



RESEARCH ARTICLE

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

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ABSTRACT

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

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

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

RESUMEN

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

poblaciones. Por ende, los rayaditos podrían estar usando estrategias específicas para lidiar con el clima local en ambientes contrastantes.

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

INTRODUCTION

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

Studies on intraspecific differences in nest morphology have shown that the nest properties of heat retention and water loss capacity, which are determined by the composition of nest materials, may differ according to climatic conditions (Mainwaring et al. 2014). For instance, populations breeding in colder environments can increase heat retention by building larger nests (Kern and van Riper 1984, Briskie 1995), using thicker and less porous nest walls (Crossman et al. 2011), or adding more feathers and/or hairs as cup-lining material (Møller 1984, Mainwaring et al. 2012). Nest structure can also differ because of local precipitation and humidity, given that bulkier nests can absorb more water and take more time to dry, which is likely disadvantageous in humid environments (Rohwer and Law 2010). Despite these findings, other studies have shown that behavioral traits other than nest structure may respond to climate regimes (e.g., nest

location; Kern 1984, Kern et al. 1993), suggesting that variation in nesting habits can be species specific or even context dependent. Further research is thus required for a better understanding of geographic variation in nest structure within species and its causal relationship with environmental factors. Unfortunately, information is still scarce and biased toward species from the Northern Hemisphere (see Mainwaring et al. 2014). Here, we address this data gap by describing interpopulation differences in nest architecture of the Thorn-tailed Rayadito (*Aphrastura spinicauda*), a secondary cavity-nesting bird that inhabits the temperate forests of southern South America.

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

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

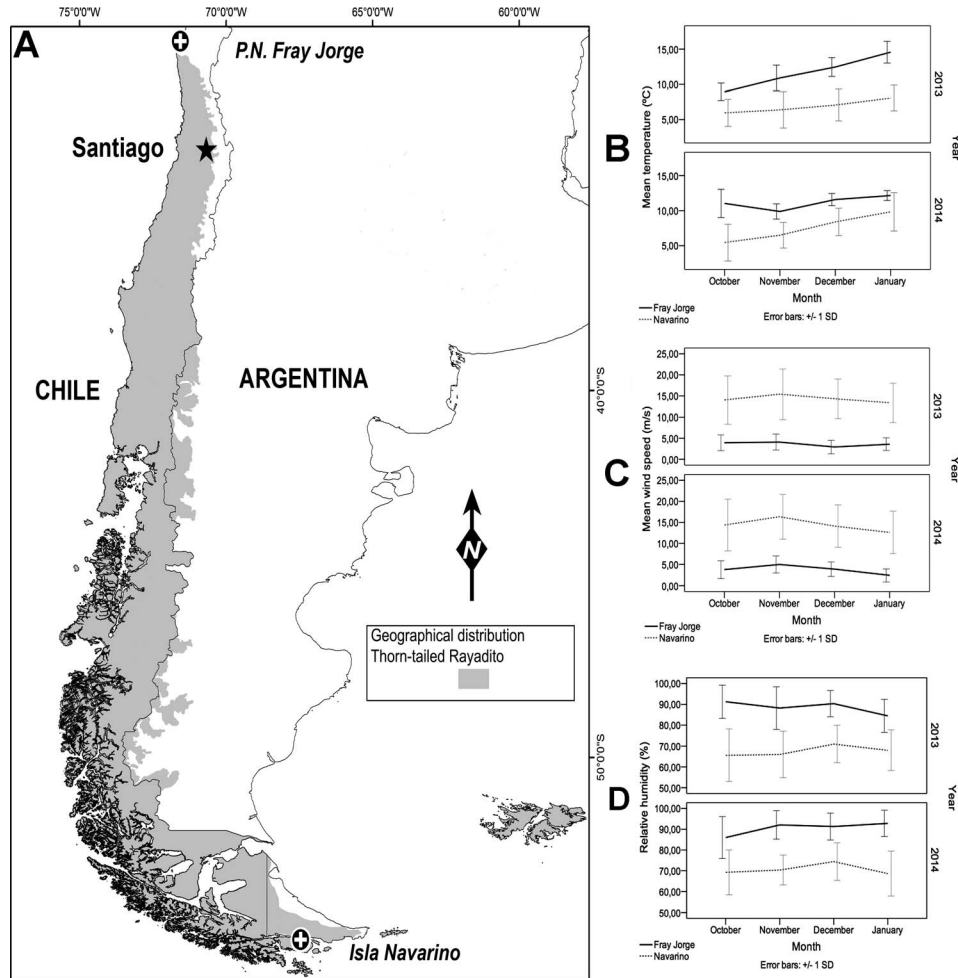


FIGURE 1. (A) Study populations of Thorn-tailed Rayaditos in the northern (Fray Jorge National Park) and southern (Isla Navarino) limits of the species' distributional range in Chile. Meteorological variables that differed between localities during the breeding season included (B) mean temperature, (C)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

