yanina Poblete.

Supplementary Material Figure S2. Photograph of the Conspecific intrusion test (CIT) used to record the aggressiveness face to conspecific taken in Navarino Island, Southern Chile. Photograph by Patricio Castwell.

Supplementary Material Figure S3. Photograph of the experimental aviary used to record the exploratory tendency taken in Navarino Island, Southern Chile. Photograph by Yanina Poblete.

Heritability in aggressiveness in an endemic bird of the sub-Antarctic Rainforests: A study based on genetic markers.

Figure 1. Representation of between-individual correlations among agonistic behaviors observed in wild thorn-tailed rayaditos. The values plotted are the individual's values for each observable behavior, during both intrusion contexts: (A) CIT, and (B) HIT, respectively.

Figure 2. Parameter estimates from SEM that best fitted the data.

Supplementary Material Figure S1. Hypothesized structural equation models explaining correlation structure among agonistic behaviors during two intrusion contexts (conspecific (CIT) and human (HIT)).

Supplementary Material Figure S2. Photograph of thorn-tailed rayadito (*Aphrastura spinicauda*) taken in Navarino Island, Southern Chile. Photograph by Yanina Poblete.

CAPÍTULO II: Personality traits and its relation with extra-pair offspring and parental investment in a sub-Antarctic Rainforest bird.

Figure 1. Boxplot showing both aggressiveness (A) and exploratory behavior (B) related to the presence of EPO in males of thorn-tailed rayaditos.

Figure 2. Relationship between personality traits and parental investment behaviors in females of thorn-tailed rayaditos. (A) Nest defense in relation to exploratory behavior; (B) offspring feeding in relation to exploratory behavior; and (C) nest defense in relation to aggressiveness.

Figure 3. Relationship between clutch volume with EPO (A), exploratory tendency (B) and aggressiveness (C) in males of thorn-tailed rayadito.

Supplementary Material Figure S1. Photograph of thorn-tailed rayadito (*Aphrastura spinicauda*) in nest box taken in Navarino Island, Southern Chile. Photograph by Yanina Poblete.

CAPÍTULO III: Behavioural compatibility and its relation with parental investment and extra-pair behaviour in an endemic bird of the sub-Antarctic rainforests

Figure 1. Compatibility relationships within parental care activities, and between aggressiveness and provisioning in 45 mates of thorn-tailed rayaditos. The plotted values are provisioning and fecal cleaning compatibilities (A); and aggressive and parental care compatibilities (B), respectively.

Supplementary Material Figure S1. Photograph thorn-tailed rayadito in nest box.

RESUMEN

La conducta agresiva junto con la conducta exploratoria son comportamientos que han mostrado ser repetibles, heredables y con impacto sobre la adecuación biológica, siendo consistentes a través del tiempo y/o bajo diferentes contextos; por estas razones son considerados rasgos de la personalidad sujetos a selección. Estas conductas pueden variar en su estructura y covariar entre sí expresando síndromes conductuales, principalmente en ambientes impredecibles y estresantes. Junto con ello, estas conductas pueden afectar diferentes aspectos asociados a la reproducción, como son el comportamiento extra-pareja, las conductas de inversión parental y/o la calidad de la descendencia, y además podrían ser rasgos considerados por los individuos durante la elección de pareja. El rayadito (*Aphrastura spinicauda*) es una modelo ideal para estudiar rasgos de la personalidad y sus implicancias en la biología reproductiva, debido a que puede nidificar en cajas anideras durante la estación reproductiva, lo cual permite realizar un seguimiento completo durante este periodo. En esta investigación, se escogió a una población de rayaditos presentes en Isla Navarino, sur de Chile, la cual presenta menores niveles de estrés y menor densidad poblacional, en comparación con otras poblaciones de estudio (e.j.Fray Jorge, Manquehue, Chiloé), y se encuentra en un ambiente continuo, con ausencia de mamíferos depredadores nativos. A través de diferentes pruebas conductuales, información reproductiva y análisis genéticos, se evidenció que la agresividad es en parte independiente de la conducta exploratoria y se determinó que es un comportamiento parcialmente heredable, el cual actúa como un carácter evolutivo en esta población. Junto con ello, se demostró que una conducta exploratoria más intensa en los machos favorece la pérdida de paternidad, mientras que una conducta agresiva más intensa la limita. Además fue posible evidenciar que una conducta exploratoria más intensa en las hembras se relaciona directamente con la defensa del nido y la frecuencia de aprovisionamiento de las crías y se detectó que en nidos con crías extra-pareja los huevos son en promedio de mayor volumen, sugiriendo posibles beneficios indirectos del comportamiento extra-pareja para las hembras. Finalmente, se evidenció que la compatibilidad en agresividad entre integrantes de una pareja se relaciona directamente con la compatibilidad en aprovisionamiento, sugiriendo que la conducta agresiva podría ser un rasgo informativo durante la elección de pareja. Los resultados de este estudio proporcionan evidencia que respalda la importancia evolutiva de los rasgos de la personalidad en la biología reproductiva de aves socialmente monógamas como el rayadito, y hacen especial énfasis en la importancia del contexto ambiental sobre la estructura, modulación y expresión de estos rasgos.

SUMMARY

Aggressive and exploratory behaviors have been shown to be repeatable, inheritable and able to influence the fitness of individuals, this being consistent over time and/or under different contexts; therefore, they are considered personality traits subject to selection. These behaviors can vary their structure and covary among themselves expressing behavioral syndromes, mainly under unpredictable and stressful environments. Moreover, these behaviors can affect different traits associated to reproduction, such as extra-pair behavior, parental investment and clutch quality, and considered by individuals during pair selection. Thorn-tailed rayadito (*Aphrastura spinicauda*) is an ideal model to study personality traits and their implications on reproductive biology, because they can nest in nest boxes, which allows a complete monitoring during the reproductive season. In this research, a thorn-tailed rayadito population located on Navarino Island, southern Chile, was studied. It shows low levels of stress and low population density regarding other study populations (e.g., Fray Jorge, Manquehue, Chiloé); besides, it inhabits a continuous environment, with absence of native predatory mammals. Different behavioral tests, reproductive information and genetic analyses provided evidence that aggressiveness is partly independent of both exploratory behavior and body size; it is a partially heritable behavior, which could act as an evolutionary character in this population, as well. Along with this, it was proved that a more intense exploratory behavior in males favors the loss of paternity, while a more aggressive behavior limits it. Results also show that a more intense exploratory behavior in females is directly related to both nest defense and feeding offspring behaviors; additionally, it was detected that in nests with extra-pair offspring, eggs are, on average, of greater volume, suggesting possible indirect benefits of extra-pair behavior for females. Finally, it was demonstrated that compatibility in aggressiveness between pair is directly related to compatibility in feeding offspring, suggesting that aggressiveness could be an informative feature during pair selection. The results of this study provide evidence supporting the evolutionary importance of personality traits on reproductive biology of socially monogamous birds such as thorn-tailed rayadito, and emphasize the importance of environmental context on structure, modulation and expression of these traits.

Introducción

El comportamiento es considerado como uno de los rasgos más flexibles presentes en la naturaleza, debido a que puede ser condicionado por múltiples factores ambientales, sociales e individuales (Kappeler y Kraus, 2010). Este mayor grado de flexibilidad, en principio, otorgaría beneficios a los individuos en su sobrevivencia y reproducción (Bergmuller, 2010). Sin embargo, a pesar de estas aparentes ventajas de la flexibilidad, se ha observado en distintos taxa que los individuos de una misma población difieren consistentemente en su comportamiento (Bell y Stamps, 2004; Dingemanse et al., 2004). Este fenómeno es conocido como personalidad animal y se define como la variabilidad conductual intra-específica consistente a través del tiempo y/o en diferentes contextos (Wilson, 1998; Gosling y John, 1999; Drent et al., 2003; Dall et al. 2004; Bergmuller y Tabosky, 2007).

Las conductas agonistas han sido ampliamente estudiadas como rasgos de la personalidad animal (Wilson, 1998; Gosling y John, 1999; Drent et al., 2003; Bell y Stamps, 2004; Bergmuller y Tabosky, 2007; Réale et al., 2007). Estas conductas que cumplen un papel crucial en la historia de vida de la mayoría de las especies, permiten a los individuos adquirir y defender diferentes recursos como fuentes de alimentación, territorios, parejas y/o crías (Ewald y Carpenter, 1978; Fox et al., 1981; Camfield, 2006; Reaney y Backwell, 2007; Maruyama et al., 2010; Toobaie y Grant, 2013). Las diferencias individuales en conductas agonistas influyen sobre los resultados de la competencia por estos recursos (Perrin et al., 2001; Bohlin et al., 2002; Yoon et al., 2012; Yuan et al., 2013), e impactan directamente sobre la adecuación biológica (Smith et al., 2008). A nivel intra-individual, las conductas agonistas generalmente se correlacionan entre sí (Verbeek et al., 1996; Garamszegi et al., 2009), por esta razón se asume que forman parte de una unidad funcional llamada agresividad (Gould et al., 1978).

El concepto de integración funcional es utilizado para referir a correlaciones entre rasgos (Wagner, 2000; Pigliucci, 2001), las cuales surgen debido a que la selección natural favorece combinaciones óptimas de atributos funcionalmente relacionados, que actúan como mediadores efectivos frente a interacciones agonistas. Por esta razón, la integración funcional entre conductas agonistas podría depender en gran medida del contexto ambiental (Schwenk, 2001; Pigliucci, 2001).

Desde un punto de vista funcional, es ampliamente aceptado que la integración funcional es modulada por genes pleiotrópicos, los cuales desencadenan una vía neurológica o fisiológica común, que conduce a la expresión de una unidad funcional que actúa como carácter evolutivo (Bakker, 1986; Mackay, 2004; Araya-Ajoy y Dingemanse, 2014), y bajo ciertas condiciones ambientales, estos mecanismos podrían conducir a la integración funcional entre caracteres (DeWitt et al., 2000).

La integración funcional entre caracteres evolutivos ha sido ampliamente documentada entre agresividad y conducta exploratoria, bajo el concepto de síndrome conductual (Verbeek et al., 1996; Carere et al., 2003; Bergmüller y Taborsky, 2007). La conducta exploratoria es un comportamiento fundamental para los individuos, porque les permite obtener información sobre fuentes de alimentación, refugios, rutas de escape y potenciales parejas, entre otros aspectos del ambiente (Dingemanse et al., 2002; van Dongen et al., 2010). Teóricamente, la relación entre agresividad y exploración es conocida como "conducta de toma de riesgo", debido a que facilitaría la adquisición de recursos, pero aumentaría los riesgos de mortalidad generados por una mayor exposición a depredadores y/o enfermedades (Bell, 2005). Empíricamente, varios estudios han demostrado que la covariación entre agresividad y exploración ocurre en poblaciones expuestas a altas presiones de depredación (Bell y Sih, 2007; Dingemanse et al., 2007) o elevados niveles de estrés (Martins et al., 2007). En general, la mayoría de los estudios están de acuerdo en que esta relación suele ser común en ambientes impredecibles (McElreath y Strimling, 2006), debido a que producir respuestas conductuales independientes hacia diferentes desencadenantes requeriría que la información sobre estos fuera confiable. Por esta razón, es esperable que en ambientes menos impredecibles, ambos comportamientos sean menos restrictivos y varíen de forma independiente uno del otro (Sih, 1992; Bell, 2005; McElreath y Strimling, 2006).

Otro caso de integración funcional ampliamente documentado a nivel intra-específico es el que ocurre entre agresividad y tamaño corporal (Rising y Somers, 1989; Gosler et al., 1998; Meiri, 2010; Porto et al., 2013). La mayoría de los estudios que han explorado esta correlación, han encontrado que la agresividad (medida en base a diferentes conductas agonistas) se asocia directamente con el tamaño corporal (Rowland, 1989; Huntingford et al., 1990; Schuett, 1997). Sin embargo, algunos estudios han encontrado que individuos más pequeños tienden a ser más agresivos, lo que se conoce como "complejo de Napoleón" (Just y Morris, 2002; Svensson et al., 2012), y en algunos casos la correlación no ha logrado ser determinada, lo cual sugiere que ambos atributos podrían variar de manera independiente (Pavey y Fielder, 1996).

La teoría de retención potencial de recursos (RPR) ofrece una alternativa que permite comprender en parte estas asociaciones. Por ejemplo, cuando la asimetría en RPR es alta, los individuos con bajo RPR (e.g., menor tamaño corporal), podrían evitar las confrontaciones, mostrándose menos agresivos (Parker, 1974; Smith y Parker, 1976, Huntingford y Turner, 1987; Arnott y Elwood, 2009; Morishita et al., 2009). Sin embargo, cuando la asimetría en RPR es baja, la agresividad podría ser un comportamiento costoso y en este escenario los individuos podrían evaluar los costos y beneficios antes de enfrentarse (Enquist y Jackobsson, 1986; Morris et al., 1995). Junto con ello, la teoría de competencia por recursos, predice que los individuos podrían ser más agresivos cuando la densidad poblacional es alta y los recursos limitados (Ashmole, 1963; Cody, 1966; Yoon et al., 2012; Yuan et al., 2013). En este contexto, es probable que un mayor tamaño corporal proporcione ventajas comparativas frente a los competidores potenciando la agresividad (Parker, 1974; Smith y Parker, 1976; Huntingford y Turner, 1987). Sin embargo, cuando la densidad poblacional es baja y los recursos no son limitados, la relación agresividad-tamaño corporal podría ser difícil de determinar. Por lo tanto, la relación entre agresividad y tamaño corporal podría depender en parte del contexto ambiental y ser explicada considerando el valor de los recursos, los costos de ser agresivo y los mecanismos que permiten evaluar la agresividad de los adversarios (Brown, 1964; Enquist y Leimar, 1990).

El reconocimiento de la agresividad como un carácter evolutivo, no solo requiere de una correcta caracterización de su estructura a través de las conductas agonistas observables, sino que también es importante que parte de su variación sea explicada por la identidad, lo cual es un reflejo de la integración funcional entre estos comportamientos (Araya-Ajoy y Dingemanse, 2014). Junto con ello, si la agresividad es reconocida como carácter evolutivo es fundamental que parte de su variación sea heredable.

La heredabilidad en sentido estricto (h^2) es un importante parámetro en biología evolutiva, porque entrega información respecto a la proporción de varianza fenotípica explicada por el efecto genético aditivo (Fisher, 1918; Wright, 1920) y permite estimar la habilidad potencial de una población para evolucionar en respuesta al contexto ambiental (Jacquard, 1983; Nyquist y Baker, 1991; Ritland, 1996; Visscher et al., 2006; Holland et al., 2010; Sillanpaa, 2011). La agresividad, caracterizada a partir de diferentes conductas agonistas, ha mostrado ser parcialmente heredable en un amplio número de poblaciones de laboratorio, donde h^2 se ha calculado con base en una estructura de pedigree conocida (Weiss et al., 2002; Fairbanks et al., 2004; Rogers et al., 2008). Sin embargo, son escasos los estudios que han calculado h^2 de la agresividad en poblaciones silvestres, principalmente porque la dispersión o la muerte de los individuos reduce las posibilidades de obtener un pedigree conocido (Boake et al., 2002; Duckworth y Badyaev, 2007). Si bien las condiciones de laboratorio proporcionan mejores oportunidades de control y replicación para los cálculos de h^2, es importante ampliar las estimaciones de h^2 a poblaciones silvestres principalmente debido a que (i) es fundamental para comprender la naturaleza evolutiva de la conducta (Boake et al., 2002), (ii) depende en gran medida del contexto ambiental (Riska et al., 1989; Dingemanse et al., 2002; Drent et al., 2003), y (iii) es improbable que la selección natural opere de forma similar sobre la variación heredable en condición de laboratorio y ambientes silvestres (Merilä y Sheldon, 2001).

A pesar de las dificultades existentes para estimar la h^2 en poblaciones silvestres, el desarrollo de marcadores genéticos ha contribuido a la generación de nuevas herramientas para calcular h^2 (Csillery et al., 2006). Estos métodos conocidos como libres de pedigree, incluyen un conjunto de técnicas dentro de las cuales destacan los métodos derivados de selección genómica y los modelos mixtos que permiten incorporar matrices de parentesco como efectos aleatorios (Lynch y Walsh, 1998; Kruuk, 2004; Goddard, 2009; Strandén y Garrick, 2009). Estos métodos han mostrado ser prominentes, debido a que entregan valores de h^2 similares a los obtenidos utilizando datos de pedigree conocido y podrían ser especialmente útiles para realizar cálculos de h^2 en rasgos complejos y donde varias réplicas de un genotipo individual se encuentran disponibles (Gay et al., 2013; Kruijer et al., 2015).

Junto con ello, la naturaleza evolutiva de los rasgos de personalidad involucra su relación con otros aspectos funcionales de la vida de los individuos como son la dominancia social (Verbeek et al., 1996), la dispersión (Dingemanse et al., 2003), la cooperación (Schürch y Heg, 2010) y una serie de aspectos asociados a la reproducción (van Oers et al., 2008; Patrick et al., 2012).

Una relación que ha recibido particular interés es aquella que trata de explicar cómo la variabilidad en rasgos de la personalidad influye sobre la variación en el comportamiento extra-pareja. Esta conducta que ha sido ampliamente descrita en aves socialmente monógamas (Petrie y Kempenaers, 1998; Griffith et al., 2002; Westneat y Stewarts, 2003), se propone como un rasgo adaptativo porque tanto machos como hembras podrían obtener beneficios asociados a un mayor número de crías o a mejoras en la calidad genética de la descendencia (Kempenaers et al., 1992; Wesneat y Stewart, 2003). Sin embargo, el comportamiento extra-pareja también tiene costos asociados a un aumento en la probabilidad de adquirir enfermedades y podría generar conflictos sexuales entre los integrantes de la pareja (Kempenaers y Schlicht, 2010). Los costos asociados a conflictos sexuales afectan en mayor medida a las hembras, debido a que los machos podrían disminuir su inversión parental frente a la infidelidad (Westneat et al., 1990).

Puesto que los costos del comportamiento extra-pareja podrían ser diferentes para cada sexo, se piensa que machos y hembras difieren intrínsecamente en su propensión a expresar este comportamiento, donde algunos individuos podrían tener una predisposición genética hacia la promiscuidad (Forstmeier, 2007), la cual podría expresarse en individuos que adquieren mayores riesgos (Dingemanse et al., 2002; van Oers et al., 2004; Martins et al., 2007). Así, la evidencia sugiere que este comportamiento es más común en individuos más exploradores, quienes tienden a ganar paternidad fuera del nido. Sin embargo, para el caso de machos más exploradores, ellos también tienden a perder paternidad en su nido social (Patrick et al., 2012).

Aunque las características conductuales individuales podrían modular diferentes aspectos asociados a la reproducción, es importante considerar la existencia de propiedades emergentes que surgen como resultado de la interacción entre los fenotipos conductuales de los integrantes de una pareja. Estas propiedades emergentes que se agrupan bajo el concepto de compatibilidad conductual (Trivers, 1972; Marzluff y Balda, 1988a; Black, 1996), hacen referencia principalmente a las similitudes entre los rasgos conductuales de los integrantes de una pareja (Marzluff y Balda, 1988a; Black et al., 1996; Dingemanse et al., 2004; Spoon et al., 2005). Si bien la compatibilidad conductual es un fenómeno que ha recibido menor atención, la evidencia señala que la compatibilidad conductual favorece la participación equitativa en las actividades reproductivas (Gabriel y Black, 2012; Adler y Ritchison, 2011; Mitrus et al., 2010) y puede influir sobre la expresión del comportamiento extra-pareja; lo que podría afectar directamente a la adecuación biológica de la pareja (Spoon et al., 2007; van Oers et al., 2007). Por esta razón, la compatibilidad conductual podría ser particularmente importante en especies monógamas que realizan cuidado biparental (Spoon et al., 2005; Ihle et al., 2015).

Por ser un ave socialmente monógama que realiza cuidado biparental (Moreno et al., 2007; Botero-Delgadillo et al., 2015; Espíndola-Hernández et al., 2017) el Rayadito *Aphrastura spinicauda* (Furnariidae), es un modelo adecuado para describir la variabilidad conductual intra-específica en rasgos de la personalidad y sus implicancias en su biología reproductiva.

El rayadito es un ave endémica de los bosques sub-antárticos de Sudamérica. En Chile se distribuye desde la región de Coquimbo, donde habita remanentes de bosques rodeados de matorral sub-xerofílico, hasta la región de Magallanes incluyendo islas cercanas al continente como Tierra del Fuego, Navarino y Diego Ramírez (Luebert y Pliscoff, 2006). El rayadito es un nidificador secundario de cavidades, que carece de dimorfismo sexual aparente al igual que otros furnáridos (Moreno et al., 2007). Habitualmente los rayaditos construyen un nido por estación reproductiva (Moreno et al., 2005), periodo durante el cual es posible reconocer un conjunto de comportamientos agonísticos desplegados en parejas cuando algún intruso ingresa a sus territorios (Ippi y Trejo, 2003; Ippi et al., 2011).

A través de un monitoreo de largo plazo ha sido posible describir la variabilidad intra-específica en repertorio vocal (Ippi et al., 2011), conducta anti-depredatoria (Ippi et al., 2013, 2017), cuidado parental (Moreno et al. 2007, Espindola-Hernandez et al. 2017), estrés fisiológico (Quirici et al., 2014) y patrones de dispersión (Botero-Delgadillo et al., 2017). En conjunto, estas investigaciones han revelado que la población de rayaditos que habita isla Navarino presenta una baja presión de depredación, debido a la ausencia de depredadores mamíferos nativos (Ippi et al. 2013, 2017), menores niveles de estrés fisiológico y menor hacinamiento, siendo en general un área menos estresante respecto a otras poblaciones monitoreadas (Quirici et al., 2014, 2016).

Isla Navarino se caracteriza por la presencia de bosque caducifolio de Magallanes, donde las especies predominantes son la lenga (*Nothofagus pumilio*) y el ñirre (*Nothofagus antarctica*) (Rozzi et al., 2004). En general, es un área expuesta a fuertes vientos y bajas temperaturas (rango: -2 a 15.8 ° C) la mayor parte del año (Dirección Meteorológica de Chile, Clima Nacional de Chile) y presenta una menor variación tanto espacial como climática respecto a otros sitios de estudio (véase e.g., Quirici et al., 2014, 2016; Botero-Delgadillo et al., 2017).

Debido a la naturaleza lábil del comportamiento, y con el propósito de disminuir el efecto que factores estresores podrían generar sobre los rasgos conductuales, se escogió a la población de rayaditos presentes en isla Navarino como población focal de esta investigación, en la cual se propone describir dos rasgos de la personalidad (agresividad y conducta exploratoria) y evaluar sus implicancias sobre la biología reproductiva de la especie.

Objetivos

Objetivo general: Evaluar la relación entre rasgos de la personalidad y sus implicancias en la biología reproductiva del rayadito, *Aphrastura spinicauda.*

Objetivos específicos:

1. Describir la estructura de la agresividad con base en un conjunto de conductas agonistas observables.
2. Evaluar la existencia de síndrome conductual entre agresividad y conducta exploratoria y la integración funcional entre agresividad y tamaño corporal.
3. Estimar la heredabilidad de la agresividad.
4. Determinar la relación entre agresividad y exploración con el comportamiento extra-pareja, la inversión parental y la calidad de la descendencia.
5. Describir el efecto de la compatibilidad conductual en exploración y agresividad sobre el comportamiento extra-pareja, la inversión parental y la calidad de la descendencia.

Hipótesis

Capítulo I: Characterizing aggressiveness as evolutionary character.

Hipótesis 1. La integración funcional de las conductas agonistas en una unidad funcional de carácter evolutivo (agresividad), es dependiente del contexto de intrusión territorial.