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

METHODS

Nest Collection

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

Meteorological Data

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

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

Nest Architecture

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

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

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

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

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

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

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

Nest Thermal Properties and Water Absorption

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

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

We obtained 60 recordings of temperature per nest from both tests, which were fitted to a cubic model using

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

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

Statistical Analyses

Statistical analyses were performed in R 2.15.2 (R Development Core Team 2012), using $\alpha = 0.05$ for hypothesis testing. We first tested all variables for normality using the Shapiro-Wilks test. None of the meteorological variables fitted the assumptions of normality, so we transformed variables using square root (daily temperature, wind speed) and log (percent humidity) transformations. Variables describing nest structure (mean nest depth, nest volume, mean inner cup diameter, cup volume, nest dry weight) were all normally distributed (all $P > 0.05$). We used the original descriptions of nest composition (percent contribution of structural layer, percent internal lining, percent woody items, percent plant fibers, percent dry grass, percent animal insulating material, percent miscellaneous) in a principal component analysis (PCA) to reduce dimensionality (correlation

matrix; Digby and Kempton 1987), generating new variables from the regression factor scores of the first 3 components because they explained 80% of the total variance (see below). These 3 new variables were normally distributed (all $P > 0.05$). Finally, all but 2 variables from the thermal and hygroscopic analyses were normally distributed (all $P > 0.05$); equilibrium temperature (convection–conduction tests) and weight loss percentage after 8 hr were log transformed.

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

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

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

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

^aA mean value was used for each nest from measurements taken on the 4 sides.
^bOnly maximum diameter is reported.

RESULTS

Climatic Patterns

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

Nest Structure and Composition

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

Although nest dry mass did not vary between localities, the remaining measurements of nest dimensions showed significant differences: on average, nests from Fray Jorge were deeper and larger (i.e. greater volume), whereas

Navarino's had wider and larger nest cups (Tables 1 and 2A). According to the first MANOVA, nest structure was significantly different between Fray Jorge and Navarino (Roy's largest root = 0.51, $F_{5,106} = 10.8$, $P < 0.001$), but there was neither an effect of the breeding season (year: 2013–2014; Roy's largest root = 0.11, $F_{5,106} = 0.97$, $P = 0.44$) nor a significant interaction between these 2 variables (Roy's largest root = 0.10, $F_{5,106} = 2.10$, $P = 0.07$). Although the analysis suggested a positive effect of clutch size on nest structure within each population (Roy's largest root = 0.11, $F_{5,110} = 2.43$, $P = 0.04$), only cup volume was significantly affected (Table 2A). There was no interaction between clutch size and the breeding season (Roy's largest root = 0.83, $F_{5,108} = 1.79$, $P = 0.12$).

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

Nest Thermal and Hygroscopic Properties

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

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

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

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

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

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

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

Relationship between Architecture and Thermal-Hygroscopic Properties

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

Nest architecture was a significant predictor of nest heat loss by convection. The Δ_5 value ($R = 0.45$, $F_{1,71} = 17.5$, $P < 0.001$) and the equilibrium temperature ($R = 0.34$, $F_{1,71} = 9.1$, $P = 0.004$) both exhibited a functional relation with the structural and/or compositional descriptors (Appendix Table 5). Nest volume was the variable that best explained variation in the Δ_5 value, whereas cup volume was the best

predictor of equilibrium temperature (Appendix Table 5 and Figure 3). There was neither autocorrelation between data points (Δ_5 value: Durbin-Watson's $d = 1.96$; equilibrium temperature: Durbin-Watson's $d = 1.98$) nor collinearity among the predictor variables (Δ_5 value: all condition index < 1.94 ; equilibrium temperature: all condition index < 4.99).