Predicciones:

a. Cuando el intruso en el territorio es un con-específico, las conductas agonistas desplegadas se correlacionarán en el mismo sentido, revelando una integración funcional entre estos observables.

b. Cuando el intruso en el territorio es un humano, las conductas agonistas no se correlacionarán en el mismo sentido, revelando la ausencia de integración entre estos observables.

Capítulo II: Personality traits and its relation with extra-pair offspring and parental investment in a sub-Antarctic Rainforest bird.

Hipótesis 2. La variación en rasgos de la personalidad se relaciona con la variación en comportamiento extra-pareja, inversión parental y calidad de cría, independientemente del sexo de los individuos.

Predicciones:

a. Hembras más exploradoras tenderán a presentar una proporción mayor de crías extra-pareja, mejor calidad de crías y mayor inversión parental respecto a hembras menos exploradoras.

b. Hembras más agresivas tenderán a presentar una proporción menor de crías extra-pareja, menor calidad de crías y menor inversión parental, respecto a hembras menos agresivas.

c. Machos más exploradores tenderán a presentar una mayor proporción de crías extra-pareja en su nido social y una menor inversión parental, respecto a machos menos exploradores.

d. Machos más agresivos tenderán a presentar una menor proporción de crías extra-pareja en su nido social y una mayor inversión parental, respecto a machos menos agresivos.

Capítulo III: Behavioural compatibility and its relation with parental investment and extra-pair behaviour in an endemic bird of the sub-Antarctic rainforests

Hipótesis 3. La variabilidad en compatibilidad en rasgos de la personalidad, se relaciona con la variación en el comportamiento extra-pareja, inversión parental y calidad de cría.

Predicciones:

a. Parejas compatibles en rasgos de la personalidad serán más compatibles en conductas de inversión parental, respecto a parejas menos compatibles en estos rasgos.

b. Parejas menos compatibles en rasgos de la personalidad presentarán una mayor proporción de crías extra-pareja y menor calidad de cría, respecto a parejas más compatible en estos rasgos.

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CAPÍTULO I

CHARACTERIZING AGGRESSIVENES AS EVOLUTIONARY CHARACTER.

Characterizing the relationship between aggressiveness, exploratory behavior and body size in Thorn-tailed rayadito.

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MANUSCRITO ENVIADO ANIMAL BEHAVIOUR (ANBEH-D-17-00999)

Lay summary

Aggressiveness plays a key role in resource acquisition. Moreover, it is predicted to be related to other attributes such as exploratory tendency or morphology. We have characterized aggressiveness using structural equation model based on the correlation of observed behaviors in order to determine evidence for a latent variable that we can define as aggressiveness, and we quantified its relation with exploratory tendency and body size in a small ovenbird inhabitant of the Sub-Antarctic rainforest of South America.

Abstract

Agonistic behaviors are an integral part of avian life-history, allowing to acquire territories and mates. In order to be effective mediators of agonistic interactions, agonistic behaviors need to be expressed in a coherent way and they should be correlated in a particular way to act as functional unit. The concept of "functional integration" is used to refer to these relations, which could evidence a latent behavioral unit, representing "evolutionary characters" under selection. Based on this background, we applied a framework that includes correlations, structural equation modelling and mixed-effect model analysis to detect whether aggressiveness acts as a "latent behavioral unit" and assessed its relation with exploratory tendency and body size. To this end, we recorded agonistic behaviors under two territorial intrusion contexts, characterized the exploratory tendency, and body size in 68 thorn-tailed rayaditos inhabiting a sub-Antarctic rainforest on Navarino Island (55°40"S, 67°40"W) southern of Chile. Our results support the presence of a latent behavioral unit, manifested as agonistic behaviors deployed toward conspecific, but not toward human, suggesting that functional integration of these behaviors is context dependent. Furthermore, we find that both exploratory tendency and body size are not good predictors of aggressiveness, suggesting that these traits are independent of one another in this population. In summary, the results of this study show that functional integration in agonistic behaviors can be context dependent, and highlights the importance of studying the correlations between behaviors to understand about the causes and consequences of the correlated expression of behaviors from a functional perspective.

Key words: Aggressiveness, functional integration, evolutionary character, exploratory behavior, body size, thorn-tailed rayadito.

Introduction

Agonistic behaviors play a crucial role in resource acquisition for most species. Several studies have shown that agonistic behaviors are positively related to the availability of food, mates, and suitable habitat (e.g., Ewald and Carpenter 1978, Fox et al. 1981, Camfield 2006, Reaney and Backwell 2007, Maruyama et al. 2010, Toobaie and Grant 2013). Thus, individual differences in agonistic behavior can affect intra-specific competition (Perrin et al. 2001, Bohlin et al. 2002, Yoon et al. 2012, Yuan et al. 2013). It has also been widely documented in many taxa that agonistic behaviors are repeatable (Verbeek et al. 1996, Kralj-Fiser et al. 2007, Duckworth 2006a, Garamszegi et al. 2006b, Pavlova et al. 2007), heritable (Duckworth and Badyaev 2007, Araya-Ajoy and Dingemanse 2017), and affect reproductive success (Smith et al. 2008). Therefore, agonistic behaviors are considered to be relevant personality traits under selection (Wilson 1998, Gosling and John 1999, Drent et al. 2003, Bell and Stamps 2004, Bergmuller and Tabosky 2007, Réale et al.2007).

Agonistic behaviors are more readily observable in reproductive season, during situations of social dominance (Verbeek et al. 1996) or territorial defense (Garamszegi et al. 2009). Agonistic behaviors have been quantified mainly using simulated territorial intrusions, where a set of behaviors deployed by the birds are recorded, when an intruder (usually a conspecific or a human), is placed inside their territory (see Wingfield et al. 1987, Carere et al. 2005).

The agonistic behaviors measured within a natural or simulated territorial intrusion are usually correlated with each other, and altogether are interpreted as expressions of aggressiveness (Verbeek et al. 1996, Garamszegi et al. 2009). Thus, most studies assume that the measured behaviors are expressions of a functional unit called aggressiveness (Gould et al. 1978). Currently, the concept of "functional integration" is used to refer to the correlations between traits (Wagner 2000, Pigliucci 2003), which arise because natural selection favors optimal combinations of traits that are functionally related (Schwenk 2001, Pigliucci 2003). Nevertheless, it is important to note that due to the labile nature of behavior, the correlations between the agonistic behaviors can be context dependent. Therefore, different observations may be good proxies of aggressiveness depending on the environmental conditions. Thus, a specific characterization of the relations among agonistic behaviors could not only affect fundamentally how we describe the structure of aggressiveness, but it would further contribute to our understanding about how these behaviors are shaped by different selective pressures (Schwenk 2001).

Birds express a wide array of behaviors during agonistic interactions and they need to be coherent in its expression in order to achieve the function of repelling intruders. For example, during highly aggressive interactions, birds respond to a conspecific intrusion by calling while approaching and attacking if the intruder does not withdraw. By contrast, during less aggressive interactions, birds may sing from far away rather than attacking the intruder. Proximately, this functional coherence is due to common mechanisms affecting the expression of all displaying behaviors (i.e. through pleiotropic effects of genetic or environmental factors) (Araya-Ajoy and Dingemanse 2014). This common (neurological or physiological) pathways enable different behaviors to be expressed as a functional unit. It is this proximate mechanism that represents the evolutionary behavioral character.

Importantly, those behavioral characters are never measured directly but are inferred from behaviors that can be measured during an aggressive interaction.

Under certain environmental conditions, evolutionary characters could also be functionally integrated with other behavioral characters (DeWitt et al. 2000). In fact, agonistic behaviors have been positively correlated with exploratory tendency in some populations (Verbeek et al.1996, Carere et al. 2003). Behavioral ecologists traditionally use the term "behavioral syndromes" when referring to these correlations between behaviors (Bell 2007, Sih and Bell 2008). For instance, it has been documented that faster explorers are more aggressive toward a con-specific (Verbeek et al.1996, Bergmüller and Taborsky 2007). This relation known as "risk-taking behavior" should facilitate the acquisition of resources, at the cost of increasing mortality risk (Bell 2005). Empirically, several studies have shown that exploration-aggressiveness covariance arises in populations with high predation pressures or higher stress levels (Bell and Sih 2007, Dingemanse et al. 2007, Martin et al. 2007). In general, it is assumed that this relation could be more frequent in unpredictable environments, because producing independent behavioral responses towards different situations (e.g., conspecific competitor and predator) would require reliable information about the environment. In contrast, it is possible that in more stable environments, behaviors are less constrained, allowing for their independent variation (Sih 1992, Bell 2005, McElreath and Strimling 2006). Thus, the functional integration among behavioral traits could depend in part on the environmental context where they are expressed.

It has also been widely documented that behavioral and morphological traits covary in multiplex taxa (Rising and Somers 1989, Gosler et al.1998, Meiri 2010, Porto et al.2013).

However, although several studies have detected positive correlations between agonistic behaviors and body size in different species (Rowland 1989, Huntingford et al.1990, Schuett 1997), the nature of this relation is yet unclear. Thus, some investigations have documented both positive and negative correlations between morphology and aggressiveness (e.g, napoleon complex, Just and Morris 2002, Svensson et al.2012). Resource-holding potential theory (RHP) could explain in part these contrasting results. For example, it is observed that when asymmetry in RHP is large, individuals with the relatively lower RHP (the probable losers) retreat, being less aggressive (Parker 1974, Smith and Parker 1976, Huntingford and Turner 1987, Arnott and Elwood 2009, Morishita et al. 2009). However, when asymmetry in RHP among individuals is small, the aggressiveness could be a costly behavior and individuals would assess costs and benefits before attacking (Enquist and Jackobsson 1986, Morris et al. 1995). Along with this, resource competition theory predicts that individuals would be less aggressive when food abundance is high and con-specific density is low, and more aggressive when density is high and resources are limited (Ashmole 1963, Cody 1966, Yoon et al. 2012, Yuan et al. 2013). Thus, when density is high and resources are limited, it is likely that a large body size provides comparative advantages to face other individuals (Parker 1974, Smith and Parker 1976, Huntingford and Turner 1987). However, when density is low and resources are plenty, competition pressures may relax and the relationship between aggressiveness and body size may disappear. Thus, the evidence suggests that covariation between aggressiveness and body size could be context dependent, where both the relation between resource value and fight cost will affect its expression (Brown 1964, Enquist and Leimar 1990).

Based on this background, we recorded a set of agonistic behaviors under two different intrusion contexts (human and con-specific), to determine if there was statistical support for a latent functional unit, that we could describe as aggressiveness. We further quantified exploratory behavior and performed morphometric measurements in order to assess their relation to aggressiveness. To this end, we studied to thorn-tailed rayadito, *Aphrastura spinicauda* (Furnariidae), an endemic bird of the sub-Antarctic rainforests of South America (Remsen 2003) (electronic supplementary material, figure S1).

The thorn-tailed rayadito is a small sub-oscine, secondary cavity nesting, socially monogamous bird, with an apparent absence of sexual dimorphism; including an equitable participation of male and female in the raising the offspring (Moreno et al 2007, Botero-Delgadillo et al. 2015, Espíndola-Hernández et al. 2017). Thorn-tailed rayaditos usually lay one clutch per breeding season, which begins in the austral spring (Moreno et al. 2005). During this season, it is possible to recognize a set of agonistic behaviors deployed in pairs for thorn-tailed rayadito, including approach toward intruders in its territory (e.g., other animals or humans) and alarm calls (Ippi and Trejo 2003, Ippi et al. 2011). In order to reduce the impact that could generate both predation pressure and high intra-specific competence over the aggressiveness, we selected a population located in Navarino island (55°4'S, 67°40'W), southern Chile. This area, characterized by deciduous Magellanic forest (Rozzi et al. 2004), is exposed to strong winds and low temperatures (range: –2 to 15.8° C) most of the year (Rozzi and Jimenez 2014). It is a continuous and less populated environment, where thorn-tailed rayadito has no native mammalian predators, and the levels of stress are lower in comparison with northern populations (e.g., Chiloé, Manquehue, Fray Jorge)(Ippi et al. 2013, Quirici et al. 2014, 2016, Botero-Delgadillo et al. 2017).

This study aimed to: (1) describe the sources of variation in ten agonistic behaviors recorded during different intrusion contexts (human and con-specific); (2) assess the correlations among agonistic behaviors in different contexts; (3) test for support of the existence of a "behavioral latent variable" that underpins the expression of the measured agonistic behaviors, and (4) assess the relationship between aggressiveness, body size and exploratory tendency.

Methods

General field procedures. The study was carried out during the reproductive season, from October to late December, during 2014 and 2015. Because rayaditos are secondary cavity nesters, we used nest boxes, which were monitored weekly until they were occupied. Adults were then captured between 7:30 am and 12:00 pm in the nest box (n=68), at 12 or 13 days post-hatch, and banded with both metal and colored bands (National Band and Tag Co., Newport, Kentucky, USA, or Split Metal Bird Rings, Porzana Ltd, UK) or with a numbered band provided by the *Servicio Agrícola y Ganadero* (Chilean Agricultural and Livestock Service, or *SAG*, Chile). The bill and tarsus length were measured to the nearest 0.01 cm with digital calipers; the whole wings were measured with a stopped rule, and mass was recorded in grams (± 0.1 g). Before releasing the birds, a small blood sample (ca. 17 µL) was taken from the brachial vein, and stored in FTA cards (Whatman®) for posterior molecular sexing (see e.g., Moreno et al 2007, Quirici et al. 2014).

Recording Agonistic behaviors.

1.-Human Intrusion Test (HIT). Thirteen days post-hatching, a focal human was placed three meters in front of the nest-box. Over a three-minute period, two observers located at 6 m, recorded the frequency of hops, flights and alarms using a digital recorder (Hollander et al. 2008). The "approach" variable was recorded as the minimum distance between the birds and the focal human as measured by laser rangefinder (CEM, LDM-40) and the "speed" variable, was estimated as the number of hops and flights performed during the first minute of the test.

2.-Conspecific Intrusion Test (CIT). At fifteen days post-hatching, a conspecific model was placed 3 m in front of the nest-box. Two observers recorded over 8 min (2 minutes of silence, 3 minutes of playback of thorn-tailed rayadito vocalizations, and 3 minutes of silence) the frequency of hops, flights and alarms using a digital voice recorder (see Ippi et al. 2013) (electronic supplementary material, figure S2). The "approach" variable was estimated as the total amount of time the individual remained close to the model (within 1 m). The "speed" was calculated as the number the hops and flights performed during the first minute of playback in the test.

Exploratory tendency

After capturing and before banding, we observed and recorded exploratory behavior via a novel environmental experiment, utilizing a large field-portable cage (270 cm length x 150 cm width x 150 cm height) made of PVC poles and semitransparent black shading cloth. In the cage, four wooden perches (80 cm long, 2 cm in diameter) were hung at varying heights between 50 and 110 cm off the ground. The floor was divided into two equally sized quadrants that when added to the four perches, four walls and two ceiling divisions yielded 14 possible perching locations (electronic supplementary material, figure S3) (see van Dongen et al. 2010). The birds were introduced into a small acclimatization cage (30 cm length x 25 cm width x 39 cm height) in a corner of the larger experimental cage and covered with a black cloth during a five-minute acclimatization period. At the beginning of the experimental period, the cloth was removed. One minute after removing the cloth, the door of the holding cage was opened and all movements made by each subject were recorded with a digital camera, over a period of ten minutes (see van Dongen et al. 2010). All recordings were reviewed using SMPlayer© (version 0.8.0) and the information was tabulated using Jwatcher (version 1.0) (Blumstein et al. 2005).

Molecular sexing

DNA was extracted from the collected blood on FTA cards using a QIAGEN DNA extraction kit (Valencia, CA, USA) in order to determine sex. The gene fragments CHD-W (unique to females) and CHD-Z (found in both males and females) were amplified using polymerase chain reactions (PCR) with primers 2550 F and 2718R (Fridolfsson and Ellegren, 1999). The PCR product was run on a 3% agarose gel in a Fluorimager (Vilber Lourmat), to separate the gene fragments. The sex was determined by visualization of the gel, with males exhibiting bands only of CHD-Z and females having bands of both CHD-W and CHD-Z, respectively.

Statistical analyses

Variance sources in agonistic behaviors. We used mixed effect models (MM) to estimate the variance explained by individual identity on the observable behaviors. The models had as dependent variable each measured agonistic behavior and included random intercepts for individual identity (n=68), and sex, age, capture year, temperature during the trial, and observer identity as fixed effects (table 1).

Correlations analysis. We estimated Pearson correlation coefficients between-individuals from each individual's mean value for each observable behavior, in order to quantify the phenotypic associations between observable behaviors, morphometric attributes and exploratory behavior (electronic supplementary material, table S1).

Structural equation modelling (SEM). SEM is a multivariate statistical technique which uses the AIC value to assess the relative support for different *a priori* hypotheses, generated from structural relationships between measured variables and latent constructs (Kline et al. 2015). Based on the correlations between agonistic behaviors, we used SEM to determine if there is evidence of a latent variable that we defined as aggressiveness underpinning the expression of the set of observed agonistic behaviors. We tested the following hypotheses: (1) absence of any latent variable (figure 1A), (2) presence of a single latent variable affecting all behaviors in both intrusion contexts (figure 1B), (3) presence of two context-specific latent variables (figure 1C), and (4) presence of two correlated but context-specific latent variables (figure 1D). Finally, we set up two additional hypothesized structural equation models to gather evidence as to which set of agonistic behaviors (within intrusion context) more closely traced the existence of a latent behavioral variable to describe aggressiveness (figure 1E; 1F). In addition, we used SEM to evidence a latent variable for body size affecting the set of morphometric attributes measured (figure 3B).

Aggressiveness, exploration and body size relations

We used MM to assess the relationship between exploratory tendency and body size with the agonistic behaviors that best predicted aggressiveness (based on SEM, *see above)*. To this end, we included the exploratory tendency quantified via Billouin's diversity index (which is appropriate to describe the exploratory diversity when the probability of obtaining any sample is not equal; see Krebs 1989), and body size (characterized as morphometric measurement that best predicted body size, *see above*) as fixed effects in the model (table 2). Finally, we used MM to assess the relationship between aggressiveness, exploratory tendency and body size. To this end, aggressiveness is modelled using the agonistic behaviors that correlated with the latent variable aggressiveness (based on SEM, *see below*) as replicates of the same character (aggressiveness), and included the exploratory tendency and body size as fixed effects in the model (Table 3). In both models, individual identity is included as random effect.

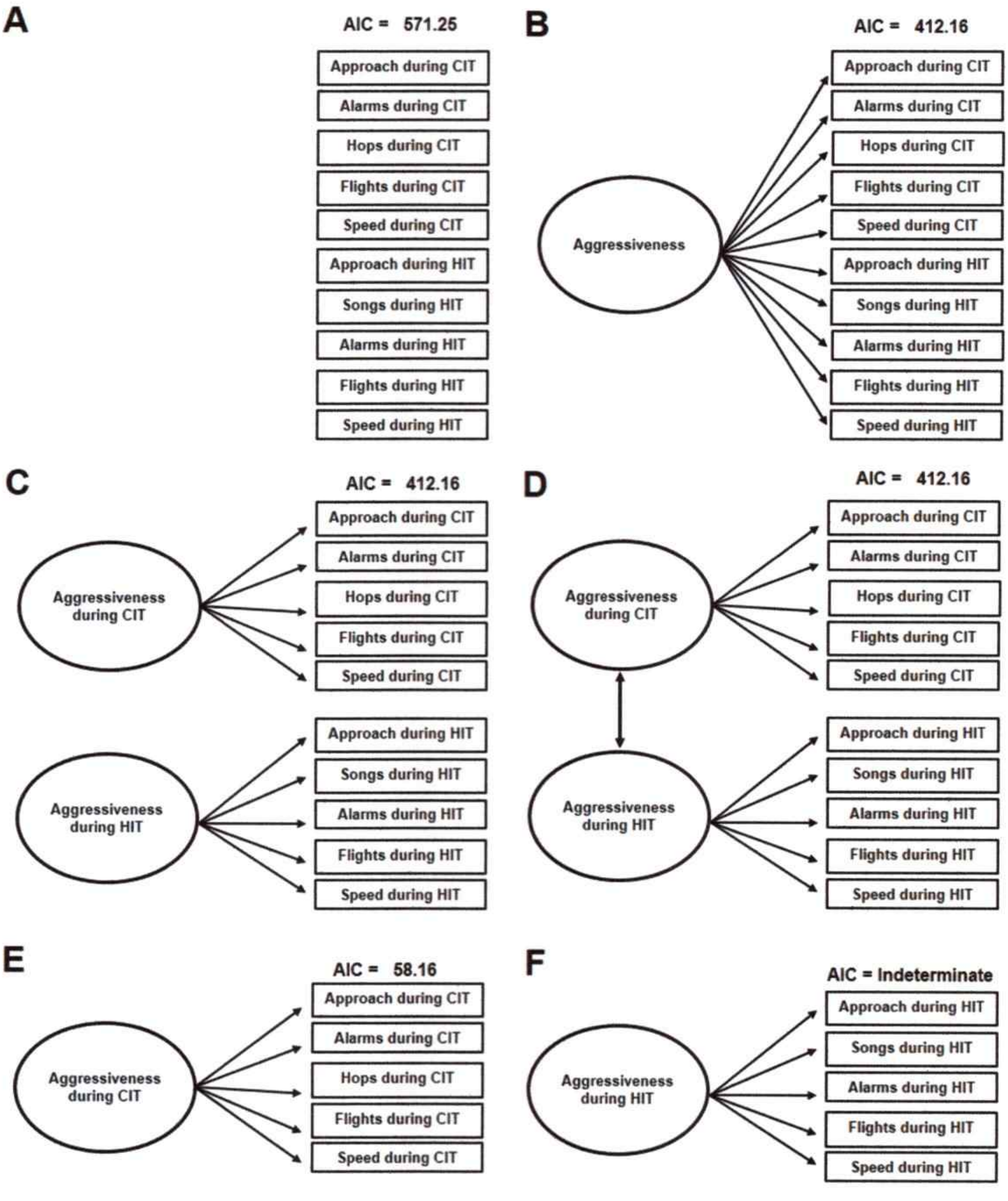

Figure 1. Six hypothesized structural equation models explaining correlation structure among agonistic behaviors during two intrusion contexts (conspecific (CIT) and human (HIT), respectively). Model (A) proposes a scenario where each combination of observable behaviors and intrusion contexts are underpinned by an independent factor (the null model); model (B) hypothesizes a latent variable is present across all observable behaviors regardless of intrusion context; model (C) hypothesizes latent variables separated for each intrusion context; model (D) hypothesizes that those latent variables are sub-units affected by an common factor. Model (E)

shows a hypothesized latent variable only at the con-specific intrusion context (CIT); and model (F) shows a hypothesized latent variable only at the human intrusion context (HIT), respectively.

All observed behaviors were standardized and the hypotheses were assessed with a 95% confidence interval (CI) for each parameter. We considered an effect as "strongly supported" when the CI did not overlap zero. Statistical analyses were performed in the R statistical environment v. 3.3.2 (R Core Team, 2016), using the MASS (Venables and Ripley 2002), SEM (Fox 2006) and MCMCglmm packages (Hadfield 2010). All mixed effect models were corroborated with lme4 packages (Bates 2010).

Results

Sources of variation in observable behaviors. The MMs showed that age, observer, temperature during trial, and capture year did not affect the observable behaviors. Sex had a significant effect only on the variable speed during CIT (β=0.55 CI=0.11,1.01). Individual identity explained a minor part of the phenotypic variance, and including random intercept for individual identity did not improve the model fit (table1). This may be caused by the modest amount of repeated measures per individual.

Table 1. Sources of variation in observable behaviors.