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

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

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

(A) Convection test		
Variable	Locality	
	Fray Jorge (<i>n</i> = 36)	Navarino (<i>n</i> = 36)
Δ_5 value ($^{\circ}\text{C}$) ^a	1.84 \pm 0.73	2.98 \pm 1.12
Rate of heat loss 1 ^b	0.76 \pm 0.20	0.98 \pm 0.31
Rate of heat loss 2 ^b	0.01 \pm 0.03	0.01 \pm 0.01
Equilibrium temperature ($^{\circ}\text{C}$) ^b	8.12 \pm 1.17	6.98 \pm 2.01
(B) Conduction test		
Variable	Locality	
	Fray Jorge (<i>n</i> = 36)	Navarino (<i>n</i> = 36)
Δ_5 value ($^{\circ}\text{C}$) ^a	3.46 \pm 0.94	1.29 \pm 0.69
Rate of heat loss 1 ^b	1.06 \pm 0.27	0.88 \pm 0.16
Rate of heat loss 2 ^b	0.02 \pm 0.02	0.02 \pm 0.01
Equilibrium temperature ($^{\circ}\text{C}$) ^b	16.64 \pm 2.02	18.53 \pm 1.23
(C) Hygroscopic test		
Variable	Locality	
	Fray Jorge (<i>n</i> = 26)	Navarino (<i>n</i> = 25)
Nest gained ratio ^b	2.04 \pm 0.85	3.29 \pm 0.97
Percent weight loss (15 min)	36.96 \pm 15.83	29.75 \pm 7.66
Percent weight loss (8 hr)	51.35 \pm 16.79	43.77 \pm 14.38

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

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

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

DISCUSSION

Variation in nest morphology is predicted to occur when environmental conditions vary temporally and/or spatially (Mainwaring et al. 2014) as birds try to regulate the nest's microclimate for optimal nestling development by adaptively modifying its structure and/or composition (Collias and Collias 1984, Webb 1987, Hansell 2000, Deeming 2002). We found that thermal and hygroscopic properties of nests in the Thorn-tailed Rayadito varied predictably between 2 populations and were related to variation in nest morphology. Furthermore, we found this variation to be consistent in both populations during 2 breeding seasons.

Contrary to our expectations, however, nests at the northern part of the species' distribution (Fray Jorge) were larger and seemed to be less affected by heat loss by convection. This finding suggests that Thorn-tailed Rayaditos could be using distinct strategies to cope with the local climate (e.g., ambient temperature) in contrasting environments, especially if there are site-specific selective pressures favoring certain types of nest structure or composition (see Hilton et al. 2004).