Observable behaviors	β (95% CI)					σ^2 (95% CI)	
	Sex	Age	Observer	T° trial	Year Cap.	Identity	Residual
Hops CIT	0.44 (-0.05,0.90)	-0.09 (-0.21,0.04)	-0.19 (-0.65,0.16)	0.04 (-0.02,0.12)	-0.04 (-0.05,0.04)	0.00 (0.00,0.00)	0.97 (0.70,1.29)
Flight CIT	0.32 (-0.05,0.72)	-0.01 (-0.12,0.10)	0.29 (-0.13,0.63)	0.02 (-0.04,0.09)	-0.06 (-0.42,0.31)	0.00 (0.00,0.00)	0.81 (0.58,1.07)
Alarms CIT	0.22 (-0.21,0.67)	-0.08 (-0.20,0.04)	0.29 (-0.17,0.70)	0.04 (-0.03,0.12)	-0.01 (-0.48,0.43)	0.01 (-0.00,0.05)	0.97 (0.67,1.30)
Approach CIT	0.34 (-0.06,0.81)	-0.02 (-0.15,0.11)	0.08 (-0.32,0.54)	0.05 (-0.01,0.13)	0.01 (-0.42,0.47)	0.01 (-0.00,0.03)	0.97 (0.67,1.39)
Speed CIT	0.55 (0.11,1.01)	-0.08 (-0.21,0.06)	-0.01 (-0.43,0.45)	0.01 (-0.07,0.08)	0.04 (-0.37,0.49)	0.03 (-0.00,0.03)	0.98 (0.64,1.36)
Hops HIT	0.00 (-0.00,0.6)	0.00 (-0.00,0.41)	0.00 (-0.00,0.38)	0.00 (-0.00,0.38)	0.00 (-0.00,0.19)	0.00 (-0.00,0.01)	1.00 (0.75,1.45)
Fligth HIT	0.00 (-0.00,0.51)	0.00 (-0.00,-0.15)	0.00 (-0.00,0.43)	0.00 (-0.00,0.23)	0.00 (-0.00,0.14)	0.02 (-0.00,0.17)	1.00 (0.69,1.41)
Alarms HIT	0.03 (-0.00,0.07)	-0.00 (-0.01,0.82)	0.00 (-0.00,0.76)	0.03 (-0.10,0.70)	0.01 (-0.04,0.40)	0.07 (-0.00,0.38)	1.00 (0.59,1.43)
Approach HIT	0.00 (-0.40,0.50)	-0.00 (-0.02,0.09)	-0.00 (-0.04,0.48)	0.02 (-0.00,-0.40)	0.03 (-0.04,0.49)	0.01 (-0.00,0.01)	1.00 (0.79,1.49)
Speed HIT	0.22 (-0.23,0.71)	0.01 (-0.13,0.14)	0.17 (-0.30,0.60)	0.04 (-0.03,0.12)	-0.18 (-0.59,0.30)	0.06 (-0.00,0.37)	0.98 (0.52,1.37)
Exploratory T.	0.01 (-0.03,0.70)	0.00 (-0.15,0.20)	-	-0.00 (-0.01,0.68)	0.06 (-0.30,0.57)	0.30 (0.00,1.00)	0.87 (0.22,1.43)

Between-individual correlations. Our results showed positive and significant correlations among most observable agonistic behaviors (electronic supplementary material, table S1). Individuals that, on average (across all agonistic observations), approached the intruders relatively closely, were also faster and performed more alarms, hops and flights, compared with individuals that, on average, maintained a greater distance (figure 2A). The mean correlation among agonistic behaviors during CIT and HIT was 0.31. When estimating these correlations with reference to the intrusion context, we found that the mean correlation among agonistic behaviors during CIT was 0.66. During HIT context, the mean correlation among agonistic behaviors was 0.45, however, only some correlations were significant (figure 2C). Regarding the correlation between exploratory tendency and the agonistic behaviors, we did not find any significant correlations (electronic supplementary material, table S1). Finally, the morphometric traits (bill, tarsus, wing length, and body mass) showed positive and significant correlations among them (electronic supplementary material, table S1). The mean correlation among these traits was 0.31. We did not find significant correlations between the morphometric traits and the observable agonistic behaviors (electronic supplementary material, table S1).

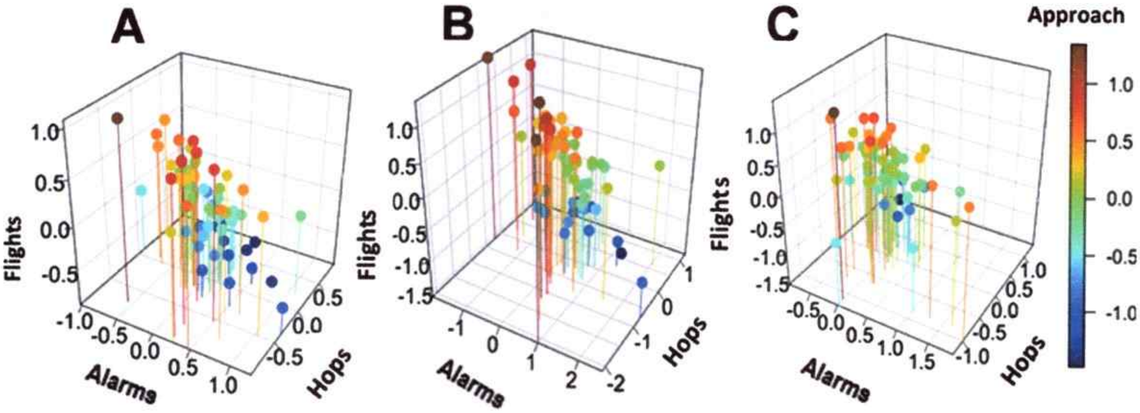

Figure 2. Representation of between-individual correlations among agonistic behaviors observed in wild Thorn-tailed rayaditos. The values plotted are the individual's values to each observable behavior, across all agonistic behaviors (A), and both intrusion contexts, CIT (B) and HIT (C), respectively.

Aggressiveness as a latent behavioral variable. The analysis of the hypothesized SEMs (based on AIC value) revealed support for the existence of a latent behavioral variable, affecting the set of agonistic behaviors observed (figure 1A; 1B). However, it was not possible to discriminate, based on AIC´s value, among models that hypothesized the presence of two un-correlated context-specific latent variables (figure 1C) versus two correlated context-specific latent variables (figure 1D). Comparing the models that hypothesized the presence of latent variables in the "within" context (figure 1E; 1F), our results indicated that the set of agonistic behaviors described in the HIT context (figure 1F) did not support the existence of any latent behavioral variable. However, the model based on the agonistic behaviors observed in the CIT context (figure 1E) supported the existence of a latent behavioral variable, at least when compared to the previously tested models (figure 3A). The SEM model based on morphometric attributes supports for the existence of a latent variable for body size, affecting the set of observed traits (Figure 3B).

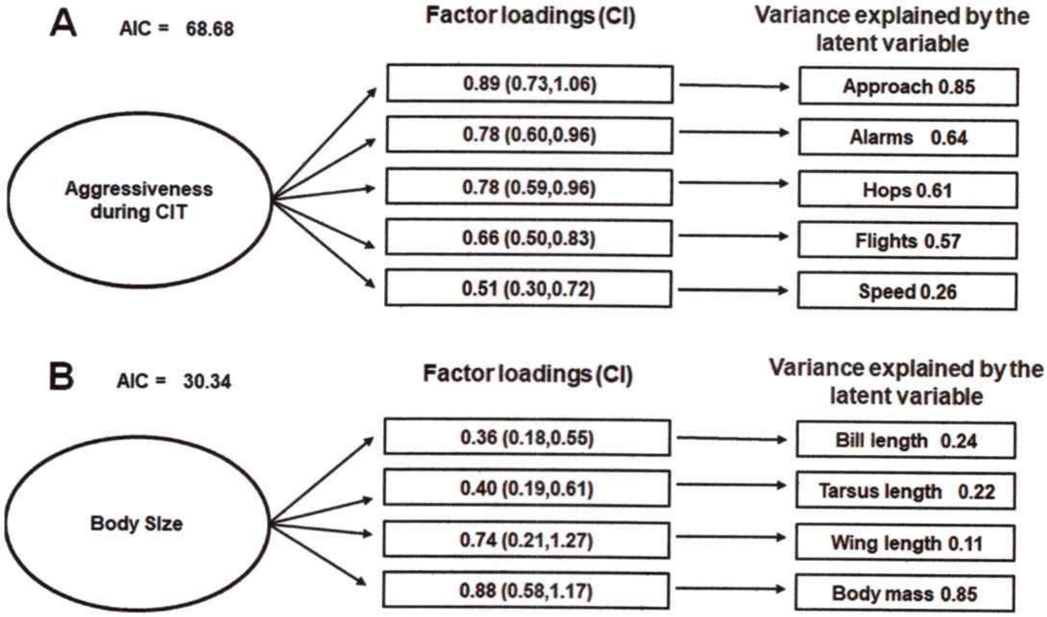

Figure 3. Parameter estimates from SEM that best support for the existence of a latent variable for aggressiveness (A) and body size (B).

Aggressiveness and its relationship with exploratory tendency and body size

Because observable agonistic behavior "approach" during CIT explains best the latent variable aggressiveness (figure 3A), we used it as proxy to characterize aggressiveness. In line with this, we selected the body mass as proxy of body size (figure 3B). Our results indicated that exploratory behavior is not a good predictor of aggressiveness (β=0.08; CI=

-0.12, 0.29); similarly, we found no relationship between body size and aggressiveness (β=0.01; CI= -0.22, 0.24) (Table 2).

Table 2. Sources of variation and fixed-effects in approach during CIT as proxy of aggressiveness.

	Aggressiveness (Approach during CIT)	
Random effects	**σ^2**	**(95% CI)**
Identity	0.10	(0.03,2.67)
Residual	0.77	(0.65,1.10)
Fixed-effect	**β**	**(95% CI)**
Exploratory tendency	0.08	(-0.12, 0.29)
Body mass	0.01	(-0.22, 0.24)

We expanded the analysis to model aggressiveness as the set of agonistic behaviors that best supported the presence of a behavioral latent variable (frequency of hops, flights, alarms, approach and speed during CIT), using this set as replicates of the same character (aggressiveness). Our results were similar to the previous model. Both the exploratory behavior (β=-0.04; CI= -0.19, 0.09), and the body size (β=0.02; CI= -0.05, 0.10) are not related with aggressiveness. However, the model indicated that individual identity explained part of the variance in aggressiveness significantly (σ2= 0.45; CI=0.29, 0.69) (table 3), reflecting the strong correlations between the different agonistic behaviors.

Table 3. Sources of variation and fixed-effects in aggressiveness.

	Aggressiveness	
Random effects	**σ^2**	**(95% CI)**
Identity	**0.45**	**(0.29,0.69)**
Residual	0.50	(0.42,0.58)
Fixed-effect	**β**	**(95% CI)**
Exploratory tendency	-0.04	(-0.19,0.09)
Body mass	0.02	(-0.05,0.10)

Discussion

In this study, we used an integrative approach to characterize aggressive responses of thorn-tailed rayaditos. We further assessed the relationship between aggressiveness, exploratory tendency, and body size. We used mixed-effect modelling, combined with structural equation modelling, to study the (co)variation between the measured behaviors and morphology. We found evidence for a latent behavioral variable, that we defined as "aggressiveness", linking five agonistic behaviors recorded during a con-specific intrusion context, but not during a human intrusion. These results suggest that stronger selection seems to select for functional integration under a conspecific threat. However, we did not find support for functional integration between aggressiveness and exploratory tendency or body size.

Variability sources in behavioral traits

Our results do not show differences in the agonistic behaviors and exploratory tendency between sexes, except in the variable "speed" during CIT, where males were faster than females in approach to intruder. Thus, we did not find sexual dimorphism in the aggressive or exploratory behavior in this species. Age is other variable that could influence behavior. For example, some studies have shown that agonistic behavior increase with age, until the beginning of senescence, after which they decrease progressively (Møller and Nielsen 2014, Ortega et al. 2017, Araya-Ajoy and Dingemanse 2017). However, other studies reported that these behaviors are not related to age (Montgomerie and Weatherhead, 1988). In general, age is difficult to estimate in wild populations, because the dispersal or death of the individual reduces the possibility to capture individual of known age. In this research, the age was estimated using the capture-mark-recapture when the individuals were banded being chicks (Clutton-Brock and Sheldon 2010). However, most individuals were captured for the first time when they were already adults. In these cases, we assumed that the individuals were one year old when they were first captured (Karlsson et al. 1986, Montalvo and Potti 1992, Botero-Delgadillo et al. 2017). Thus, our results showed that age is not related to observed behaviors. However, more accurate estimations of age are needed to obtain definitive results.

The influence of temperature during different trials, as well as capture year, were negligible. This is the expected result, because the study location shows low temperatures (range: –2 to 15.8° C) most of the year (Rozzi et al.2004), with a low fluctuation in general, both daily and seasonal.

Finally, the variance explained for individual identity was very small on observed behaviors, being these the expected results, because of a reduced number of repeated measures for each observable behaviors (two in thirteen individuals only) (Dingemanse and Dochtermann 2013). However, a significant variance explained by individual identity was detected when repeated measures of observable behaviors are available.

Phenotypic correlations and latent variable

We quantified the correlations among all the observed behaviors, and morphometric traits to determine the existence of a "latent variable" resulting from the functional integration pressures that cause adaptive correlations between behavior and morphology. However, we did not find a significant correlation between any agonistic behavior and exploratory tendency or morphology. Nevertheless, our results showed positive and significant correlations among agonistic behaviors (figures 2A; 2B; 2C), which were stronger among the agonistic behaviors recorded during CIT.

We tested six hypothesized scenarios to determine the presence of a latent behavioral variable called "aggressiveness" using SEM. These analyses suggested that the expression of the agonistic behaviors recorded during the HIT are not underpinned by the same mechanisms (for statistical argument see Kline et al. 2015). Based on this observation, we consider that the behavioral expression during HIT were not necessarily solely reflecting aggressiveness, likely because the "human" used as a stimulus could be reflecting boldness or aversion to predation risk. Furthermore, human intrusion does not represent a habitual environmental stimulus that will trigger a normal aggressive response. Human intrusions are usually used to measure anti-predatory behaviors (Hollander et al. 2008), it is likely that the less defined aggressive responses in this population under HIT can also be caused by the low predation exposure of individuals in this population (Ippi et al.2013).

Instead, we found a greater covariance between agonistic behaviors measured under the CIT and the latent behavioral unit, which did indeed reveal an underlying behavioral variable (figure 3A). These results suggest that a conspecific intrusion triggers a response where the different observables need to be tightly coordinated to be an effective adaptive response. This is expected because during reproductive season, aggressiveness toward a conspecific is a crucial behavior in the evolutionary history of birds (van Oers and Naghi 2013). Under this context, it is likely that stronger selection acts on functional integration of the observed agonistic behaviors. This contrast with the correlation patterns during HIT, which don't seems to require such a tight functional coordination of these behaviors. Thus, the functional integration of agonistic behaviors into a functional unit could depend to a large extent on environmental context.

Based on this result, we suggest caution when selecting tests to characterize aggressiveness, especially when describing the structure of aggressive behavior.

Moreover, we found a greater covariance between morphometric attributes and a latent unit called "body size" (figure 3B). This result is expected, due to the extensive evidence for a positive covariation among morphological attributes in different taxa (see e.g., Rising and Somers 1989, Gosler et al.1998, Calsbeek and Irschick 2007, Meiri 2010, Porto et al.2013).

Aggressiveness and exploratory tendency

Our results indicated that aggressiveness and exploratory tendency are not related, which suggests that both behaviors could be, in part, independent. Although these results are similar to other studies (Araya-Ajoy and Dingemanse 2014), it is important to note that other investigations have reported significant correlations between some agonistic behaviors and exploratory tendency (Verbeek et al. 1996, Dingemanse et al. 2007). These relations called "behavioral syndromes" describe the co-variation among different behaviors (Réale and Dingemanse 2010). However, environmental pressures seem to be very important on the detection of behavioral syndromes. For example, some studies have concluded that these syndromes are found mainly when populations are exposed to high predation pressure (Bell 2005), or higher than normal stress levels (Martins et al. 2007), and they could be more common in unpredictable environments (McElreath and Strimling 2006). The relationship aggressiveness-exploratory tendency is not detected in the study population, possibly because this population is not exposed to environmental pressures, like predation, that select for strong functional integration between aggressiveness and exploratory behavior (Bell 2005). Nevertheless, understanding the behavioral syndromes causes requires considering social, environmental and genetic information, and assessing this relation in populations exposed to different conditions.

Aggressiveness and body size

Our results indicated that aggressiveness and body size are not related. In line with this, it is reported that some individuals seem to be more aggressive than others, irrespective of their body size (Pavey and Fielder 1996). However, body size modulates aggressive encounters, where the largest individuals are generally dominating (Arnott and Elwood 2009, Morishita et al 2009). While the relationship between aggressiveness and body size be explained by the interaction between "resource-holding potential", competence and personality (Wilson et al. 2011), and the relative importance of the different processes could depend partly on the environmental context. This is because the decision of whether or not to display an aggressive behavior depends on several factors, including competitor density, resource density, and resource distribution in space and time (Brown 1964). Thus, the relationships between aggressiveness and body-size could arise depending on these factors. Accordingly, the mechanisms that determine the aggressive behavior could be in part independent of the body size, particularly when the resources are abundant, as arise in the study area. Thus, we suggest that understanding the relation between aggressiveness and body size requires including specific information about available resources, because it is likely that the body size is a good predictor of aggressiveness when those are limited.

Variance explained for identity in aggressiveness

We expanded our behavioral analysis using the agonistic behaviors recorded via CIT as repeated measures of aggressiveness, since this set of agonistic behaviors best supported the presence of a latent behavioral variable according to SEM analysis. Thus, in our MM, we included the identity of individuals as a random effect in the model. In this way, it was possible to determine that most of the variance in this trait was attributable to the identity of individuals, reflecting the strong within-individual correlation between agonistic behaviors displayed toward conspecifics. Thus, our results suggest that the characterization of "evolutionary behavioral characters" from functionally integrated observable attributes could be a novel alternative to quantify the variability attributable to the identity over these characters. Along with this, and despite the genetic aspects involved in the behavior are still unclear (van Oers and Mueller 2010), most researchers agree that personality traits like aggressiveness are modulated by pleiotropic effect of genes (van Oers and Sinn 2013). In that sense, this hypothesis would also explain in part the existence of functional integration among observed agonistic behaviors.

Concluding remarks

We identified a "latent behavioral variable" which we defined as aggressiveness, causing the coordinated expression of the agonistic behaviors that wild thorn-tailed rayadito express during agonistic interactions. Our results also suggest that the functional integration of these behaviors depend to a large extent on environmental context, where differences in functional pressures between contexts, affect the observed correlation between agonistic behaviors. Furthermore, we found no evidence that aggressive behavior is related to exploratory tendency or body size in this population. The results of this study highlight the importance of studying the correlations between behaviors and morphology in different contexts to gain a deeper understanding about the causes and consequences of the correlated expression of behaviors and morphology from a functional perspective.

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Data accessibility statement: Should the manuscript be accepted, the data supporting the results will be archived in an appropriate public repository such as Dryad or Figshare and the data DOI will be included in the article.

Author contributions: YP conceived the idea, conducted the research, analyzed data and wrote the manuscript. PEH assisted with the fieldwork, carried laboratory work and edited the manuscript. EBD participated in the design of field protocols and carried laboratory work. GPS assisted with the fieldwork and edited the manuscript. YAA provided assistance with the analysis and edited the manuscript. RAV supervised the research, participated in the design of protocols and edited the manuscript.

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Characterizing the relationship between aggressiveness, exploratory behavior and body size in Thorn-tailed rayadito.

Yanina Poblete, Pamela Espíndola-Hernández, Esteban Botero-Delgadillo, Gabriela Paz Südel, Yimen Araya-Ajoy, and Rodrigo A.Vásquez.

Electronic Supplementary Material

Contents

Table S1. Correlation matrix among agonistic behaviors, exploratory tendency and morphometric measured.

Figure S1. Photograph Thorn-tailed Rayadito.

Figure S2. Photograph of the conspecific intrusion test used to record the aggressiveness.

Figure S3. Photograph of the experimental aviary used to record the exploratory tendency.

Table S1. Correlation matrix among agonistic behaviors, exploratory tendency and body size

	Hops.CIT	**Flight.CIT**	**Alarms.CIT**	**Approach.CIT**
Hops.CIT	1.0000000000	0.52069177*	0.56039132*	0.77596804*
Flight.CIT	0.5206917704*	1.00000000	0.73435310*	0.61687982*
Alarms.CIT	0.5603913234*	0.73435310*	1.00000000	0.74984204*
Approach.CIT	0.7759680406*	0.61687982*	0.74984204*	1.00000000
Speed.CIT	0.5931010709*	0.48014629*	0.30897252*	0.36181701*
Hops.HIT	0.1293023731	0.08788757	0.11882168	0.17882246
Flight.HIT	-0.1022238475	0.11326347	0.06699765	0.01619412
Alarms.HIT	0.1239361922	0.04418032	0.05519224	0.11427403
Approach.HIT	0.0971757441	0.12138678	0.16784429	0.22978766
Speed.HIT	0.0675426844	0.09447612	0.10344187	0.14199814
Exp.Tend.	0.0283162997	0.20874021	0.12981818	0.13214747
Bill length	0.0509419367	0.02793476	-0.01789191	0.10246553
Tarsus length	0.0133577809	-0.01235871	-0.01183821	-0.04295509
Wing length	-0.0369533344	0.12157058	0.09552708	-0.01324867
Body.Mass	0.0737732669	0.17501892	0.07163827	0.13769437
CPmorph1	0.0443026705	0.11658527	0.04831527	0.07645866

	Speed.CIT	**Hops.HIT**	**Flight.HIT**	**Alarms.HIT**
Speed.CIT	1.000000000	0.31689282*	-0.009778914	0.295103998*
Hops.HIT	0.316892819*	1.00000000	0.338272994	0.271058061*
Flight.HIT	-0.009778914	0.33827299	1.000000000	0.231006314*
Alarms.HIT	0.295103998*	0.27105806	0.231006314*	1.000000000
Approach.HIT	-0.018493472	0.08525025*	0.277667792*	0.135039476
Speed.HIT	0.260646107*	0.95623646*	0.577529341*	0.294676967*
Exp.Tend.	-0.008010201	-0.18869509	-0.037922452	-0.188660009
Bill length	0.073018571	-0.26939888	-0.124799686	0.071498040
Tarsus length	0.015424584	-0.06808478	0.148535435	-0.127237277
Wing length	0.025529859	-0.04237491	-0.098535103	-0.178056432
Body.Mass	0.081668874	-0.12212725	-0.059587620	-0.059501511
CPmorph1	0.072776449	-0.17771110	-0.042010928	-0.096785652

	Approach.HIT	**Speed.HIT**	**Expl. Tend.**
Approach.HIT	1.00000000	0.16823583	0.16419238
Speed.HIT	0.16823583	1.00000000	-0.18087251
Expl.Tend.	0.16419238	-0.18087251	1.000000000
Bill length	0.21717346	-0.26116434	0.342790543*
Tarsus length	0.07120156	-0.03256995	-0.009881697
Wing length	0.14910643	-0.06719249	0.071164028
Body.Mass	0.21241438	-0.14062584	0.08619307
CPmorph1	0.23158577	-0.17766693	0.177354207

	Bill length	**Tarsus length**	**Wing length**
Exp.Tend.	0.34279054*	-0.009881697	0.071164028
Bill length	1.00000000	0.109214091	0.086193069
Tarsus length	0.10921409	1.000000000	0.446912632
Wing length	0.177354207	0.086193069	1.000000000
Body.Mass	0.50434839*	0.417638127*	0.369451712*
CPmorph1	0.61285242	0.696006904	0.623636582

	Body.Mass
Body.Mass	1.00000000
CPmorph1	0.86054064

*** $p<0.05$**

Figure S1. Photograph of Thorn-tailed Rayadito (*Aphrastura spinicauda)* taken in Navarino Island, Southern Chile. Photograph by Yanina Poblete.

Figure S2. Photograph of the Conspecific intrusion test (CIT) used to record the aggressiveness face to conspecific taken in Navarino Island, Southern Chile. Photograph by Patricio Castwell.

Figure S3. Photograph of the experimental aviary used to record the exploratory tendency taken in Navarino Island, Southern Chile. Photograph by Yanina Poblete.

Heritability in aggressiveness in an endemic bird of the sub-Antarctic rainforests: A study based on genetic markers.

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MANUSCRITO ENVIADO A JOURNAL ANIMAL ECOLOGY (JAE-2017-00824)

Abstract

1. Behavioral heritability has been studied in a number of well-known laboratory animal populations. However, fewer studies have examined heritability of behavioral traits in wild populations, mainly because dispersal and/or the death of individuals reduces the possibility of obtaining a known pedigree, which makes difficult its estimation by classic methods.
2. However, the emerging availability of genetic markers in wild populations has allowed to calculate heritability estimates based on those markers, using genetic kinship relationships matrices combined with mixed models. Using this approach to estimating heritability, some studies have produced similar results to those that used a known pedigree.
3. We characterized aggressiveness in 68 Thorn-tailed Rayaditos (*Aphrastura spinicauda*) inhabiting a sub-Antarctic rainforest on Navarino island (55°40¨S, 67°40¨W) in the south of Chile. We used structural equation modeling (SEM) to detect a latent behavioral unit that we defined as "aggressiveness". Thirteen species-specific polymorphic microsatellite loci markers were used to estimate the narrow-sense heritability (h^2) in this trait, from a mixed model containing random additive genetic effects whose covariance structure was estimated from a relatedness coefficient matrix based on these 13 markers.
4. We detected a latent behavioral unit to characterize aggressiveness from observations of five agonistic behaviors recorded during a conspecific intrusion test, and derived an estimate for h^2 of 0.33.

5. Our results not only supported the presence of a latent behavioral unit characterizing aggressiveness, but also produced an estimation of h^2 similar to those reported in other studies, in which the h^2 in aggressiveness was estimated via phenotypic variance analysis using a known pedigree. In summary, we suggest that the approach we used could be a novel alternative to estimate behavioral h^2 in wild animal populations, mainly when pedigree information is limited.

Key words: Aggressiveness, narrow-sense heritability, genetic markers, mixed-effect model, wild population, Thorn-tailed rayadito.

Introduction

Aggressiveness is a behavior which plays a crucial role in the life-history of birds because it allows them to acquire resources, dominate territory and obtain mates (van Oers and Naguib 2013). It has been described mainly through observation of the agonistic behaviors deployed by birds during dominance, docility or territorial intrusion tests (Verbeek et al. 1996, Garamszegi et al. 2009, Duckworth 2006a, Kralj-Fiser et al. 2007, Blas et al. 2007, Ippi et al. 2013). Based on those tests, it has been demonstrated that agonistic behaviors differ consistently between individuals across time or context (Verbeek et al. 1996, Duckworth 2006a, Pavlova et al. 2007), being usually studied as animal personality traits (Wilson 1998, Gosling and John 1999, Drent et al. 2003, Bell and Stamps 2004, Bergmuller and Tabosky 2007, Réale et al. 2007). Thus, it is observed that agonistic behaviors are repeatable (Kralj-Fiser et al 2007, Garamszegi et al. 2006b, Araya-Ajoy and

Dingemanse 2014), and able to influence the fitness of individuals (Smith and Blumstein 2008).

Agonistic behaviors need to be expressed in a coherent way in order to be effective mediators of agonistic interactions. Therefore, their expression needs to be correlated in a particular way in order to be used as a functional unit. Thus, notwithstanding the assumption that agonistic behaviors are parts of a "functional unit" shaped by evolutionary processes (Gould et al. 1978), an exploration of the adaptive significance of a particular trait could require a specific approach; in this case, evaluating the relationship between agonistic behaviors and linking it to a functional unit recognizable as "aggressiveness" (Araya-Ajöy and Dingemanse 2014). In this context, the "evolutionary character hypothesis" proposes the existence of functional units called "evolutionary characters" which, identified through the correct characterization of their observable parts, could represent the ultimate meta-units exposed to selective processes (Wagner 2000, Houle 2001, Wagner and Stadler 2003, Wagner et al. 2007). Based on this hypothesis and using structural equation modeling (SEM), it has been possible to support the existence of a functional behavioral unit to describe "aggressiveness" (Araya-Ajöy and Dingemanse 2014; Poblete et al. Chapter I), suggesting that this aggressiveness could be acting as an "evolutionary character", understood through the functional integration of its observable parts (the agonistic behaviors) into a latent construct (aggressiveness) (Wagner 2000, Pigliucci 2003, Kline et al. 2015).

In order to explore the adaptive nature of "aggressiveness" it would not only be necessary to deepen our knowledge regarding the structure of this behavior, but also to estimate its narrow-sense heritability (h^2) in wild populations. Heritability is an important parameter in evolutionary biology, because it estimates the proportion of phenotypic variance present in a population, due to additive genetic effects (Fisher, 1918, Wright, 1920); thus permitting an understanding of the potential ability of a population to evolve in response to novel selective challenges (Jacquard 1983, Nyquist and Baker 1991, Ritland 1996, Visscher et al. 2006, Holland et al. 2010, Sillanpaa 2011). In fact, agonistic behaviors have been shown to be heritable in several well-known captive animal populations, where h^2 is estimated by relating the phenotypic covariance with the proportion of shared genes by descent between relatives, using a kinship relationship which is known via pedigree data (Bakker 1994, Weiss et al. 2002, Fairbanks et al. 2004, Rogers et al. 2008). Much fewer studies have examined h^2 in agonistic behaviors in wild animal populations, mainly because the dispersal and/or death of individuals reduces the possibility of obtaining individuals with a known pedigree, complicating its assessment by classic methods (Boake et al. 2002, Duckworth and Badyaev 2007, Araya-Ajoy and Dingemanse 2017). Although captivity conditions have advantages with respect to control and replication opportunities, it is important to estimate h^2 in wild animal populations for several reasons. Firstly, heritability is essential to understanding the evolutionary nature of behavior (Boake et al. 2002). Secondly, heritability depends on environment context (Riska et al.1989, Dingemanse et al.2002, Drent et al. 2003), and thirdly, it is unlikely that selection operates in the same way on the heritable variation as it would under wild conditions (Merilä and Sheldon 2001). Thus, natural selection might produce distinct patterns of genetic variation in aggressiveness depending on the environmental conditions, with corresponding differences in selection between wild and somewhat artificial captive conditions (Van Oer and Sinn 2013).

Currently, increasing availability of genetic markers in wild populations is allowing the assessment of h^2 using marker-based relatedness coefficients (Csillery et al. 2006). Altogether these methods are known as 'pedigree-free', and include: i) estimating heritability via covariance between pairwise phenotypic similarity and pairwise relatedness, otherwise known as the Ritland method (Ritland 2000); ii) classification of individuals into known classes of relatedness (for example siblings verses unrelated), in conjunction with the use of mixed models (Mousseau et al. 1998); iii) complete pedigree reconstruction from relatedness coefficients, in conjunction with the use of the animal model (mixed model) (Blouin et al.2003, Jonson et al. 2010); iv) the "multilocus association method", derived from genomic selection (Sillanpaa 2011); and finally, v) the "mixed model method" using the full pairwise relatedness matrix estimated via molecular markers (Lynch and Walsh 1998, Kruuk 2004, Goddard 2009, Strandén and Garrick 2009). The accuracy of these methods has been analyzed through comparing h^2 estimations obtained from both empirical and data simulations using classic and pedigree-free methods, and it appears that the estimation of heritability by both Ritland (i) and pedigree reconstruction methods (ii and iii) worsen the estimations. On the other hand, estimations of h^2 via the multi-locus association method derived from genomic selection (iv), and mixed models using marker-based pairwise relatedness (v) are promising. In fact, it has been demonstrated that mixed models using marker-based pairwise relatedness can be applied to any complex traits where multiple replicates of individual genotypes can be scored (Gay et al 2013, Kruijer et al. 2015).

Within this context, we proposed to estimate h^2 in aggressiveness based on genetic markers in a wild animal population, using as our subject species the thorn-tailed rayadito, *Aphrastura spinicauda* (Furnariidae: Passeriformes), an endemic bird of the sub-Antarctic rainforests of South America (Remsen 2003) (electronic supplementary material, Fig. S2). The thorn-tailed rayadito is a small suboscine (~11 g), secondary cavity nesting, socially monogamous bird, with an apparent absence of sexual dimorphism. Males and females participate equitably in the raising of offspring (Moreno et al. 2007, Botero-Delgadillo et al. 2015, Espíndola-Hernández et al. 2017). Thorn-tailed Rayadito usually lay one clutch per breeding season, which begins in the austral spring (Moreno et al. 2005). During this season, it is possible to recognize a set of agonistic behaviors deployed by pairs of thorn-tailed rayadito, including approaches toward intruders in their territory (e.g., other animals or humans) and alarm calls (Ippi and Trejo 2003, Ippi et al. 2011, 2013, 2017). Based on these observable behaviors and using SEM, we expected to recognize a latent behavioral unit to describe "aggressiveness" as a functional unit, and to estimate h^2 in this trait from a mixed model containing random additive genetic effects whose covariance structure is estimated from a relatedness coefficients matrix based on markers. Thus, we hypothesize that aggressiveness acts as functional unit, in which case it should be, in part, heritable.

Methods

Study location. The study site was located in the sub-Antarctic rainforest of Navarino island (UNESCO Cape Horn Biosphere Reserve), Southern Chile (55°4′ S, 67°40′ W).

Vegetation is characterized by deciduous Magellanic forest, whose typical species are Lenga Beech (*Nothofagus pumilio*), and Ñirre Beech (*Nothofagus antarctica*) (Rozzi et al. 2006). In general, this area is exposed to strong winds and low temperatures (range: –2 to 15.8° C), with precipitation in the form of rain and snow falling every month of the year (see Rozzi et al. 2004, Rozzi and Jiménez 2014).

General field procedures. The study was carried out over the reproductive season, from October to late December, during the years 2014 and 2015. Because rayaditos are secondary cavity nesters, we used nest boxes, which were monitored weekly until they were occupied (Moreno et al. 2005, 2007). The adults were then captured between 7:30 am and 12:00 pm in the nest box (n=68), 12 or 13 days after the hatching of their offspring, and banded with both numeric metal and colored bands (National Band and Tag Co., Newport, Kentucky, USA, or Split Metal Bird Rings, Porzana Ltd, UK or with a numbered band provided by the *Servicio Agrícola y Ganadero* (Chilean Agricultural and Livestock Service), Chile). The bill and tarsus length were measured to the nearest 0.01 cm with digital calipers, the wings were measured with a stopped rule, and mass was recorded in grams (± 0.1 g). Before releasing the birds, a small blood sample (ca. 17 μL) was taken from the brachial vein, and stored in FTA cards (Whatman®) for posterior molecular analysis (see Quirici et al. 2014, Yañez et al. 2015, Botero-Delgadillo et al. 2017).

Recording Agonistic behaviors. We used two different intrusion context (human and con-specific), to characterized aggressiveness in thorn-tailed rayadito:

1. Human Intrusion Test (HIT). Thirteen days post-hatch, a focal human was placed three meters in front of the nest-box. Over a three-minute period, two observers recorded the frequency of hops and flights, and alarm sounds using a digital voice recorder (Ippi et al. 2013, Botero-Delgadillo et al. 2017). The "approach" variable was recorded as the minimum distance between the birds and the focal human as measured by laser rangefinder, and the "speed" variable, was estimated as the number of hops and flights performed during the first minute of the test (Poblete et al.Chapter I)

2. Conspecific Intrusion Test (CIT). Fifteen days post-hatch, a conspecific model was placed three meters in front of the nest-box. Two observers recorded during eight minutes (two minutes of silence, three minutes of playback of thorn-tailed rayadito vocalizations, and three minutes of silence) the frequency of hops and flights, and alarm sounds using a digital voice recorder (see Ippi et al. 2013, Botero-Delgadillo et al. 2017). The "approach" variable was estimated as the total amount of time the individual remained within 1 m of the conspecific intruder. The "speed" was calculated as the number the hops and flights performed during the first minute of playback in the test (Poblete et al.Chapter I).

Molecular analysis

DNA was extracted from the collected blood on FTA cards using a QIAGEN DNA extraction kit (Valencia, CA, USA), and the individuals were genotyped at 13 polymorphic microsatellites loci (supplementary material, table S1.), using eight species-specific markers, As1, As7, As18, As25-1, As25-5,As25-8, As25-10, and As25-14 (*see* Yañez et al. 2015; Botero-Delgadillo et al. 2017), and five cross-species amplifying markers: Asµ 15_ZEST,CcaTgu23 (Olano-Marín et al. 2010), Tgu06 (=CK307697), Tgu05 (=DV946651) (Slate et al.2007), and marker ZF_AC138573 (van Oosten et al. 2016). The genetic relatedness included 12 of 13 markers, which showed no significant deviations from the Hardy-Weinberg equilibrium (HWE; all P>0.1) and the frequencies of null alleles were below 0.05. Maximum likelihood coefficients of pairwise genetic relatedness (*r*) were calculated using the ML-Relate software (Kalinowski et al. 2006, *see* Botero-Delgadillo 2017 for details).

Because thorn-tailed rayadito sexual dimorphism is not identifiable by observation, we used molecular techniques, including the primers 2550 F and 2718R (Fridolfsson and Ellegren, 1999) to amplify the gene fragments CHD-W (unique to females) and CHD-Z (found in both males and females) using polymerase chain reactions (PCR). The PCR product was run on a 3% agarose gel in a Fluorimager (Vilber Lourmat), to separate the gene fragments, and sex was determined by visualization of the gel, with males exhibiting bands only of CHD-Z and females having bands of both CHD-W and CHD-Z, respectively.

Statistical analyses

Correlations analysis. To describe the initial relationships among agonistic behaviors, we calculated correlation coefficients for each observable behavior (electronic supplementary material, table S2; but see Poblete et al. Chapter I for details), in order to determine the phenotypic relationships among the observed behaviors.

Structural equation modelling (SEM). SEM is a multivariate statistical technique based on AIC value, allowing to assess the relative support for different *a priori* hypotheses, generated from structural relationships between measured variables and latent constructs (Kline et al. 2015). Based on the results of the correlations analysis described above, we used SEM to determine if "aggressiveness" acts as a latent behavioral unit, considering the set of the agonistic behaviors we had recorded, testing the following *a priori* hypotheses: (i) absence of any latent variable (supplementary material, Fig. S1A); (ii) presence of a single latent variable affecting all behaviors in both intrusion contexts (supplementary material, Fig. S1B); (iii) presence of two context-specific latent variables (supplementary material, Fig. S1C); and (iv) presence of two correlated but context-specific latent variables (supplementary material, Fig. S1D). Finally, we set up two additional hypothesized structural equation models, to gather evidence as to which set of agonistic behaviors (within each intrusion context) more closely traced the existence of a latent behavioral unit to describe aggressiveness (supplementary material, Fig. S1E; S1F) (Poblete et al. ChapterI).

Mixed-effect model (MM). We used a MM to estimate h^2 in aggressiveness, modeled using the agonistic behaviors that best supported a latent behavioral unit as replicates of the same behavioral character trait (aggressiveness). The additive genetic effects were included as a random effect in the model, estimated from the relatedness coefficients matrix based on markers.

Before setting up the analysis, all recorded behaviors were standardized and with the MM we estimated the variance explained by individual identity on the recorded behaviors, including this variable as a random effect in the models. In addition, we included body size (characterized as a component variable obtained by Principal Component Analysis

(PCA) from the set of morphometric traits measured, supplementary material, table S3), sex, age, capture year, environmental temperature during the trial, and observers as fixed effects (supplementary material, table S4).

Hypotheses were assessed with a 95% confidence interval (CI) for each parameter, and we considered an effect as "strongly supported" when the CI did not overlap zero. The statistical analyses were performed in the R statistical environment v. 3.3.2 (R Core Team, 2016), using the MASS (Venables and Ripley 2002), SEM (Fox 2006), MCMCglmm (Hadfield 2010); and Heritability (Kruijer et al. 2016) packages.

Results

Initial investigation suggested that individual identity, body size, sex, age, capture year, environmental temperature during the trial, and observers are unrelated to the observed behaviors (supplementary material, table S4).

Aggressiveness as a latent behavioral unit. Our results indicated non-zero correlations among most of the recorded agonistic behaviors (supplementary material, table S2). Individuals that on average (across all agonistic observations) approached the intruders relatively closely, also tended to be "faster" in the sense of displaying a greater number of hops and flights during the first play-back minute, and to perform more alarm sounds, than individuals that on average maintained a greater distance. Assessing these relationships with reference to the intrusion context, we found positive correlations among observable agonistic behaviors during CIT (mean correlation=0.66; Fig. 1A; supplementary material, table S2). However, although similar observations were detected in the HIT (Fig. 1B), only some correlations were significant (mean correlation=0.31; supplementary material, table S1).

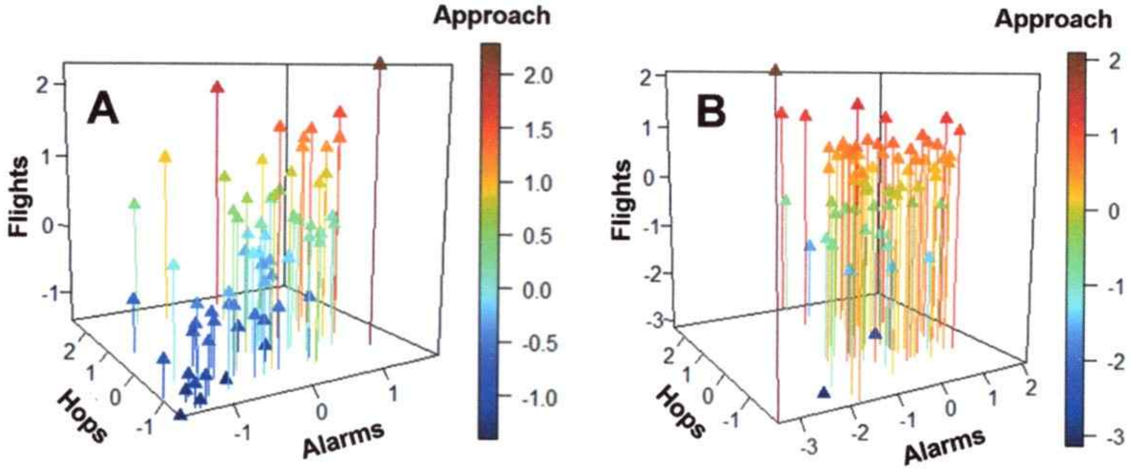

Figure 1. Representation of between-individual correlations among agonistic behaviors observed in wild thorn-tailed rayaditos. The values plotted are the individual's values for each observable behavior, during both intrusion contexts: (A) CIT, and (B) HIT, respectively.

Analysis of the hypothesized SEMs (based on AIC value) revealed support for the existence of a latent behavioral unit affecting the set of agonistic behaviors observed, although only in the CIT context (supplementary material, Fig. S1E), which supported more strictly the existence of a latent behavioral unit, at least when compared to the previously tested models (Fig. 2).

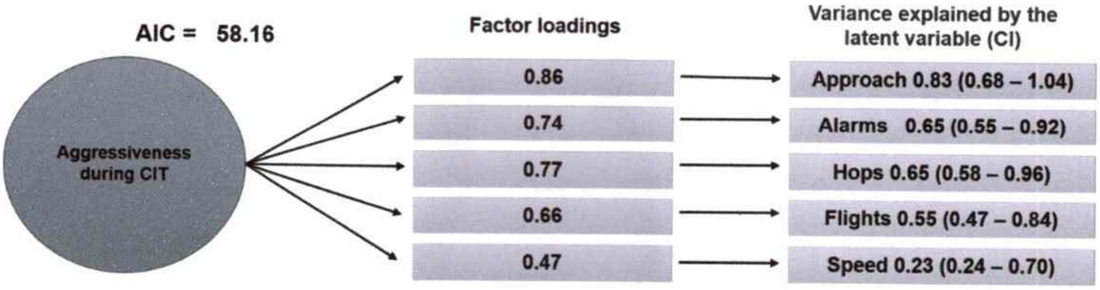

Figure 2. Parameter estimates from SEM that best fitted the data.

Narrow-sense heritability (h^2) in aggressiveness

The narrow-sense heritability model showed an h^2 value = 0.33 (CI=0.22, 0.43) in aggressiveness, with 0.32 additive variance and 0.65 environmental variance.

Discussion

In this research we used field data to characterize aggressiveness as a functional unit, and assessed its h^2 in a wild thorn-tailed rayadito population. Analysis of the data was carried out using mixed-effect modeling, combined with correlations and structural equation modeling. Analysis of the results provided evidence for a latent behavioral unit called "aggressiveness", linking the five agonistic behaviors recorded during a con-specific intrusion context, and we were able to determine that the trait is partially heritable in this population.

Aggressiveness as functional unit

The characterization of behavioral units as being based on an evolutionary character is a novel approach to deepen our understanding of the adaptive nature of behavior, mainly because it evidences the phenotypic relations among observable behaviors; showing a possible functional coherence among them (Araya-Ajoy and Dingemanse 2014). Based on this, we first detected non-zero correlations among agonistic behaviors (Figs. 1A; 1B), where we found stronger correlations among the agonistic behaviors recorded during the CIT. Then, we tested hypothesized scenarios to determine both the structural relationships among agonistic behaviors and the presence of a latent behavioral unit (i.e., aggressiveness) via SEM. Our results suggested that the agonistic behaviors recorded during the HIT do not reveal an underlying behavioral unit, because of limited covariance among the observable variables and the latent behavioral unit (for statistical argument see Kline et al. 2015). Based on this observation, we consider that the HIT was not the most appropriate test to capture the presence of a latent behavioral unit for aggressiveness. In the case that aggressiveness is considered an adaptive characteristic, two possible alternatives could explain this result. Firstly, it is possible that the human used as a stimulus could be inducing less defined aggressive responses, because human intrusion does not represent an habitual environmental stimulus which would thus automatically be capable of triggering an aggressive response. Secondly, it remains difficult to quantify any effects on the observed behavior caused by the monitoring, manipulation and release process. Notwithstanding this however, the human as an intruder is often used to measure anti-predatory behaviors (Hollander et al. 2008). Hence, to address the question of how the human is perceived by the subject species, it is likely that the less defined aggressive responses to humans in this thorn-tailed rayadito population arise because they are less affected by predator pressure, given that, for the Navarino island population at least, they have no native mammalian predators (Ippi et al. 2013). To validate this hypothesis it would be necessary to assess if anti-predator behavior (via the HIT) is more defined in populations where predation pressure is high, in particular due to native predators (e.g. in other regions of Chile such as Fray Jorge, Manquehue, or Chiloé) (Ippi et al. 2011, 2013, Quirici et al. 2014, Botero-Delgadillo et al. 2017). For these reasons, we cannot support the use of this test to describe the structure of the aggressiveness in this study (see also Ippi et al. 2013). Instead, we found greater covariance between the agonistic behaviors recorded under the CIT and the latent behavioral unit, which did indeed reveal an underlying behavioral unit (Fig. 2). These results suggest that a conspecific is better used as stimulus, and is more effective in triggering aggressiveness as a behavioral adaptive response, because during the reproductive season such aggressiveness toward a conspecific is a crucial behavior in the evolutionary history of the birds (van Oers and Naghi 2013). In line with this, an expanded behavioral analysis conducted by Poblete et al. (Chapter I), using the set of agonistic behaviors best supported the presence of a latent behavioral unit according to SEM as repeatable measures of aggressiveness, detected that most of the variance in this trait was attributable to the identity of individuals ($\sigma2= 0.45$; CI=0.29, 0.69), thus, reflecting the strong within-individual correlation between agonistic behaviors displayed toward conspecific.

Based on these results, is likely that natural selection favors phenotypic integration among agonistic behaviors toward conspecific, giving rise to a functional unit subject to selection (aggressiveness). Thus, we suggest caution when selecting tests to characterize aggressiveness, especially when the focus is on describing the structure of this behavior.

Narrow-sense heritability in aggressiveness

The adaptive nature of aggressiveness as a functional unit subject to evolutionary change requires that part of its variation must be heritable (Endler 1986). Supporting this, several studies have described h^2 estimates in agonistic behaviors ranging from 0.21 to 0.89, this being broadly consistent across studies on behavioral heritability for several taxa (van Oers and Sinn, 2013). However, most h^2 estimates in agonistic behaviors have been obtained from studies where the data is collected from individuals of known pedigree in captive populations, and it is therefore likely that these estimations could be not a good predictor of heritability in wild conditions, as heritability is strongly dependent on environment context (Roff and Mousseau 1987, Riska et al. 1999, Dingemanse et al. 2002, Drent et al. 2003).

As part of our preliminary analysis, we were able to discard the possibility that age, sex, body size, capture year, temperature during trials or observers were affecting our observations. Any of these variables could potentially exert an influence on phenotypic variance, and thus affect h^2 estimations (Réale et al. 1999, Coltman et al. 2005, Kruuk et al. 2008). Then used agonistic behavior linked to a latent behavioral unit defined as aggressiveness as replicates of the same evolutionary character trait, and a relatedness coefficients matrix based on markers, to estimate h^2 (Kruijer et al. 2015, Kruijer et al. 2016). In this way, it was possible to derive a value of 0.33 for h^2 in aggressiveness, this result being similar to other studies in which h^2 was estimated using individuals of known pedigree and varied sets of observed behaviors as proxies for aggressiveness in wild populations (Bakker 1994, Araya-Ajoy and Dingemanse 2017). This is possible given that there is substantial additive genetic variation in aggressiveness to respond to selection in this population, being this variation in part responsible of phenotypic variation observed on the trait under the environmental conditions of the study place.

Although the genetic basis responsible of behavior is still unclear, it is widely accepted that aggressiveness and other behavioral traits could be modulated by pleiotropic genes (van oer et al. 2005, van Oers and Mueller 2010). Similarly, the functional integration among observable agonistic behaviors in a functional unit partially heritable, could be the result of this modulation. However, it is possible that different h^2 estimations in that trait are detected, depending mainly on the environmental context. For this reason, more heritability studies are necessary, including data across time and from different populations under different environmental conditions (Dingemanse et al. 2009).

Concluding remarks

Our approach suggests that the agonistic behavior deployed in a con-specific intrusion context act as a functional unit we called "aggressiveness", which could act as "evolutionary character" due to its variability and heritability. Thus, this result support the use of relatedness coefficient matrices based on markers combined with MM as a proper methodology to explore h^2 in complex traits such as behavior, supporting that the replicates of each genotype are part of the same trait.

In summary, we suggest that behavioral unit recognition, along with h^2 estimations based on markets, could bring new possibilities for characterizing the behavior from an evolutionary point of view, particularly in wild species.

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Author contributions: YP conceived the idea, conducted the research, analyzed data and wrote the manuscript. EBD participated in the design of field protocols and carried laboratory work. PEH assisted with the field work and carried laboratory work. GPS assisted with revision audiovisual. RAV supervised the research and edited the manuscript.

Data accessibility statement: Should the manuscript be accepted, the data supporting the results will be archived in an appropriate public repository such as Dryad or Figshare and the data DOI will be included in the article.

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Heritability in aggressiveness in an endemic bird of the sub-Antarctic Rainforests: A study based on genetic markers

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Electronic Supplementary Material

Contents

Table S1. Details of 13 polymorphic microsatellite loci and one chromosome-linked marker (Ps/P) for thorn-tailed rayadito.

Table S2. Correlation matrix among agonistic behaviors in thorn-tailed rayadito

Table S3. Eigenvalues of correlation matrix among morphometric traits to characterize body size.

Table S4. Sources of variation in observable behaviors.

Figure S1: Hypothesized structural equation models explaining correlation structure among agonistic behaviors during two intrusion contexts (conspecific (CIT) and human (HIT)).

Figure S2. Photograph of a Thorn-tailed Rayadito in Navarino Island.

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) (with permission Botero-Delgadillo et al. 2017)

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

Table S2. Correlation matrix among agonistic behaviors

	Hops.CIT	Flight.CIT	Alarms.CIT	Approach.CIT
Hops.CIT	1.0000000000	0.52069177*	0.56039132*	0.77596804*
Flight.CIT	0.5206917704*	1.00000000	0.73435310*	0.61687982*
Alarms.CIT	0.5603913234*	0.73435310*	1.00000000	0.74984204*
Approach.CIT	0.7759680406*	0.61687982*	0.74984204*	1.00000000
Speed.CIT	0.5931010709*	0.48014629*	0.30897252*	0.36181701*
Hops.HIT	0.1293023731	0.08788757	0.11882168	0.17882246
Flight.HIT	-0.1022238475	0.11326347	0.06699765	0.01619412
Alarms.HIT	0.1239361922	0.04418032	0.05519224	0.11427403
Approach.HIT	0.0971757441	0.12138678	0.16784429	0.22978766
Speed.HIT	0.0675426844	0.09447612	0.10344187	0.14199814

	Speed.CIT	Hops.HIT	Flight.HIT	Alarms.HIT
Speed.CIT	1.000000000	0.31689282*	-0.009778914	0.295103998*
Hops.HIT	0.316892819*	1.00000000	0.338272994	0.271058061*
Flight.HIT	-0.009778914	0.33827299	1.000000000	0.231006314*
Alarms.HIT	0.295103998*	0.27105806	0.231006314*	1.000000000
Approach.HIT	-0.018493472	0.08525025*	0.277667792*	0.135039476
Speed.HIT	0.260646107*	0.95623646*	0.577529341*	0.294676967*

	Approach.HIT	Speed.HIT
Approach.HIT	1.00000000	0.16823583
Speed.HIT	0.16823583	1.00000000

*** $p<0.05$**

Table S3. Eigenvalues of correlation matrix among morphometric traits to characterize body size.

Factor	Eigenvalue	% Total variance	Cumulative Eigenvalue	Cumulative %
1	2,157673	55,96122	2,157673	55,9612
2	0,979383	12,98972	4,137056	68,9509
3	0,759638	12,66063	4,896694	81,6116
4	0,520751	8,67919	5,417446	90,2908
5	0,393437	6,55728	5,810883	96,8480
6	0,189117	3,15196	6,000000	100,0000

Table S4. Sources of variation in observable behaviors.

Observable behaviors	β						σ		
	Sex	**Age**	**Body size**	**Observer**	**T° trial**	**Year Cap.**	**Identity**	**Residual**	**DIC**
Hops CIT	0.42 (-0.02,0.81)	-0.09 (-0.21,0.04)	0.02 (-0.13,0.18)	-0.19 (-0.65,0.16)	0.05 (-0.02,0.12)	-0.02 (-0.49,0.42)	0.01 (0.00,0.36)	0.97 (0.65,1.31)	240.4
Flight CIT	0.32 (-0.05,0.72)	-0.01 (-0.12,0.10)	0.03 (-0.12,0.18)	0.28 (-0.13,0.63)	0.02 (-0.04,0.09)	-0.06 (-0.42,0.31)	0.03 (0.00,0.02)	0.77 (0.51,1.10)	224.5
Alarms CIT	0.24 (-0.16,0.70)	-0.07 (-0.20,0.04)	-0.01 (-0.19,0.13)	0.29 (-0.17,0.70)	0.04 (-0.03,0.12)	-0.01 (-0.48,0.43)	0.00 (-0.00,0.01)	0.99 (0.68,1.33)	242.0
Approach CIT	0.34 (-0.06,0.81)	-0.02 (-0.15,0.11)	0.04 (-0.12,0.19)	0.08 (-0.32,0.54)	0.05 (-0.01,0.13)	0.01 (-0.42,0.47)	0.02 (-0.00,0.16)	0.97 (0.63,1.29)	241.0
Speed CIT	0.55 (0.11,1.01)	-0.08 (-0.21,0.06)	0.01 (-0.16,0.05)	-0.01 (-0.43,0.45)	0.01 (-0.07,0.08)	0.04 (-0.37,0.49)	0.00 (-0.00,0.00)	0.99 (0.72,1.38)	244.6
Hops HIT	0.00 (-0.00,0.6)	0.00 (-0.00,0.41)	-0.00 (-0.00,0.18)	0.00 (-0.00,0.38)	0.00 (-0.00,0.38)	0.00 (-0.00,0.19)	0.00 (-0.00,0.01)	1.00 (0.75,1.45)	248.5
Fligth HIT	0.02 (-0.02,0.71)	0.04 (-0.01,-0.18)	-0.05 (-0.23,0.18)	0.18 (-0.26,0.66)	0.00 (-0.00,0.23)	0.03 (-0.48,0.14)	0.02 (-0.00,0.17)	1.00 (0.69,1.41)	249.8
Alarms HIT	0.03 (-0.00,0.07)	-0.00 (-0.01,0.82)	-0.00 (-0.01,0.06)	0.00 (-0.00,0.76)	0.03 (-0.10,0.70)	0.01 (-0.04,0.40)	0.07 (-0.00,0.38)	1.00 (0.59,1.43)	247.1
Approach HIT	0.00 (-0.40,0.50)	-0.00 (-0.02,0.09)	-0.01 (-0.05,0.28)	-0.00 (-0.04,0.48)	0.02 (-0.00,-0.40)	0.03 (-0.04,0.49)	0.00 (-0.00,0.00)	1.00 (0.79,1.49)	249.2
Speed HIT	0.22 (-0.23,0.71)	-0.01 (-0.13,0.14)	-0.12 (-0.27,0.50)	0.21 (-0.20,0.69)	0.03 (-0.03,0.12)	-0.18 (-0.59,0.30)	0.03 (-0.00,0.26)	0.99 (0.62,1.42)	242.5

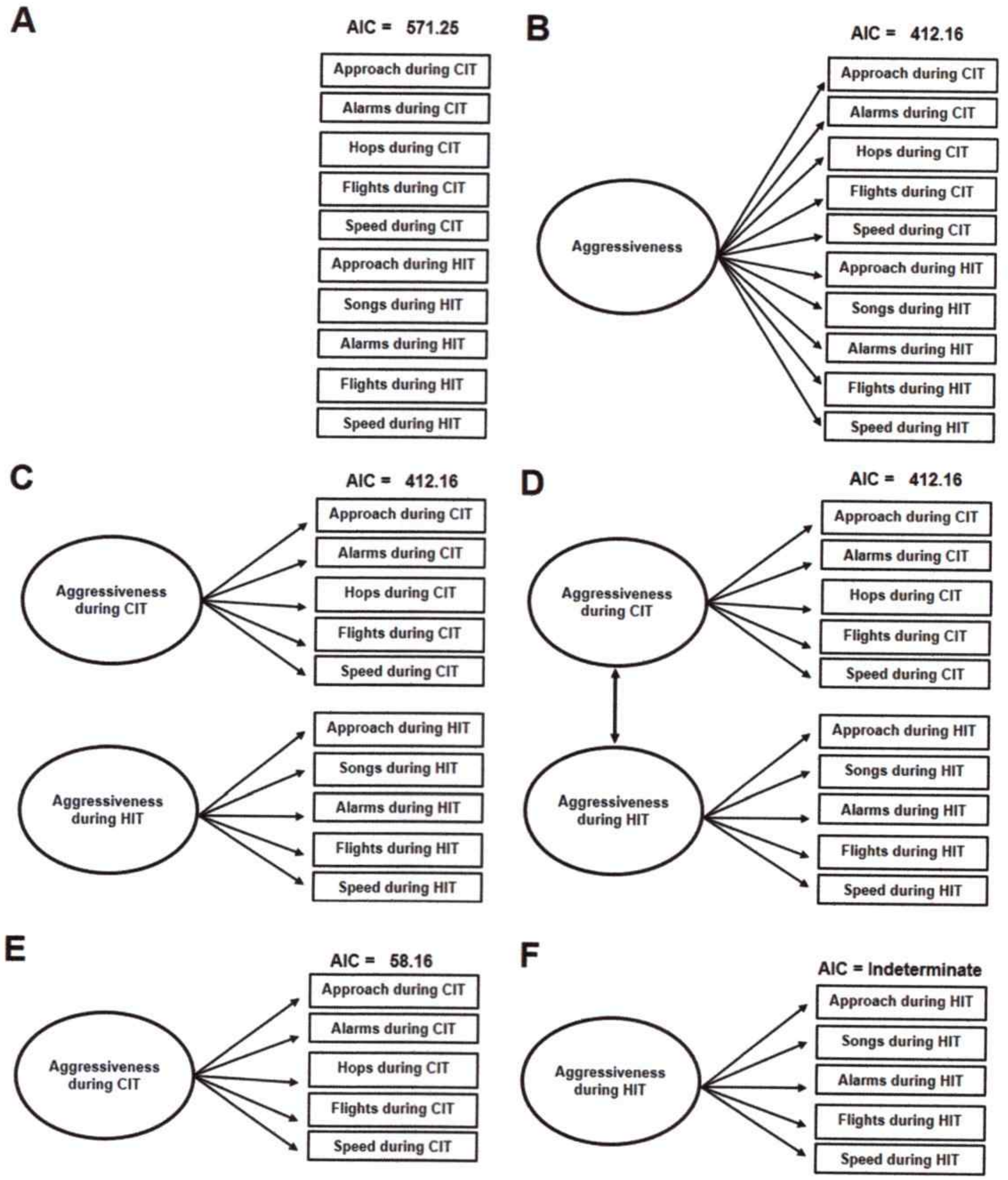

Figure S1. Six hypothesized structural equation models explaining correlation structure among agonistic behaviors during two intrusion contexts (conspecific (CIT) and human (HIT), respectively). Model (A) proposes a scenario where each combination of observable behaviors and intrusion contexts are underpinned by an independent factor (the null model); model (B) hypothesizes a latent unit is present across all observable behaviors regardless of intrusion context; model (C) hypothesizes latent units separated for each intrusion context; model (D) hypothesizes that those latent units are sub-units affected by an common factor. Model (E) shows a hypothesized latent unit only at the con-specific intrusion context (CIT); and model (F) shows a hypothesized latent unit only at the human intrusion context (HIT), respectively.

Figure S2. Photograph of Thorn-tailed Rayadito (*Aphrastura spinicauda)* taken in Navarino Island, Southern Chile. Photograph by Yanina Poblete.

CAPITULO II

PERSONALITY TRAITS AND ITS RELATION WITH EXTRA-PAIR OFFSPRING AND PARENTAL INVESTMENT IN A SUB-ANTARCTIC RAINFOREST BIRD

Personality traits and its relation with extra-pair offspring and parental investment in a sub-Antarctic Rainforest bird

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Abstract

Personality traits have shown to be repeatable, heritable and with impact on animal fitness. Indeed, they could affect different aspects associated to reproduction such as extra-pair mating, parental investment and/or clutch quality. Current evidence suggests that personality traits are commonly associated to risk-taking behavior as extra-pair behavior, where individuals exhibiting a more exploratory behavior would lose paternity in their nests, but could gain paternity outside their nests, while more aggressive individuals could reduce infidelity by their couple of the nest. Along with this, variability in those traits could also explain the detected variability in parental investment. However, extra-pair behavior could lead to sexual conflict, reducing parental investment by males. In this study, we recorded aggressiveness, exploratory behavior and parental investment, and detected extra-pair offspring (EPO) in the Thorn-tailed Rayadito (*Aphrastura spinicauda*), an endemic bird of the Sub-Antarctic rainforests. Results showed that aggressiveness and exploratory behavior in males are related with extra-pair behavior, where more exploratory males loss paternity in social nests, while more aggressive males seem to avoid the infidelity by their pairs. Moreover, we also detected that personality traits in females is positively related with parental investment behaviors. In addition, we found that in nests with EPO, clutch volume increased, suggesting that females could obtain indirect benefits of extra-pair behavior.

Keywords: Aggressiveness, exploratory behavior, parental investment, EPO, clutch quality.

Significant Statement

Birds have developed a set of interrelated reproductive and behavioral strategies to increase their fitness. Individual characteristics, such as personality traits could favor acquisition of extra-pair offspring, since it would allow gathering information about the best opportunities to display extra-pair behavior, but extra-pair behavior could lead to a sexual conflict and reduce parental investment. Here, we demonstrate that personality traits are related with extra-pair behavior in males, and with parental investment in females. Although, we did not detect evidence of reduced parental investment in males experiencing infidelity, we found that females seem to obtain indirect benefits of extra-pair behavior, like increasing clutch volume.

Introduction

The intraspecific variability in aggressive and exploratory behaviors has been demonstrated in multiplex taxa, where different behavioral phenotypes have been found co-existing in the same population (Carere and Maestripieri 2013). These behaviors are often repeatable (e.g. individuals differ consistently across time or contexts) (Verbeek et al. 1996, Gosling 2001, Dingemanse et al. 2002, Garamszegi et al. 2006b, Duckworth 2006a, Pavlova et al. 2007, van Dongen et al. 2010), heritable (Benus et al. 1991, Dingemanse et al. 2002, Duckworth and Badyaev 2007, Poblete et al. Chapter II), and affect individual fitness (Clark and Ehlinger 1987, Wilson 1998, Dingemanse et al.2004, Smith et al. 2008). For these reasons, aggressive and exploratory behaviors are commonly considered as a main component of animal personality (Wilson 1998, Gosling and John 1999, Drent et al. 2003, Bell and Stamps 2004, Bergmuller and Tabosky 2007, Réale et al.2007), as they can affect different aspects associated to reproduction such as extra-pair behavior, parental investment and/or nest quality (Dingemanse et al. 2002, van Oers et al.2008, Patrick et al. 2012, Baldassarre et al. 2016).

In socially monogamous birds with biparental care, extra-pair behavior has been widely demonstrated in several species (Petrie and Kempenaers 1998, Griffith et al.2002, Westneat and Stewarts 2003, Castaño-Villa 2015). In general terms, it is assumed to be an adaptive behavior (Griffith et al.2002, Anderson and Simmons 2006, Wilson and Nussey 2010), since both males and females could achieve additional offspring, increasing the probability of improving genetic quality of their offspring (Kempenaers et al. 1992, Wesneat and Stewart 2003), or decreasing the risk of failure clutch if social pair is infertile

(Krokene et al. 1998). However, the extra-pair behavior of the female is costly for its social pair because it involves investment in time and energy raising more offspring (Kempenaers and Schlicht 2010). Based on this, it is likely that aggressiveness helps males to avoid extra-pair behavior of their pairs, because the aggression toward intruders may serve to repel rivals and decrease the likelihood that the male is cuckolded (Raouf et al.1997, Kokko et al.2005). For this reason, during the reproductive season, individual differences in aggressiveness of the males could influence the presence of extra-pair offspring in their social nests, where it is expected that more aggressive males tend to loss paternity in their nests in relation to less aggressive males.

Although for a long time it was assumed that males that spend more time engaged in aggressive territorial spend less time in parental investment behaviors (eg. feeding offspring) (Hegner and Wingfield 1987, Ketterson and Nolan 1992), current evidence suggests that different measurements of paternal investment are positively correlated with aggressiveness (Trainor and Marler 2001). Based on this, it is likely that both more aggressive males and females are more active in parental investment activities such as nest defense and feeding offspring. Along with this, extra-pair behavior has associated costs to increase in both predation and infection risks (Kempenaers and Schlicht 2010). For this reason, it is likely that this behavior is more common in individuals that take more risks or display a more exploratory behavior, because those individuals could have a genetic predisposition toward this kind of behaviors (Forstmeier 2007). In fact, evidence suggests that more exploratory individuals tend to experience more risk (Dingemanse et al.2002, van Oers et al. 2004) and to display extra-pair behaviors (Patrick et al. 2012). Thus, it is likely that more exploratory males lose more paternity in their social nests, although they could gain paternity outside their nests, while that more exploratory females could acquire more extra-pair offspring.

Although empirical evidence is scant, it suggests that more exploratory individuals are more actives in nest defense towards an intruder (Hollander et al.2008), and feed more their offspring (Budaev et al 1999). Thus, individual differences in exploratory behavior could be important in explaining variation in parental investment.

In addition, extra-pair behavior has potential costs related to sexual conflicts that could lead to lessen parental investment of the males when extra-pair behavior in females is detected (Westneat et al.1990, Kempenaers and Schlicht 2010). In general, it is assumed that males could decrease nest defense or offspring feeding in response to extra-pair behavior by the female, which could affect clutch quality (Kempenaers and Sheldon 1997, Sheldon 2002). Although in species with bi-parental care, the female behavior could favor facultative behavioral responses in males reducing parental investment (Birkhead and Møller 1993), empirical evidence is still scarce (Royle et al.2012).

In this study, we characterized aggressive, exploratory, nest defense and parental provisioning visits in the thorn-tailed rayadito, *Aphrastura spinicauda* (Furnariidae: Passeriformes), an endemic bird of the Sub-Antarctic rainforests of South America (Remsen 2003). We also assessed the presence of EPO in their nests. In addition, we characterized the clutch volume and body condition of the offspring, in order to assess its relation with those behaviors and possible benefits on individual fitness.

Within this framework, our investigation aimed to: (1) determine if aggressiveness and exploratory behaviors predict EPO; (2) describe the relationship between aggressiveness and exploratory behavior with nest defense and feeding behavior; and (3) assess if there are differences in nest defense and feeding behavior between nests with and without EPO. In addition, we assessed if there are differences in both clutch volume and offspring body condition between nests with and without EPO, in order to evidence possible comparative advantages for females as a result of extra-pair behavior, and analyzed if these attributes are related to personality or parental investment behaviors.

Methods

Species and study site

The thorn-tailed rayadito is a socially monogamous and secondary cavity nesting bird, with an apparent absence of sexual dimorphism (Moreno et al. 2007). Thorn-tailed rayadito usually lays one clutch per breeding season, and males and females participate equitably in the raise of offspring (Moreno et al. 2005, Moreno et al 2007, Botero-Delgadillo et al. 2015, Espíndola-Hernández et al. 2017). We selected a thorn-tailed rayadito population located on Navarino island (55°4'S, 67°40'W), southern Chile. This area, characterized by deciduous Magellanic forest (Rozzi et al. 2004), it is generally exposed to strong winds and low temperatures (range: –2 to 15.8° C) most of the year (Dirección Meteorológica de Chile, Chilean National Weather Service). It presents a continuous and less populated environment (Rozzi and Jiménez 2014, Botero-Delgadillo et al.2017), where aggressive and exploratory behaviors are not correlated (Poblete et al. Chapter I), likely because this population is not exposed to environmental pressures that could modulate the functional integration of these behaviors (e.g. high density, stress or predation pressure) (Bell 2005; see Ippi et al. 2013 for an anti-predator study in the species).

General field procedures. The study was carried out over the reproductive season, from October to late December, since 2013 to 2015. Because thorn-tailed rayaditos are secondary cavity nesting, we used 220 nest boxes, which were monitored weekly to record the start laying. During laying, we measured length and width of eggs to estimate the clutch volume used the formula ¾ πr^3. At days 12 and 13 after hatching of their offspring, each adult was captured in the nest box (n=130) between 7:30 AM and 12:00 PM, and banded with both numbered metal and colored bands (National Band and Tag Co., Newport, Kentucky, USA, or Split Metal Bird Rings, Porzana Ltd, UK or with a numbered band provided by the Servicio Agrícola y Ganadero (Chilean Agricultural and Livestock Service, or SAG), Chile). The chickens were banded with metal numbered bands during the capture of first adult 12 days post-hatch. To calculate the body condition index (BCI) of the offspring, tarsus length and mass were recorded (see Hayes and Shonkwiler 2001). Before releasing birds, a small blood sample (ca. 17 µL) was taken from the brachial vein of both adults and chickens, and each of them was stored in FTA cards (Whatman®) for posterior molecular analysis (see Quirici et al. 2014).

Exploratory behavior. After capturing and before banding birds, we recorded exploratory behavior of 130 adults via a novel environmental experiment, utilizing a large field-portable cage (270 cm length x 150 cm width x 150 cm height) made of PVC poles and semitransparent black shading cloth (see van Dongen et al. 2010; Poblete et al. chapter

I). In the cage, four wooden perches (80 cm long, 2 cm in diameter) were hung at varying heights between 50 and 110 cm off the ground. The floor was divided into two equally sized quadrants that resulted in 14 possible perching locations, when the four perches, four walls and two ceiling divisions were added. Birds were introduced into a small acclimatization cage (30 cm length x 25 cm width x 39 cm height) in a corner of the larger experimental cage and covered with a black cloth during a five-minute acclimatization period. At the beginning of the experimental period, the cloth was removed, and one minute after removing the cloth, the door of the holding cage was opened, and each subject was free to go out the acclimatization cage. Hops and total area visited by each subject was recorded with a digital camera over a period of ten minutes, to calculate speed, richness and diversity exploratory index (Verbeek et al.1994, van Dongen et al. 2010, Poblete et al. Chapter I).

Aggressiveness toward conspecific. Fifteen days post-hatch, we recorded aggressiveness in 87 adults by simulated territorial intrusion (STI). To this end, a conspecific model was placed three meters in front of the nest-box. Two observers recorded over eight minutes (two minutes of silence, three minutes of playback of thorn-tailed rayadito vocalizations, and three minutes of silence) the frequency of hops and flights, and alarms using a digital voice recorder (see Ippi et al. 2013). The "approach" variable was estimated as the total amount of time the individual remained close to the model (within 1 m). The "speed" was calculated as the number the hops and flights performed during the first minute of playback in the test (see Poblete et al. Chapter I).

Nest defense behaviors. Thirteen days post-hatch, a focal human was placed three meters in front of the nest-box. Over a three-minute period, two observers recorded the frequency of hops and flights, and alarms using a digital voice recorder (Hollander et al. 2008). The "approach" variable was recorded as the minimum distance between the birds and the focal human as measured by laser rangefinder, and the "speed" variable, was estimated as the number of hops and flights performed during the first minute of the test. The focal human was the same person and used the same cloth in all experiments (see Poblete et al. Chapter I).

Feeding offspring behavior. Seventeen days post-hatch a digital video camera (Sony DCR-68) was positioned at 3-4 m from the nest box to record a 4 hour period, between 07:00 and 14:00, the frequency of offspring feeding behavior in each nest box (see Espíndola-Hernández et al. 2017).

All recordings were reviewed using SMPlayer© (version 0.8.0) and the information was tabulated using Jwatcher (version 1.0) (Blumstein et al. 2005).

Molecular analysis

DNA was extracted from the collected blood on FTA cards using a QIAGEN DNA extraction kit (Valencia, CA, USA), and the individuals were genotyped at 13 polymorphic microsatellites loci, using eight species-specific markers, As1, As7, As18, As25-1, As25-5, As25-8, As25-10, and As25-14 (see Yañez et al. 2015) and five cross-species amplifying markers: Asμ 15_ZEST,CcaTgu23 (Olano-Marín et al. 2010), Tgu06 (=CK307697), Tgu05 (=DV946651) (Slate et al.2007), and marker ZF_AC138573 (van

Oosten et al. 2016, *see* Botero-Delgadillo et al. 2017 for PCR details). Paternity analyses included 12 of 13 markers, which did not show significant deviations from the Hardy-Weinberg equilibrium (HWE; all P>0.1) and their frequencies of null alleles were below 0.05. The EPO estimation was obtained after performing parentage analyses under a combination of assignment and exclusion approaches (see Jones et al. 2010; Botero-Delgadillo 2017). We used CERVUS 3.07 (Kalinowski et al.2006) to perform parentage analyses, using the logarithm of odds (LOD score) and critical Delta for assigning paternity. These results were checked in order to confirm or exclude paternity, 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 (Kalinowski et al. 2007). When the social father was the most likely candidate, assignment was confirmed regardless of the confidence around it. If a set of candidates (excluding the social father) showed no mismatches and positive LOD scores, but relaxed confidence (80%), the whole set was excluded. As EPO were not always confidently assigned to any sampled male, it was not possible to establish gained paternity (*see* Botero-Delgadillo 2017).

Because thorn-tailed rayadito sexual dimorphism is almost nil, the sex must be determined by molecular techniques (Moreno et al. 2007). Thus, we used the primers 2550 F and 2718R (Fridolfsson and Ellegren, 1999) to amplify the gene fragments CHD-W (unique to females) and CHD-Z (found in both males and females) using polymerase chain reactions (PCR). The PCR product was run on a 3% agarose gel in a Fluorimager (Vilber Lourmat), to separate the gene fragments; and sex was determined by visualization of the gel, with males exhibiting bands only of CHD-Z and females having bands of both CHD-W and CHD-Z, respectively.

Statistical analyses

We used general lineal model (GLM) with binomial error distribution to assess if personality traits predicts the presence of EPO in social nests. Lineal model (LM) was used to analyze relations between personality traits and parental investment behaviors. ANOVA test was used to determine differences in clutch quality between nests with and without EPO. Finally, we used LM to describe the relationship between personality traits and parental investment behaviors with clutch quality.

We considered an effect was "strongly supported" with $P < 0.05$ for each parameter. Statistical analyses were performed in the R statistical environment v. 3.3.2 (R Core Team, 2016), using nlme (Pihneiro et al. 2017), MASS (Venables and Ripley 2002), glm2 (Marschner 2011).

Results

Personality traits and EPO in social nests

During 2013-2015, the thorn-tailed rayadito population occupied 65 nest-boxes, and in 61 of them, paternity was assigned, detecting 18% of nests with EPO. Our results indicated that both aggressiveness and exploratory behaviors predicts EPO, where more aggressive males showed no EPO ($Z=-2.19$; $P=0.02$) (Figure 1A), while more exploratory males tended to have EPO in their nests ($Z=2.75$; $P=0.00$) (Figure 1B). However, when assessed theses relations to females is not found significant results in both aggressiveness (Z=-0.89; P=0.37) and exploratory tendency (Z=0.13; P=0.89).

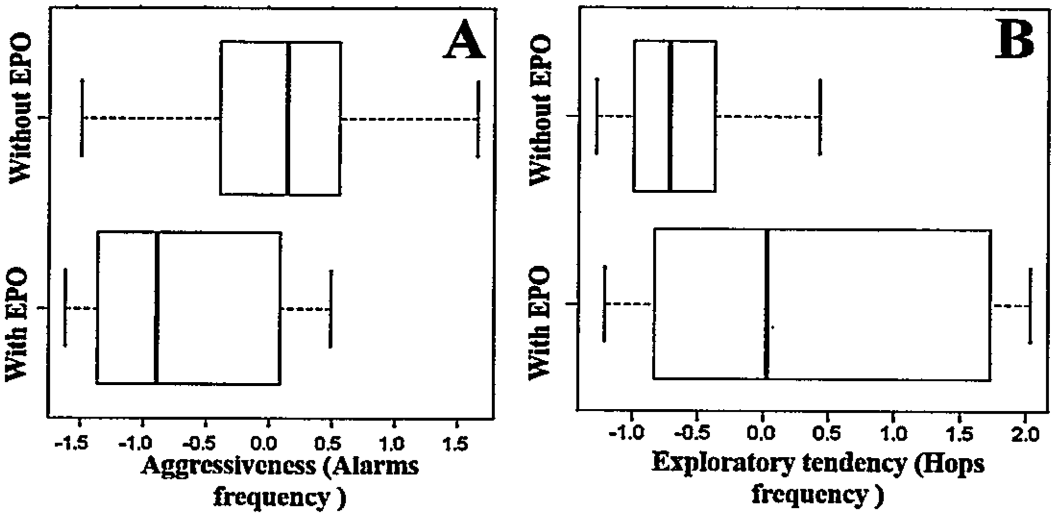

Figure 1. Boxplot showing both aggressiveness (A) and exploratory behavior (B) related to the presence of EPO in males of thorn-tailed rayaditos.

Personality traits and parental investment

We found no relationships between exploratory behavior and nest defense in males (F=0.55; P=0.46). However, we found tend that more aggressive males defend more intensely their nests (β=0.29; F= 3.95; P=0.05). We found no significant results in the relation both between aggressiveness (F=0.11; P=0.73) and exploratory behavior (F=0.02; P=0.87) with feeding offspring behavior in males, while in females, we found that more explorer females defend (β=0.42; F= 6.61; P=0.01; Figure 2A) and feed their offspring (β=0.29; F= 4.55; P=0.03; Figure 2B) more than less explorer females, and more aggressive females defend more actively their nests (β=0.40; F= 6.71; P=0.01; Figure 2C). However, aggressiveness in females is not related with feeding offspring (F=0.09; P=0.75).

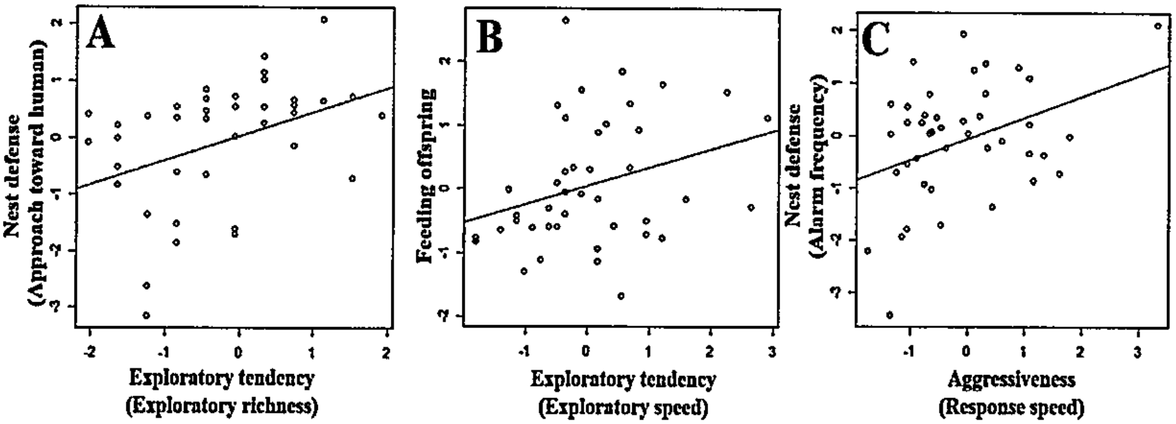

Figure 2. Relationship between personality traits and parental investment behaviors in females of thorn-tailed rayaditos. (A) Nest defense in relation to exploratory behavior; (B) offspring feeding in relation to exploratory behavior; and (C) nest defense in relation to aggressiveness.

Parental investment and EPO

Our results showed that both nest defense (males: Z=-0.59; P=0.55; females: Z=-0.29; P=0.76) and feeding offspring (males: Z=-0.44; P=0.65; females: Z=-0.55; P=0.57) are no related with EPO.

Behavioral traits, clutch quality and EPO

We analyzed if there are differences in clutch volume and BCI of the offspring comparing nests with and without EPO. We detected that nests with EPO had a higher clutch volume in comparison to nests without EPO (F=14.76; P=0.001; Figure 3A). However, there were no significant differences in BCI of offspring between nests with and without EPO (F=0.76; P=0.38). Regarding the relationship between exploratory behavior and clutch volume, males with a more exploratory behavior had a higher clutch volume in social nests compared to males with a less exploratory behavior (β=0.39; F=9.33; P=0.001; Figure 3B). Moreover, we found that in nests with larger clutch volume, males were less aggressive (β=-0.27; F= 4.15; P=0.04; figure 3C). However, for females, we did not find significant differences in aggressiveness (Z=-0.95; P=0.33) and exploratory behaviors (Z=-0.73; P=0.46) between nests with and without EPO, nor any relationship between these traits and clutch volume (aggressiveness: F=0.04; P=0.82; exploratory tendency: F=2.32; P=0.13) and BCI of the offspring (aggressiveness: F=0.001; P=0.92; exploratory tendency: F=3.01; P=0.09). We did not find significant results between nest defense with clutch volume (males: F=0.03; P=0.84; females: F=1.20; P=0.27) and BCI of the offspring (males: F=0.36; P=0.54; female: F=0.00; P=0.92). Finally, any significant result is detected between feeding offspring with BCI of the offspring (males: F=2.65; P=0.11; females: F=0.25; P=0.62).

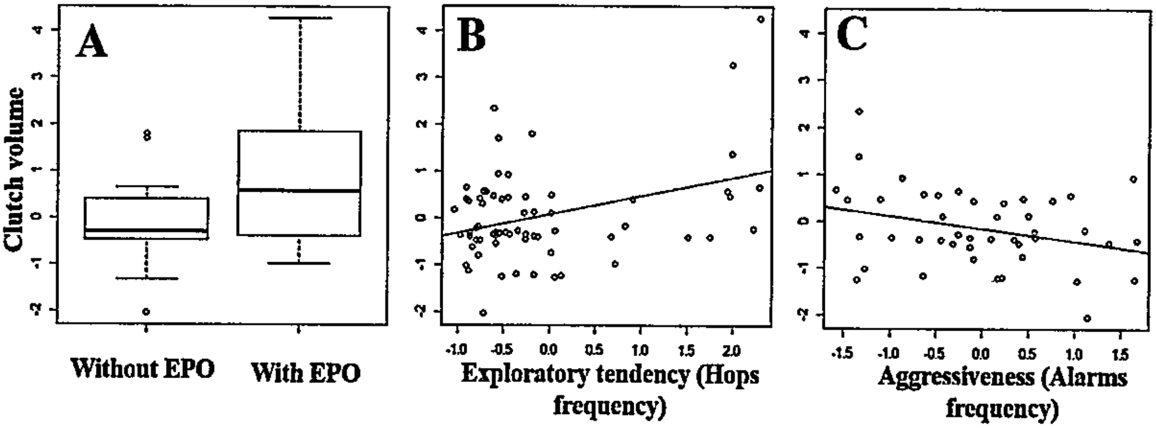

Figure 3. Relationship between clutch volume with EPO (A), exploratory tendency (B) and aggressiveness (C) in males of thorn-tailed rayadito.

Discussion

Analysis of the results showed that exploratory behavior is more intense in males with EPO in their nests. Besides, in those nests, males were less aggressive compared to those without EPO. Moreover, we found that more exploratory and aggressive females invest more in parental activities. However, we did not detect any relationship between personality traits and parental investment in males. Along with these results, we detected that nests with EPO had a higher clutch volume than those without EPO, and aggressiveness and exploratory behaviors in males were related to clutch volume in the same way they are connected to presence and/or absence of EPO.

Personality traits and loss of paternity in social nests

Evidence suggests that exploratory behavior could explain the variation in EPO, mainly because exploratory behavior is strongly associated to risk-taking behavior (Dingemanse et al.2002, van Oers et al. 2004, Martins et al. 2007). In relation to this, it has been reported that males with more exploratory behavior tend to lose paternity in social nests, but they gain it outside their nests, making more difficult to assess the influence of EPO on fitness. As a result, the adaptive nature of promiscuity is yet questioned, in spite of extensive evidence supporting that exploratory behavior, a trait that increases extra-pair mating, is an adaptive trait (van Oers and Naguib 2013). For this reason, it is likely that promiscuity is not an adaptive trait by itself, but a consequence of its association with other behaviors under selection (Patrick et al. 2012). In this study, we could not detect gained paternity outside social nests, but 18% of pairs with EPO were identified, finding evidence supporting that males with a more exploratory behavior lose paternity in their nests. Along with this, we found that more aggressive males tend to have less EPO in their nests. However, we did not find significant differences in aggressiveness and exploratory behavior between nests with and without EPO in females. Thus, our result suggests that during the reproductive season, different behavioral phenotypes would partly explain variation in EPO in social nests in males but not in females.

Some studies have reported that extra-pair behavior in females could depend on ecological factors that favor the probability of meeting an extra-pair partner, such as population density (e.g., Stutchbury and Morton 1995) or vegetation density (e.g., Valera et al.2003). Along with those findings, sexual conflicts due to differences in optimal fitness between sexes, predict that evolution favors male traits to manipulate female behavior, while females resist this manipulation through sexual selection. For these reasons, it is likely that males and females intrinsically differ in a variety of ways to reach an optimal fitness (Parker 1979, Andersson 1994, Gavrilets et al. 2001). Thereby, males with a more exploratory behavior could obtain offspring outside their nests to increase their total fitness, even considering the risk to lose some paternity in their social nests, while females could face associated costs such as less parental investment in reproductive activities during pre-laying, but they increase their fitness by meeting an extra-pair partner when social pair is not in their territory (Kempenaers and Schlicht 2010). Accordingly to this, evidence from a well studied model, *Drosophila*, has shown that effects of sexual conflicts cannot always be attributed to female behavior (Partridge and Farquhar 1981, Chapman et al.1995, Rice 1996, Holland and Rice 1999). It is likely that extra-pair behavior in females of thorn-tailed rayadito arises as a consequence of male behavior, combined with both specific characteristics of the environment and potential sexual conflicts between breeding pairs, which could generate greater opportunities of extra-pair encounter for females, independently of their behavioral phenotype.

Personality traits and parental investment

Because there is considerable variation in parental investment in several taxa, it is expected that those behaviors covariate with personality traits (Royle et al 2012). In this study, it was not possible to detect any relationship between those behaviors in males, even where we detected a positive tendency between aggressiveness and nest defense. However, we found that more exploratory females defended more intensively their nests and fed their offspring with more frequency in comparison to less exploratory females. Along with this, we also detected that more aggressive females defended more intensively their nests. Thus, our results suggest that variability in personality traits could be related with variation in parental investment activities. Although current evidence is scarce (see Budaev et al.1999), personality traits may provide a mean to reliably indicate parental ability during mate choice and reduce sexual conflicts over parental care. More studies are necessary to understand how personality traits could to modulate these relationships (Roulin et al. 2010).

Benefits and costs of extra-pair behavior in females

A main indirect benefit of extra-pair behavior for females is the possibility of improving quality of their offspring by increasing fertilization by extra-pair males of higher quality (Kempenaers and Schlicht 2010). Although the mechanisms to detect genetic quality of males are yet unclear, it has been reported that females prefer specific males within a population, and females copulating with those preferred males lay eggs of greater size and produces offspring with better body condition (Cunningham and Russell 2000, Osorno et al. 2006). Accordingly, some studies have reported that paternity may determine differences in the reproductive value of the eggs (Sheldon 2000, Krist et al. 2005). Even though this study did not provide conclusive information to associate each egg with its parents or with a specific offspring, it was detected that nests with EPO had a greater clutch volume. Therefore, our results suggest that females could be obtaining indirect benefits as a result of extra-pair behavior in this population.

We studied possible differences in body condition of offspring between nests with and without EPO. However, significant differences were not detected, since body condition of the offspring cannot be attributed only to paternal or maternal genetic effects (Cunningham and Russell 2000). On the contrary, it has been demonstrated that body condition of the offspring is affected by multiplex factors, namely parental care (Clutton-Brock 1991), nutritional quality (Agosta 2008), and incubation behavior (Kovarik et al. 2009), among others. Therefore, it is necessary to include more information that can allow assigning each egg to an offspring and to its biological father, in combination with ecological and behavioral information to assess real benefits of extra-pair behavior on fitness of females. In relation to this, associated costs of extra-pair behavior for females, being part of sexual conflicts, include a set of behaviors that males could display when they discover have suffered infidelity. However, our results did not reveal reduced parental investment by males. Although in species with bi-parental care, mate selection could favor facultative behavioral responses in males, it is difficult to determine if in fact the presence of EPO triggers a facultative response of males toward female infidelity, because a reduced parental investment could depend on facts such as quality territory, age or condition of the male (Kempenaers and Sheldon 1997, Sheldon 2002). Hence, EPO could be a consequence of the personality of some males combined with ecological factors that could favor extra-pair mating. Therefore, while perception mechanisms used by males to detect infidelity are not clear, costs of extra-pair behavior on females will remain not yet identified.

Concluding remarks

Our approach allowed to find that males with a more exploratory behavior tend to lose paternity in social nests, independently of the exploratory behavior of their nest pair, and we detected that more aggressive males tend to have less EPO in social nests. Consequently, personality traits in males seem to favor extra-pair behavior in females. Along with this, we found that variability in personality traits could regulate at least partially, parental investment behavior, especially in females, who could to be acquiring indirect benefits of extra-pair behavior. In summary, our results support the idea that variability in personality traits could to modulate different aspects associated to reproduction in socially monogamous birds.

Data accessibility statement: Should the manuscript be accepted, the data supporting the results will be archived in an appropriate public repository such as Dryad or Figshare and the data DOI will be included in the article.

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Personality traits and its relation with extra-pair offspring and parental investment in a sub-Antarctic Rainforest bird.

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Electronic Supplementary Material

Contents

Figure S1. Photograph Thorn-tailed Rayaditos in nest box.

Figure S1. Photograph of Thorn-tailed Rayadito (*Aphrastura spinicauda)* in nest box taken in Navarino Island, Southern Chile. Photograph by Yanina Poblete.

CAPITULO III

BEHAVIOURAL COMPATIBILITY AND ITS RELATION WITH PARENTAL INVESTMENT AND EXTRA-PAIR BEHAVIOUR IN AN ENDEMIC BIRD OF THE SUB-ANTARCTIC RAINFORESTS

Behavioural compatibility and its relation with parental investment and extra-pair behaviour in an endemic bird of the sub-Antarctic rainforests

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MANUSCRITO ENVIADO A ETHOLOGY (ETH-17-0230)

Abstract

The concept of behavioural compatibility is used to refer to properties emerging from the interaction between behaviours of the pair, and it moulds different aspects of reproduction. Evidence suggests that preference for a social partner with similar behavioural phenotype could favour cooperation between breeding pairs, resulting in a higher compatibility in parental care activities, and, as a consequence, increasing quality of their offspring. Moreover, is reported that behavioural compatibility could have influenced the decision mechanisms of decision behind underlying extra-pair behaviour. In this study, we characterised behavioural compatibility in aggressiveness, nest defence and parental care in 45 mating pairs of Thorn-tailed rayadito, *Aphrastura spinicauda* (Furnariidae: Passeriformes), an endemic bird of the Sub-Antarctic rainforests. Our aims were to (1) describe the relationship between compatibility in aggressiveness and compatibility in parental care; (2) determine whether compatibility in aggressiveness predicts EPO in social nests; (3) analyse whether compatibility in aggressiveness explains body condition of the offspring; and (4) assess whether the presence of EPO in social nests lessens compatibility in parental investment activities. Our results indicated that compatibility in aggressiveness predicts compatibility in parental care behaviour, which means that behavioural compatibility could result in an equitable participation in parental care. However, did not find conclusive information to detect if behavioural compatibility influences extra-pair behaviour or offspring's body condition, or if extra-pair offspring affect compatibility in parental investment. In sum, our study provide evidenced that behavioural compatibility could be an important aspect in the process of paternity choice, in which a high behavioural compatibility seems to ensure an equitable participation in parental care. Nevertheless evidence did not provide conclusive information to detect if behavioural compatibility affect extra-pair behaviour or offspring qualities.

Key words: Behavioural compatibility, parental investment, extra-pair offspring, Thorn-tailed Rayadito

Introduction

In monogamous species with biparental care, breeding partners need to be efficient on parental activities in order to increase reproductive success (Spoon et al. 2006, Ihle et al. 2015). Achieving this efficiently depends not only on individual characteristics of each member of the pair, but also on properties emerging from their interaction (Ens te al. 1993, Zeh and Zeh 2001, Dingemanse et al. 2004). These properties are referred as compatibility and mould different attributes, such as pair bonds, parental behaviour, divorces and mate choice, among others (e.g. Trivers 1972, Marzluff and Balda 1988, Black 1996). Although both mice and human individuals seem favour partner with major histocompatibility complex (MHC) genotypes that differ from their own (Yamazaki et al. 1976, Potts et al. 1991, Ober et al. 1997, Wedekind et al. 1995) and is assumed that animals tends to avoid inbreeding (Bateson 1980; Shields 1983), some studies focused both physical and behavioural traits had demonstrated that individuals in a variety of species prefer partners with traits similar to their own phenotype (Burley 1983; Cooke & Davies 1983; Marzluff and Balda 1988, Choudhury et al. 1996). In this sense, it has been reported that a great similarity in weight, age, body mass and behaviour has positive effects on reproductive success (Marzluff and Balda 1988a, Black et al. 1996, Dingemanse et al.2004, Spoon et al. 2006). Although compatibility concept has not been explicitly defined, mainly because it depends on variation between mate traits, which means it could vary among species (e.g. temporal synchrony in foraging could indicate compatibility or not, depending on how it affects competence between mates), is accepted that similarities between mates are directly proportional to compatibility (Marzluff and Balda 1988, Black and Owen 1995, Choudhury et al. 1996, Marzluff et al. 1996, Spoon et al. 2006, Gabriel et al.2012), leading to improved fitness particularly in socially monogamous species (Rowley 1983, Ens et al. 1996, Black 2001, Ryan and Altmann 2001, Spoon et al. 2006).

A behaviour having significant effects during mating is aggressiveness, with a crucial role in the evolutionary history of birds, affecting defence of resources like territories, offspring, mates and sources of food (van Oers and Naguib 2013). Aggressiveness has been characterised mainly by using simulated territorial intrusions (STI), i.e., an intruder is placed inside a given territory to record a set of agonistic behaviours deployed by the owner of that territory (Wingfield et al. 1987, Carere et al. 2005). This behaviour has shown to be repeatable, where different individuals differ consistently across time and/or context (Verbeek et al. 1996, Gosling 2001, Dingemanse et al. 2002, Garamszegi et al. 2006, Duckworth 2006, Kralj-Fiser et al 2007, Pavlova et al. 2007, van Dongen et al.2010), heritable (Benus et al. 1991, Dingemanse et al.2002, Duckworth and Badyaev 2007, Poblete et al. Chapter II), and it affects individual fitness (Clark and Ehlinger 1987, Wilson 1998, Dingemanse et al.2004, Smith et al. 2008). For those reasons, it is considered as an animal personality trait under selection (Wilson 1998, Gosling and John 1999, Drent et al. 2003, Bell and Stamps 2004, Bergmuller and Tabosky 2007, Réale et al.2007). Thus, preference for a compatible social partner regarding aggressiveness could favouring cooperation between partners, resulting in a high compatibility in parental care activities, as well as increasing quality of the offspring (Gabriel and Black, 2012, Adler and Ritchison 2011, Mitrus et al. 2010)

On the other hand, some studies have reported significant relationships between behavioural compatibility and extra-pair behaviour. Although detection of extra-pair behaviour via field observations is difficult, the development of genetic markers for wild species has made possible the detection of extra-pair offspring (EPO) during raising (Griffith et al. 2002). Accordingly, it has been reported that mates with extreme and compatible behavioural phenotype tend to have EPO in social nests (van Oers et al. 2007). Since personality traits have a genetic component (van Oers et al. 2004), this relationship has been approached from the "good genes hypothesis" perspective, predicting that mates with high behavioural compatibility increase extra-pair behaviour in order to acquire more genetic variability in the offspring (Krokene et al. 1998). However, it has also been detected that mates with low behavioural compatibility have more probabilities of engaging in extra-pair behaviour than those with high compatibility (Spoon et al.2007). An alternative hypothesis to explain this relationship states that mates with low behavioural compatibility may benefit from dissolving their current relationship and establishing a new one. Therefore, engaging in extra pair behaviour may represent a way of having a new partner (Colwell and Oring 1989, Wagner 1991b, Kempenaers and Dhondt 1993).

The extra-pair behaviour has been widely reported in socially monogamous birds (Petrie and Kempenaers 1998, Griffith et al.2002, Westneat and Stewarts 2003). It is considered an adaptive behaviour (Griffith et al.2002, Andersson and Simmons 2006, Wilson and Nussey 2010), since it allows individuals to achieve additional offspring, as well as increase probabilities of improving its genetic quality (Kempenaers et al. 1992, Wesneat and Stewart 2003). However, this behaviour has associated costs, such as a development of sexual conflicts that mainly affect females, lessening parental investment when extra-pair behaviour is detected by their social pair (Westneat et al.1990, Kempenaers and Schlicht 2010). As a response, males can reduce intensity of nest defence against predators (Kempenaers and Sheldon 1997, Sheldon 2002), a behaviour usually associated to parental investment (Royle et al. 2012). In line with this, when EPO arises, mate compatibility in nest defence could decrease.

Notwithstanding that variation in extra-pair behaviour is yet unclear (Kempenaers 2010) and results of compatibility studies are not conclusive, evidence suggests that behavioural compatibility could influence the mechanisms of decision behind extra-pair behaviour.

Based on this information, we characterised behavioural compatibility in aggressiveness, nest defence and parental care in 45 mates of thorn-tailed rayadito, *Aphrastura spinicauda* (Furnariidae: Passeriformes), an endemic bird of the Sub-Antarctic rainforests of South America (Remsen 2003) (electronic supplementary material, figure S1), and detected presence of EPO in social nests. We also characterised body condition of the offspring, in order to assess its relationship with behavioural compatibility of parents.

The thorn-tailed rayadito is a secondary cavity nesting bird, with an apparent absence of sexual dimorphism (Moreno et al. 2007). It is socially monogamous, but displays extra-pair behaviour (Castaño 2015, Botero-Delgadillo 2017; Poblete et al. chapter III); besides, males and females equitably invest in caring for the offspring (Moreno et al 2007, Botero-Delgadillo et al. 2015, Espíndola-Hernández et al. 2017). Our study population is located on Navarino island (55°4'S, 67°40'W), southern Chile, an area characterised by deciduous

Magellanic forest (Rozzi et al. 2004), and exposed to strong winds and low temperatures (range: –2 to 15.8° C) most of the year (Dirección Meteorológica de Chile, the Chilean National Weather Service). It presents a continuous and less populated environment, where the thorn-tailed rayadito has no native mammalian predators (Ippi et al. 2013, 2017, Rozzi and Jiménez 2014, Botero-Delgadillo et al. 2017).

Within this framework, our investigation aimed to: (1) describe the relationship between compatibility in aggressiveness and compatibility in parental care; (2) determine whether compatibility in aggressiveness predicts EPO in social nests; (3) analyse whether compatibility in aggressiveness explains body condition of the offspring; and (4) assess whether the presence of EPO in social nests lessens compatibility in nest defence and parental care.

Methods

General field procedures. The study was carried out over the reproductive season, from October to late December, during the years 2014 and 2015. We weekly monitored 220 nest boxes until they were occupied. 12 and 13 days after the hatching of their offspring, each adult (n=90) was captured in the nest box (n=45) between 7:30 am and 12:00 pm; they were banded with both metal and coloured bands (National Band and Tag Co., Newport, Kentucky, USA, or Split Metal Bird Rings, Porzana Ltd, UK or with a numbered band provided by the Servicio Agrícola y Ganadero (Chilean Agricultural and Livestock Service, or SAG), Chile). Chickens were banded with a metal numbered band when capturing the first adult, 12 days post-hatch. To calculate body condition index (BCI) of the offspring tarsus length and mass were recorded (see Hayes and Shonkwiler 2001).

Before releasing the birds, a small blood sample (ca. 17 μL) was taken from the brachial vein in both adults and chickens, and it was stored in FTA cards (Whatman®) for posterior molecular analysis (Quirici et al. 2014).

Recording behaviours

1. Nest defence behaviour. 13 days post-hatching, a focal human (used to simulate predator, see Hollander et al 2008), was placed 3 meters in front of the nest-box. Over a three-minute period, two observers recorded the frequency of hops and flights and alarm sounds using a digital voice recorder (Ippi et al. 2013, 2017). The "approach" variable was recorded as the minimum distance between the target birds and the focal human as measured by laser rangefinder, and the "speed" variable, was estimated as the number of hops and flights performed during the first minute of the test.

2. Aggressive behaviour. 15 days post-hatching, a stuffed decoy of an adult male rayadito was placed 3 min in front of the nest-box. Two observers recorded over 8 min (2 min of silence, 3 min of playback of thorn-tailed rayadito vocalisations, and 3 min of silence) the frequency of hops and flights, and alarm sounds using a digital voice recorder (see Ippi et al. 2013, 2017). The "approach" variable was estimated as the total amount of time the individual remained within 1m of the conspecific intruder. The "speed" was calculated as the number the hops and flights performed during the first minute of playback in the test (see Poblete et al chapter I).

3. Parental care behaviours. 17 days post-hatching, a digital video camera (Sony DCR-68) was positioned 3-4 m from the nest-box in order to record the frequency of offspring feeding and fecal cleaning behaviour in each nest box over a four-hour period, between 07:00 and 14:00 (see Espíndola-Hernández et al. 2017).

All recordings were reviewed using SMPlayer© (version 0.8.0). Information about aggressive and nest defence behaviours was tabulated using Jwatcher (version 1.0) (Blumstein et al. 2005).

Molecular analysis

DNA was extracted from the collected blood on FTA cards using a QIAGEN DNA extraction kit (Valencia, CA, USA). The individuals were genotyped at 13 polymorphic microsatellites loci, using eight species-specific markers, As1, As7, As18, As25-1, As25-5,As25-8, As25-10, and As25-14 (see Yañez et al. 2015; Botero-Delgadillo et al. 2017), and five cross-species amplifying markers: Asμ 15_ZEST,CcaTgu23 (Olano-Marín et al. 2010), Tgu06 (=CK307697), Tgu05 (=DV946651) (Slate et al.2007), and marker ZF_AC138573 (van Oosten et al. 2016; Botero-Delgadillo et al.2017). For the purpose of paternity analyses, 12 of 13 markers were included; they showed no significant deviations from Hardy-Weinberg equilibrium (HWE; all P>0.1) and the frequencies of null alleles were below 0.05. EPO estimation was obtained after performing parentage analyses under a combination of assignment and exclusion approaches (Jones et al.2010). CERVUS 3.07 (Kalinowski et al.2006) was used to perform parentage analyses. Paternity was assigned based on logarithm of odds (LOD score) and critical Delta. These results were checked to confirm or exclude paternity, whenever the most likely father showed no loci mismatches with putative offspring, and there was 95% confidence around the assignment based on LOD or Delta scores (Kalinowski et al.2007). When social father was the most likely candidate, assignment was confirmed regardless of the confidence around it. If a set of candidates (excluded social father) showed no mismatches and positive LOD scores, but relaxed confidence (80%), the whole set was excluded. Since EPO were not always confidently assigned to sampled males, gained paternity could not be determined (See Botero-Delgadillo for details).

The sex must be determined by molecular techniques, because Thorn-tailed Rayadito sexual dimorphism is not possible to determine visually (Moreno et al. 2007). To this end, we used the primers 2550 F and 2718R (Fridolfsson and Ellegren, 1999) to amplify the gene fragments CHD-W (unique to females) and CHD-Z (found in both males and females) using polymerase chain reactions (PCR). The PCR product was run on a 3% agarose gel in a Fluorimager (Vilber Lourmat), to separate the gene fragments; and sex was determined by visualization of the gel, with males exhibiting bands only of CHD-Z and females having bands of both CHD-W and CHD-Z, respectively.

Statistical analyses

Before performing the analyses, all behaviours were standardised. As frequencies of provisioning and cleaning depend on brood size, scores were corrected according to this variable.

1. Compatibility index (CI). We calculated CI indicating to what extend both partners of a social pair are compatibles in aggressiveness, nest defence, provisioning and cleaning behaviour. Mates with low CI are considered to be more compatibles in the described behaviours (David et al. 2015)

$$\mathrm{CI} = \Delta \text{ score partners}$$

2. Behavioural compatibility, EPO in social nests and body condition of the offspring

During descriptive analysis, we detected positive and significant correlations among agonistic behaviour compatibilities recorded during conspecific intrusion tests, as well as among agonistic behaviour compatibilities recorded during human intrusion tests. For this reason, component variables obtained by Principal component analysis (PCA) were used to characterise aggressiveness and nest defence respectively (supplementary material table S1).

We used lineal model (LM) to describe the relationships between compatibility in aggressiveness and parental care, and body condition of the offspring. Moreover, we used general lineal model (GLM) with binomial distribution to determine if compatibility in aggressiveness predicts the presence of EPO in nests. Finally, we used ANOVA test to assess differences in compatibility during nest defence and parental care between nests with and without EPO.

We considered an effect to be significant with p value < 0.05 for each test. Statistical analyses were performed in the R statistical environment v. 3.3.2 (R Core Team, 2016), using nlme (Pihneiro et al.2017), MASS (Venables and Ripley 2002), glm2 (Marschner 2011) packages.

Results

Aggressiveness and parental care compatibilities

Our results showed a positive and significant relationship between offspring feeding and fecal cleaning, with females of a pair showing similar levels of each behaviour to their male pairs, i.e., meaning high compatibilities in parental care behaviours (β=0.57; R^2=0.37; F=24.95; P<<0.01; Fig. 1A). Results also showed a positive and significant relationship when assessing compatibility in aggressiveness as a predictor of compatibility in provisioning behaviour (β=0.23; R^2=0.10; F=4.43; P=0.04) (Fig. 1B). This effect was not significant regarding fecal cleaning (β=0.18; R^2=0.01; F=1.57; P=0.21).

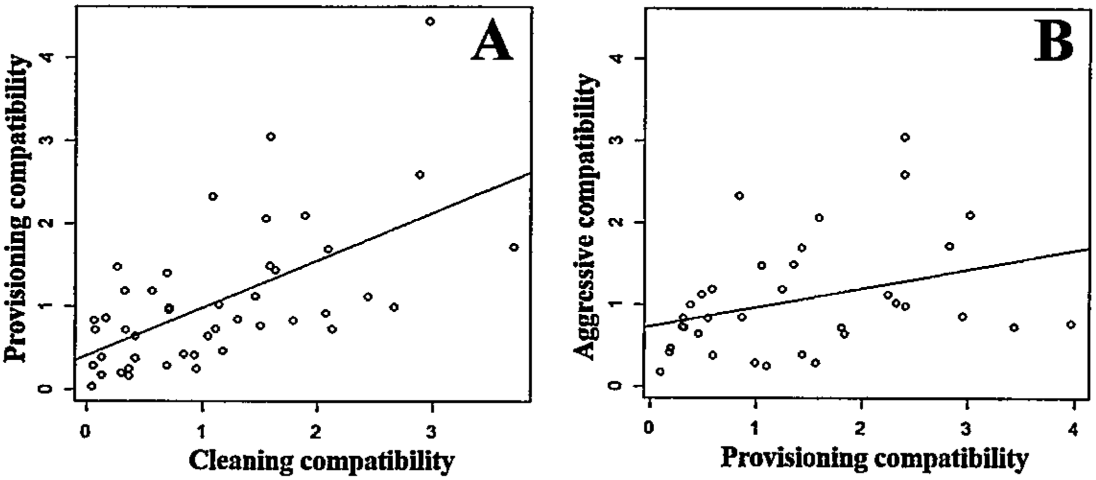

Figure 1. Compatibility relationships within parental care activities, and between aggressiveness and provisioning in 45 mates of thorn-tailed rayaditos. The plotted values are provisioning and fecal cleaning compatibilities (A); and aggressive and parental care compatibilities (B), respectively.

Behavioural compatibility, EPO in social nests and body condition of the offspring

We did not find significant results when assessing compatibility in aggressiveness as a predictor of the presence of EPO in social nests ($Z=0.24$; $P=0.80$) and body condition of the offspring ($\beta=0.04$; $R^2=-0.02$; $F=0.09$; $P=0.75$). A similar result was detected when analysing if the presence of EPO is related to low compatibility in nest defence ($F=1.54$; $P=0.69$) and parental care activities ($F=1.37$; $P=0.24$).

Discussion

We found that compatibility in aggressiveness predicts compatibility in parental care behaviour, but we failed to detect if compatibility in aggressiveness is related to both EPO in social nests and body condition of the offspring. An influence of EPO over compatibility in nest defence or parental care was not detected either.

Compatibility in aggressiveness and parental investment

We found that mates with a higher degree of compatibility in aggressiveness had a higher degree of compatibility in parental care, as well. This result is not surprising, since in species with biparental care, like the thorn-tailed rayadito, behavioural compatibility in personality traits has shown to be fundamental for different aspects associated to reproduction, as most of the partners share a common reproductive success (Spoon et al. 2006, Schuett et al. 2011, Mariette and Griffith 2012, 2015, Harris and Siefferman 2014). Although investigation on compatibility is limited, evidence suggests that self-selected pairs reproduce better than forced pairs (Klint and Enquist 1981, Lupo et al.1990, Cunninghan and Russell 2000, Ryan and Altmann 2001). Along with this, mate choice based on behavioural compatibility could be considered as the first step in the process of paternity choice, in which a high behavioural compatibility would ensure the provision of material advantages, such as a high territorial defence, parental care or protection. Besides, it could be an important mechanism to decrease the costs associated to mate choice, such as loss of energy and time (Anderson and Simmons 2006). Furthermore, behavioural compatibility could help females to avoid the negative consequences of sexual conflicts, allowing them to increase its resistance toward males that are less compatible with their own behavioural phenotype. Although females could bias paternity toward preferred mates by means of a range of potential mechanisms (see Rice et al. 2005), it is important to point out that behavioural traits such as aggressiveness could be considered during the mate choice not only because of its importance for acquisition and defence of resources, but also because it is a key behaviour on the evolutionary history of birds (van Oers and Naghib 2013). Therefore, it is likely that behavioural compatibility in aggressiveness is an important aspect during mate choice, to ensure an equitable participation in parental care activities (Spoon et al 2006).

As nest defence is usually associated to parental investment (Royle et al. 2012), we tried to characterise this behaviour against predators using as proxy a human intrusion test (Montgomery and Weatherhead 1988, Hollander et al.2008, Rodriguez-Prieto et al. 2010). However, we did not find significant relationships between compatibility in aggressiveness and compatibility in nest defence. That is, behavioural compatibility in nest defence seems not to be affected by aggressiveness compatibility. However, it is worthy to mention that "human" used as a stimulus could induce a less defined nest defence behaviour, as human intrusion does not represent a usual environmental stimulus automatically capable of triggering this response. Furthermore, if selection favours behavioural responses based on environmental context, nest defence behaviour against human become confusing (in case that this behaviour is an adaptive characteristic) in populations where predation pressure is low, like our thorn-tailed rayadito population (see Ippi et al 2013,2017, Poblete et al. Chapter I). In this context, it remains difficult to quantify any effects caused by the monitoring, manipulation and release process on the observed behaviour. Consequently, relationships between compatibility in aggressiveness and compatibility in nest defence were not detected in this study.

Behavioural compatibility, EPO and body condition of the offspring

We failed to find significant results regarding compatibility in aggressiveness as a predictor of the presence of EPO in social nests. Although previous results suggest that during the reproductive season, different behavioural phenotypes in males of thorn-tailed rayadito would partly explain variation in EPO in social nests, our results did not support this hypothesis for females (see Poblete et al chapter III). Some studies have reported that extra-pair behaviour in females could depend on ecological factors that favour the probability of meeting extra-pair partner, such as population density (Stutchbury and Morton 1995) or vegetation density (Valera et al.2003). As a consequence, it is likely that extra-pair behaviour in females is not related to its behavioural phenotype. Hence, detecting the effects of behavioural compatibility on EPO could require ecological and genetic information for a deeper understanding of the causes of extra-pair behaviour in thorn-tailed rayadito females.

The assessment of a potential relationship between the presence of EPO and low compatibility in nest defence and parental care did not provide significant results. Although in species with biparental care, selection could favour facultative behavioural responses in males, reducing nest defence behaviour or parental care (Birkhead and Møller 1993), empirical evidence to support this effect is scarce. In this context, it is difficult to determine if the presence of EPO or any other sexual conflict effectively trigger a facultative behavioural response, because a reduced parental investment could depend on factors like quality of the territory, age and/or condition of the male (Kempenaers and Sheldon 1997, Sheldon 2002).

Finally, no significant relationship between body condition of the offspring and characterized behavioural compatibilities was detected, probably because body condition of the offspring is affected by multiple factors, such as parental care (Clutton-Brock 1991), nutritional quality (Agosta 2008), and incubation behaviour (Kovarik et al. 2009), among others. Therefore, ecological and behavioural information should be included to assess the real benefits of behavioural compatibility on reproductive success.

Concluding remarks

Our approach allowed detecting a relationship between compatibility in aggressiveness and compatibility in parental care in a wild thorn-tailed rayadito population. We have evidenced that behavioural compatibility could be an important aspect in the process of paternity choice, in which a high behavioural compatibility seems to ensure an equitable participation in parental care. However, this research fails to detect if behavioural compatibility has any influence on extra-pair behaviour or body condition of the offspring.

In this context, it is necessary to achieve a deeper understanding of ecological and genetic factors that favour extra-pair behaviour and mould body condition of the offspring in this population.

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Data accessibility statement: Should the manuscript be accepted, the data supporting the results will be archived in an appropriate public repository such as Dryad or Figshare and the data DOI will be included in the article.

Author contributions: YP conceived the idea, conducted the research, analysed data and wrote the manuscript. PEH assisted with the field work, carried laboratory work and revised audiovisual material. GPS assisted with the field work and revised audiovisual material. EBD participated in the design of field protocols and carried laboratory work. RAV supervised the research and edited the manuscript.

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Behavioural compatibility and its relation with compatibility in parental investment in an endemic bird of the sub-Antarctic rainforests

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Electronic Supplementary Material

Contents

Table S1. Principal component analysis (PCA) to characterize aggressiveness and nest defence.

Figure S1. Photograph Thorn-tailed Rayadito in nest box.

Table S1. Eigenvalues of correlation matrix, and related statistics by PCA among observable behaviours during conspecific (CIT) and human intrusion tests (HIT).

Observable behaviours	Eigenvalue	% Total	Cumulative Eigenvalue	Cumulative %
Hops CIT	1,988059	39,76118	1,988059	39,7612
Flight CIT	1,475192	29,50384	3,463251	69,2650
Alarms CIT	0,710946	14,21892	4,174197	83,4839
Approach CIT	0,475689	9,51377	4,649886	92,9977
Speed CIT	0,350114	7,00229	5,000000	100,0000
Hops HIT	2,465282	49,30564	2,465282	49,3056
Flight HIT	1,170591	23,41181	3,635873	72,7175
Alarms HIT	0,718397	14,36794	4,354270	87,0854
Approach HIT	0,587712	11,75425	4,941982	98,8396
Speed HIT	0,058018	1,16036	5,000000	100,0000

Figure S1. Photograph of a couple of Thorn-tailed Rayadito (*Aphrastura spinicauda)* in nest box taken in Navarino Island, Southern Chile. Photograph by Yanina Poblete.

Discusión

En esta investigación se utilizó un punto de vista integrador de las conductas agonistas con el propósito de evidenciar la naturaleza evolutiva de la agresividad como un rasgo de la personalidad sujeto a selección. La organización de la personalidad animal como una unidad funcional de carácter evolutivo se puso a prueba, evaluando su estructura e independencia respecto a otros rasgos con los cuales podría integrarse funcionalmente bajo ciertas condiciones ambientales. Con este propósito, se seleccionó una población de rayadito expuesta a condiciones que podrían limitar su integración con otros rasgos como la conducta exploratoria o el tamaño corporal. Junto con ello, su potencial capacidad de responder a la selección fue evaluada al estimar su heredabilidad en sentido estricto. Su impacto sobre la biología reproductiva se determinó al describir la relación de las conductas agonistas con el comportamiento extra-pareja, las conductas de inversión parental y la calidad de las crías. Asimismo, se utilizó la compatibilidad conductual entre los integrantes de la pareja para profundizar el posible impacto que la agresividad podría generar sobre la biología reproductiva, especialmente como un rasgo importante durante la selección de pareja.

Si bien en este estudio no fue posible describir la estructura de la conducta exploratoria desde un punto de vista integrativo, debido al limitado número de conductas observables obtenidas durante cada prueba experimental, la naturaleza adaptativa de este comportamiento y su reconocimiento como rasgo de la personalidad animal han sido ampliamente documentados (Verbeek et al., 1996; Dingemanse et al., 2002; van Dongen et al., 2010; van Oers y Naghib, 2013). Por esta razón, en esta tesis se evaluó el impacto de este comportamiento sobre la biología reproductiva a partir de la relación entre las conductas observables durante la prueba de exploración, con el comportamiento extra-pareja, las conductas de inversión parental y la calidad de las crías, incluyendo la compatibilidad en conducta exploratoria en los análisis.

En la primera etapa de este trabajo se evaluó la relación de las conductas agonistas y la tendencia exploratoria con el sexo, debido a que en varias especies se ha demostrado que los machos tienden a ser más agresivos y exploradores, probablemente por los mayores niveles de testosterona que presentan durante la estación reproductiva (Wingfield et al., 1987; Soma, 2006). Sin embargo, nuestros resultados en general no muestran un dimorfismo sexual evidente en estos comportamientos (Tabla 1; Capítulo I), reflejando que la variación en estas conductas es independiente del sexo. En relación con esto, el estudio previo de Moreno et al. (2007), evidenció que en el cuidado parental, los machos y las hembras de cada pareja, se comportan de manera muy similar, con ambos padres realizando una alta labor de cuidado parental.

La edad es otro factor que podría influir sobre el comportamiento. Por ejemplo, algunas investigaciones han reportado que las conductas agonistas aumentan con la edad, pero disminuyen progresivamente con el inicio de la senescencia (Møller y Nielsen, 2014; Ortega et al., 2017). No obstante, también se ha reportado que estos comportamientos no estarían relacionados con la edad (Montgomerie y Weatherhead, 1988). La edad en especies silvestres en su mayoría es difícil de estimar, puesto que la dispersión o la muerte de los individuos reducen las posibilidades de recapturar individuos con edad conocida.

En esta investigación, la edad se determinó utilizando el método captura-marcaje-recaptura, a partir de cuando los individuos fueron anillados por primera vez siendo crías (Clutton-Brock y Sheldon, 2010). Sin embargo, la mayoría de los individuos fueron capturados por primera vez siendo adultos y en este caso se asumió que tenían 1 año de edad al momento de ser capturados (Karlsson et al., 1986; Montalvo and Potti, 1992). Con base a estas estimaciones, nuestros resultados revelaron que la edad no se relaciona significativamente con las conductas observadas (Tabla 1, Capítulo I). Posiblemente estos resultados hacen evidente que es necesario incluir estimaciones más precisas de la edad para obtener resultados concluyentes al respecto.

Durante el anillamiento se realizaron mediciones morfológicas, como largo del culmen, ala, tarso y peso con el propósito de evaluar si estos rasgos se relacionan con las conductas observadas, dado que algunos estudios señalan que las conductas agonistas podrían covariar con el tamaño corporal (Rowland, 1989; Huntingford et al., 1990; Schuett, 1997; Just y Morris, 2002; Svensson et al., 2012). No obstante, nuestros resultados revelaron que las conductas agonistas y la conducta exploratoria no se relacionan con las dimensiones corporales en el rayadito (material suplementario Tabla S1, Capítulo I). Aunque el tamaño corporal podría modular especialmente los encuentros agonistas, la evidencia sugiere que la importancia relativa de esta relación podría depender en gran medida del contexto, porque la decisión de expresar un determinado comportamiento podría depender de factores como la densidad poblacional y la densidad de recursos, considerando su distribución en el espacio y el tiempo (Brown, 1964). Por este motivo, es probable que dadas las características del área de estudio, las conductas agonistas sean en parte independientes del tamaño corporal.

Considerando la naturaleza lábil del comportamiento, durante las diferentes pruebas se registró la temperatura ambiente con el propósito de evaluar si su variación influye sobre la variabilidad de las conductas observadas y también se consideró el año en el cual se realizaron las pruebas conductuales. Con esta información fue posible corroborar que las conductas observadas no se relacionan con la temperatura presente durante las pruebas, ni tampoco con el año en el cual se realizaron (Tabla 1, Capítulo I).

En línea con la mayoría de los estudios que exploran rasgos de la personalidad animal, nuestros resultados revelaron que la variabilidad de estas conductas es independiente de factores como el sexo, edad, tamaño corporal y fluctuaciones ambientales (van Oers y Naguib, 2013), lo cual respalda la idea de que el comportamiento en su mayoría presenta una flexibilidad limitada, con diferencias conductuales entre individuos modeladas por procesos evolutivos que podrían actuar de manera particular sobre el comportamiento (Bergmuller, 2010).

Posteriormente, nos centramos en el concepto de integración funcional para caracterizar una unidad conductual que representa un carácter evolutivo (Wagner, 2000; Schwenk, 2001; Pigliucci, 2003). Con este fin, se utilizaron modelos de ecuaciones estructurales (SEM) (Araya-Ajoy y Dingemanse, 2014) que permitieron generar diferentes escenarios *a priori* con el propósito de evidenciar una unidad conductual capaz de integrar las conductas agonistas registradas bajo dos contextos de intrusión territorial (Figura 1, Capítulo I), en los cuales se utilizó siempre al mismo humano focal (HIT, human intrusión test) y a un con-específico (CIT, cospecific intrusión test) como intrusos, respectivamente (Hollander et al., 2008; Ippi et al., 2013).

Por medio de este análisis, nuestros resultados revelaron que las conductas agonistas desplegadas durante HIT mostraron una escasa covariación con la unidad conductual modelada, por lo que no fue posible respaldar la integración funcional de estas conductas observables (Kline et al., 2015). Basados en estos resultados, se sugiere que HIT no es una prueba apropiada para capturar la presencia de una unidad conductual para describir agresividad, probablemente porque el humano utilizado como intruso no representa un estímulo ambiental habitual que sea automáticamente percibido por los individuos como un desencadenante de agresividad, sobre todo si la agresividad ha evolucionado como un rasgo adaptativo a determinados estímulos existentes en el ambiente natural. Junto con ello, es importante señalar que el humano habitualmente es utilizado como un estímulo que representa a un depredador (Hollander et al., 2008). Por esta razón, también es probable que una respuesta agresiva menos definida frente a un humano en esta población, sea resultado de la menor presión de depredación a la que han estado expuestos estos individuos (véase Ippi et al. 2011, 2013). Además y debido a que es difícil evidenciar el efecto que la presencia humana puede generar en los individuos durante el monitoreo y anillamiento, en este estudio no fue posible respaldar la utilización de HIT para describir la estructura de la agresividad.

No obstante, se encontró una gran covariación entre las conductas agonistas registradas durante CIT con una unidad funcional a la cual llamamos agresividad (Figura 3A, Capítulo I). Sobre esta base, nuestros resultados sugieren que un con-específico es un estímulo más efectivo para desencadenar agresividad como una respuesta adaptativa, probablemente porque la agresividad hacia un con-específico es un comportamiento fundamental en la historia de vida de las aves (van Oers and Naghi, 2013). En este contexto, es probable que la selección actúe fuertemente en la integración funcional de las conductas agonistas registradas durante CIT. Sin embargo, podría actuar débilmente en la integración funcional de estas conductas durante HIT. Con base en ello, en esta tesis se propone que la integración funcional de las conductas agonistas depende en gran medida del contexto ambiental, por lo cual se sugiere precaución en la selección de las pruebas experimentales cuando el propósito sea caracterizar el comportamiento desde un punto de vista evolutivo.

La integración funcional también puede surgir entre diferentes atributos bajo ciertas condiciones ambientales. El concepto de síndrome conductual es utilizado para referirse a la integración funcional entre diferentes comportamientos (Réale y Dingemanse, 2010). Particularmente, la integración entre agresividad y conducta exploratoria conocida como "comportamiento de toma de riesgos" es un fenómeno descrito principalmente en poblaciones expuestas a altas presiones de depredación y que comúnmente son afectadas por diversos factores que generan estrés (Bell, 2005; Martins et al., 2007; McElreath y Strimling, 2006). En esta investigación, quisimos evaluar la presencia de este síndrome conductual bajo condiciones menos estresantes. De este modo, fue posible evidenciar que la covariación agresividad-conducta exploratoria no es detectable en la población de isla Navarino, probablemente porque en dicha localidad los individuos presentan menor presión de depredación y en general, presentan bajos niveles de estrés, en comparación con otras poblaciones de rayadito (Ippi et al., 2013; Quirici et al., 2014; 2016; Botero-

Delgadillo et al., 2017). Sobre la base de estos resultados, es posible respaldar la idea de que en ambientes menos estresantes y/o impredecibles, estos comportamientos se encuentran menos restringidos, por lo que pueden variar de forma independiente uno del otro (Sih, 1992; Bell, 2005; McElreath y Strimling, 2006).

Debido al limitado número de medidas repetidas por cada conducta observada, no fue posible estimar cuánto de la variabilidad de cada conducta observada es explicada por la identidad de los individuos. Sin embargo, fue posible expandir nuestro análisis cuando detectamos que las conductas agonistas descritas durante CIT integraban una unidad funcional. Para ello, las conductas agonistas registradas durante CIT se consideraron medidas repetidas del mismo rasgo (agresividad) y la identidad individual se incluyó como efecto aleatorio en el modelo (véase Dingemanse y Dochtermann, 2013). De esta forma, se encontró que una parte importante de la variación en agresividad es explicada por la identidad de los individuos (Tabla 3, Capítulo I), lo cual respalda la fuerte integración funcional entre las conductas agonistas a nivel intra-individual. Estos resultados son interesantes porque además coinciden con otros estudios donde la variabilidad explicada por la identidad es evaluada sobre medidas repetidas del mismo comportamiento observable (e.g., llamados de alarma) (Araya-Ajoy y Dingemanse, 2014; Moiron et al., 2016). Considerando estos resultados, se sugiere que la descripción de caracteres evolutivos podría ser una novedosa alternativa para cuantificar la variabilidad de un rasgo atribuible a la identidad individual.

Sin embargo, la naturaleza adaptativa de la agresividad como una unidad sujeta a cambio evolutivo, requiere que parte de su variación sea heredable (Endler, 1986). Así también, la evidencia disponible principalmente a través de estudios realizados en cautiverio con información de pedigree, muestra que las conductas agonistas son parcialmente heredables en un rango de valores de heredabilidad que va entre 0.21 a 0.89 (van Oers y Sinn, 2013). Gracias a la disponibilidad de marcadores genéticos y nuevos métodos estadísticos, actualmente también es posible estimar la heredabilidad en sentido estricto (h^2) en poblaciones silvestres. En este estudio se modeló la agresividad con base en las conductas agonistas que mejor explican la presencia de una unidad conductual latente (Figura 2, Capítulo II) y se utilizaron coeficientes de parentesco obtenidos a partir de marcadores genéticos especie-específicos de rayadito (Yañez et al., 2015; Botero-Delgadillo et al., 2017), los cuales se organizaron en una matriz de parentesco para ser incluidos como efecto aleatorio en un modelo mixto (Kruijer et al., 2016). De esta forma, se estimó un valor de 0.33 de (h^2) (Tabla 1, Capítulo II). Este resultado es interesante, ya que se encuentra dentro del rango (h^2) calculado sobre las conductas agonistas cuando se dispone de información sobre pedigree y, además, es muy similar a los valores obtenidos en condiciones naturales con datos de pedigree en un estudio realizado por Bakker en 1994. Con ello, es posible señalar que en esta población la agresividad cuenta con variación genética suficiente para responder a la selección y que parte de la variabilidad de este rasgo es modulada genéticamente.

Aunque las bases genéticas responsables del comportamiento son todavía inciertas, es ampliamente aceptado que los rasgos de la personalidad son modulados por genes pleiotrópicos (van Oers et al., 2005; van Oers y Mueller, 2010). Del mismo modo, es probable que esta modulación sea en parte responsable de la integración funcional detectada entre las conductas agonistas en una unidad conductual parcialmente heredable. No obstante, es importante señalar que la heredabilidad de un rasgo puede variar en función del contexto, dado que la selección puede actuar de distinta forma sobre la variación heredable en función del ambiente (Dingemanse et al., 2009).

Hasta el momento nuestros resultados coinciden con la mayoría de los estudios, demostrando la importancia evolutiva que la conducta agresiva tiene en la historia de las aves (van Oers and Naghi, 2013). Sin embargo y con el objetivo de profundizar nuestro conocimiento respecto al papel que los rasgos de la personalidad podrían tener particularmente en la biología reproductiva, se evaluó cómo las conductas agonistas y la conducta exploratoria se relacionan con el comportamiento extra-pareja, las conductas de inversión parental y la calidad de cría. Debido a que el comportamiento extra-pareja es complejo de evidenciar a través de observaciones de campo, se utilizaron marcadores genéticos para detectar la presencia de crías-extra pareja (CEP) y este dato se utilizó como indicador de comportamiento extra-pareja (van Oers et al., 2008; Patrick et al., 2012). La inversión parental se estimó a través de la conducta de defensa frente a un potencial depredador (Hollander et al., 2008) y con base en la frecuencia de aprovisionamiento corregida por el número de crías, obtenida a través de grabaciones realizadas en cada nido (Espíndola-Hernández et al., 2017). La calidad de cría se caracterizó a través del volumen de la nidada y el índice de condición corporal de las crías (Hayes y Shonkwyles 2001). De esta manera, fue posible encontrar que una conducta exploratoria más intensa en los machos favorece la presencia de CEP en el nido social (Figura 1A, Capítulo III). Sin embargo, no fue posible detectar paternidad ganada fuera del nido social, por lo cual no podemos concluir que estos machos compensen la paternidad perdida en su nido a través de crías extra-pareja, aunque la evidencia señala que esto ocurre en algunas especies (Patrick et al., 2012). Asimismo, se encontró que los machos más agresivos frente a un con-específico presentan en promedio menos CEP en su nido social en relación a machos menos agresivos (Figura 1B, Capítulo III). Respecto a la hembra, no fue posible detectar una relación entre conducta exploratoria o conducta agresiva con la presencia de CEP en el nido. Por esto, nuestros resultados sugieren que durante la estación reproductiva, diferentes fenotipos conductuales en los machos podrían explicar la variación en la conducta extra-pareja, pero no es posible respaldar esta hipótesis para las hembras. En línea con ello, algunos estudios han reportado que la promiscuidad de la hembra podría depender de factores ecológicos que favorecen la probabilidad de encuentros extra-pareja, como son la mayor densidad poblacional (Stutchbury y Morton, 1995) o la vegetación más abundante y densa (Valera et al., 2003). Por otra parte, la teoría de conflictos sexuales dada por diferencias entre la adecuación óptima entre machos y hembras, predice que la evolución favorecería rasgos de los machos que permiten manipular a las hembras, mientras que las hembras resistirían esta manipulación a través de la selección sexual (Parker, 1979). Por esta razón, es probable que machos y hembras difieran intrínsecamente en los mecanismos para maximizar su adecuación biológica a través de comportamiento extra-pareja. Por lo tanto, es probable que la conducta más exploradora de algunos machos genere mayores oportunidades de encuentros extra-pareja para las hembras, mientras que una mayor agresividad en los machos parece limitar el comportamiento extra-pareja de las hembras. En este sentido, el comportamiento extra-pareja en las hembras parece ser una consecuencia de la conducta de los machos, lo cual podría estar asociado a características ecológicas que en conjunto favorecen los encuentros extra-pareja para ellas. Aunque la evidencia es escasa, algunos estudios realizados en *Drosophila* muestran que el resultado de los conflictos sexuales podría ser independiente de la conducta de la hembra (Partridge and Farquhar, 1981; Chapman et al., 1995; Rice, 1996; Holland and Rice, 1999) y en general la mayoría de las investigaciones no han logrado dilucidar si el comportamiento extra-pareja es un rasgo adaptativo sujeto a selección o una consecuencia de su relación con rasgos asociados a conductas de riesgo como la conducta exploratoria (Patrick et al., 2012).

Uno de los principales beneficios del comportamiento extra-pareja para la hembra es la posibilidad de mejorar las cualidades de su descendencia, si es que el macho extra-pareja tiene una mejor calidad genética respecto a su pareja social (Kempenaers y Schlicht, 2010). Aunque los mecanismos para detectar la calidad genética de los machos son todavía poco claros, la evidencia señala que las hembras tienen preferencias por machos específicos y que cuando copulan con ellos colocan huevos de mayor volumen y generan crías con mejor condición corporal (Cunninghan and Russell, 2000; Osorno et al. 2006). Si bien en esta investigación no fue posible asociar cada huevo con un padre biológico, se logró detectar que en los nidos con CEP la puesta fue de mayor volumen (Figura 3A, Capítulo III). Sin embargo, no logramos detectar alguna relación entre la condición corporal de las crías respecto a la presencia de CEP o diferencias significativas entre las crías extra y la crías de la pareja, probablemente porque este atributo depende de múltiples factores como el cuidado parental (Clutton-Brock, 1991), la calidad nutricional (Agosta, 2008) y/o la conducta de incubación (Kovarik et al., 2009), entre otros. Al respecto, parece ser que la hembra recibe beneficios indirectos de la conducta extra-pareja, pero nuestros resultados no lograron ser totalmente concluyentes.

Entre los costos asociados al comportamiento extra-pareja de la hembra, los conflictos sexuales incluyen un conjunto de conductas que el macho podría realizar si descubre la infidelidad. En teoría, es esperable que la selección favorezca conductas facultativas en los machos, quienes podrían reducir su conducta de defensa del nido o aprovisionamiento cuando existen CEP en el nido (Birkhead and Møller, 1993). En esta investigación, no fue posible detectar una reducción en la inversión parental en nidos que presentaron CEP. Del mismo modo, la evidencia que respalda la existencia de respuestas facultativas en los machos frente a la infidelidad de la hembra es bastante escasa, puesto que es difícil determinar si los machos tienen mecanismos efectivos para detectar la infidelidad y porque una menor inversión parental puede estar asociada a factores difíciles de aislar como son la calidad del territorio, edad o condición del macho (Kempenaers and Sheldon, 1997; Sheldon, 2002).

Independientemente de la relación entre inversión parental y comportamiento extra-pareja, la variabilidad conductual en inversión parental ha sido documentada en múltiples taxa. Por ello, se ha propuesto que su variación podría estar asociada a la variabilidad presente en rasgos de la personalidad (Royle et al. 2012). En esta tesis, se encontró que las hembras más exploradoras defendieron su nido de forma más intensa y alimentaron a la nidada de forma más frecuente. Junto con ello, se encontró que hembras más agresivas fueron más intensas en la defensa del nido respecto a hembras menos agresivas (figura 2; Capítulo III). Sin embargo, no fue posible detectar estas relaciones en los machos, a excepción de una tendencia positiva entre agresividad y defensa de nido. Con base en esto, nuestros resultados sugieren que la variabilidad en rasgos de la personalidad podría explicar en parte la variación en conductas de inversión parental, particularmente en las hembras.

Aunque la evidencia sugiere que los rasgos de la personalidad parecen influir sobre algunos aspectos de la biología reproductiva, es importante reconocer la existencia de propiedades emergentes que surgen de la interacción de estos comportamientos entre los integrantes de una pareja y que podrían modular aspectos reproductivos (Spoon et al., 2007; van Oers et al., 2008). Estas propiedades agrupadas bajo el concepto de compatibilidad en su mayoría reflejan el grado de similitud entre los integrantes de una pareja (Trivers, 1972; Marzluff y Balda, 1988a; Balck, 1996). Con base en ello, en esta investigación se utilizó un índice de similitud (David et al., 2015) para describir la compatibilidad en rasgos de la personalidad y en conductas de inversión parental. De esta forma, fue posible evidenciar que parejas compatibles en agresividad resultaron ser más compatibles en aprovisionamiento de la nidada (figura 1; Capítulo IV). Este resultado sugiere que la compatibilidad en agresividad podría ser un aspecto considerado durante la elección de pareja, el cual podría representar una señal para la hembra que asegure una participación equitativa en las actividades de cuidado parental y que contribuya positivamente en la descendencia (Gabriel y Black, 2012; Adler y Ritchison, 2011; Mitrus et al., 2010).

Asimismo, algunos estudios han reportado que la compatibilidad conductual podría influir en la decisión de tener encuentros extra-pareja (Spoon et al., 2007; van Oers et al., 2007).

Sin embargo, no fue posible encontrar una relación entre compatibilidad conductual y presencia de CEP en el nido social. Finalmente y aunque los estudios en compatibilidad conductual aún son escasos, la evidencia sugiere que parejas que se escogen se reproducen mejor en relación a parejas forzadas (Klint and Enquist, 1981; Lupo et al., 1990; Cunninghan y Russell, 2000; Ryan y Altmann, 2001). Por este motivo, es esperable que parejas menos compatibles tengan nidadas de menor calidad. No obstante, en esta investigación no fue posible evidenciar una menor calidad de nidada en parejas menos compatibles. Sobre la base de estos resultados, es probable que la compatibilidad conductual sea un factor considerado durante la elección de pareja, particularmente en especies socialmente monógamas con cuidado biparental como el rayadito, ya que ambos integrantes de la pareja comparten una descendencia común (Spoon et al., 2006; Schuett et al., 2011; Mariette y Griffith, 2012, 2015; Harris y Siefferman, 2014). Sin embargo, en este estudio no fue posible concluir si la compatibilidad conductual impacta sobre la adecuación biológica de los individuos.

En resumen, esta tesis proporciona evidencia que respalda la importancia evolutiva de los rasgos de la personalidad en la biología reproductiva de aves socialmente monógamas como el Rayadito, y hace especial énfasis en la importancia del contexto ambiental sobre la modulación y expresión de dichos rasgos. Con base en ello, es importante destacar que los rasgos conductuales en poblaciones silvestres parecen tener un carácter adaptativo, el cual podría ser local y, por lo tanto, las perturbaciones ambientales que generan rápidos cambios en la disponibilidad y/o distribución de los recursos, podrían afectar profundamente a estas poblaciones, porque probablemente no logren ajustar su comportamiento al ritmo que ocurren estos cambios.

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