Differences in Nest Structure and Composition

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

Functional Properties and the Role of Nest Morphology

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

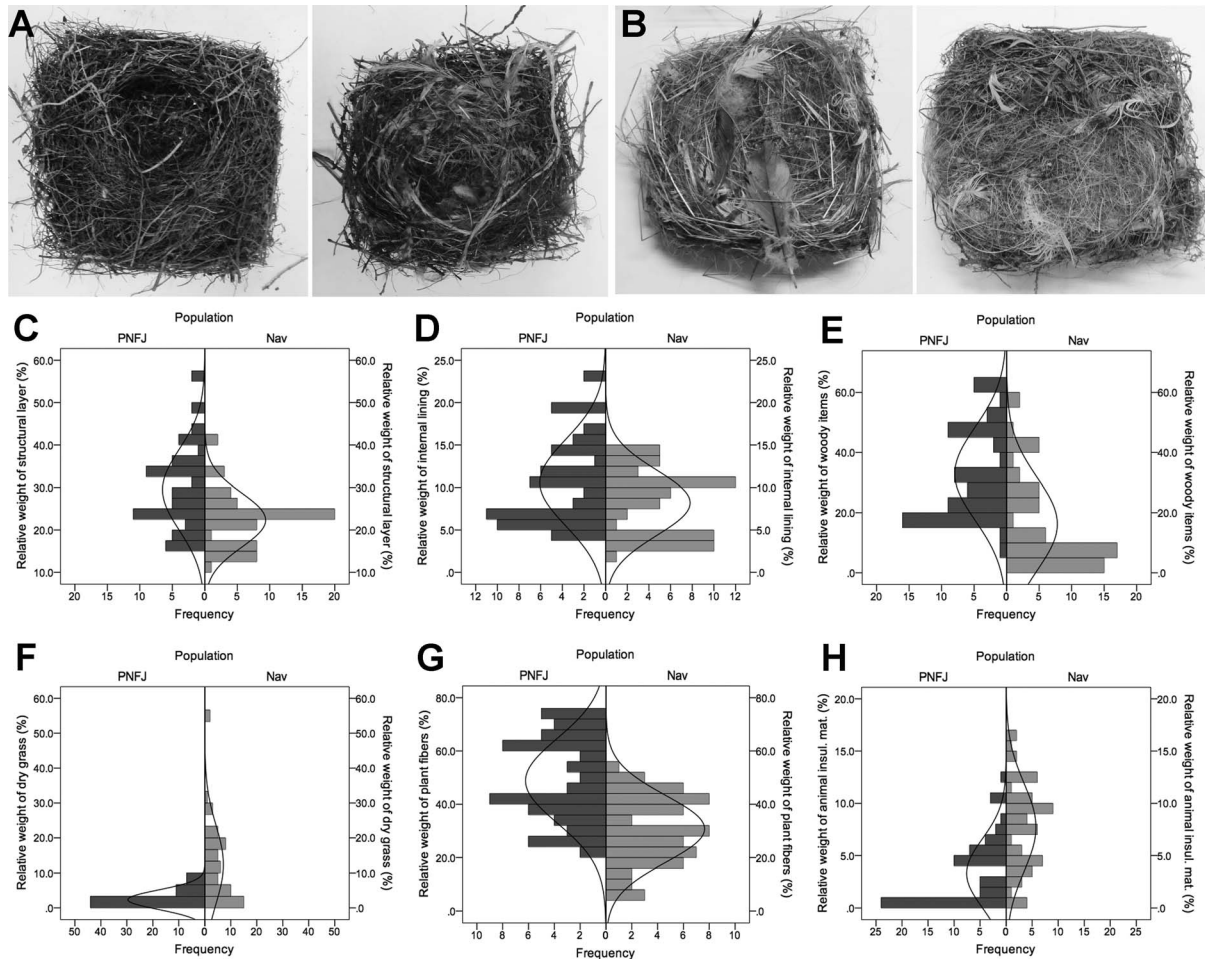


FIGURE 2. Composition of Thorn-tailed Rayadito nests from (A) Fray Jorge National Park and (B) Isla Navarino, Chile. We quantified the relative contributions of (C) the structural layer and (D) the internal lining to total nest weight. We also estimated the relative contributions of constitutive components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

Although Fray Jorge is located at a subtropical latitude, weather conditions in the coastal forest remnants at this site during the beginning of the breeding season are similar to those in other temperate humid forests in the Southern Hemisphere during the first weeks of October (relative humidity usually $>80\%$, with temperatures of $5\text{--}7^\circ\text{C}$; CEAZA). The constant presence of sea fog over the coastal hills of Fray Jorge results in high levels of horizontal precipitation inside forest remnants, with water constantly running down through the tree trunks or dropping down directly (Villagrán et al. 2004, del-Val et al. 2006). This means that the Thorn-tailed Rayaditos of Fray Jorge will often have to use cold and humid cavities and wet materials for nest construction. A possible way to deal with this challenge is to build a well-insulated and nonhygroscopic structure; this presumes a trade-off between nest insulation and hygroscopic properties, given that fluffy materials such as feathers or animal hairs, though providing good thermal

insulation (see Møller 1991, Lombardo et al. 1995, McGowan et al. 2004, Schöll and Hille 2014), tend to absorb more water (Hilton et al. 2004, Rohwer and Law 2010, Deeming 2011). As we observed in the hygroscopic tests, Fray Jorge nests absorbed less water than Navarino nests, and this difference was likely related to less use of animal insulating materials, particularly feathers (Figure 3), which may be explained by differences in resource availability between locations, or it may be a result of the insulation–humidity trade-off (see Hilton et al. 2004). Whatever the cause, plant fibers and roots were more likely to be used in the humid environment of Fray Jorge.

How do birds at Fray Jorge deal with low temperatures if using large amounts of animal insulating materials is not the most suitable way to do so? Increasing nest size can be an alternative, and this may explain why Fray Jorge nests were larger, and lost heat at a lower rate in the convection test, compared to Navarino nests (see Table 3). Aside from

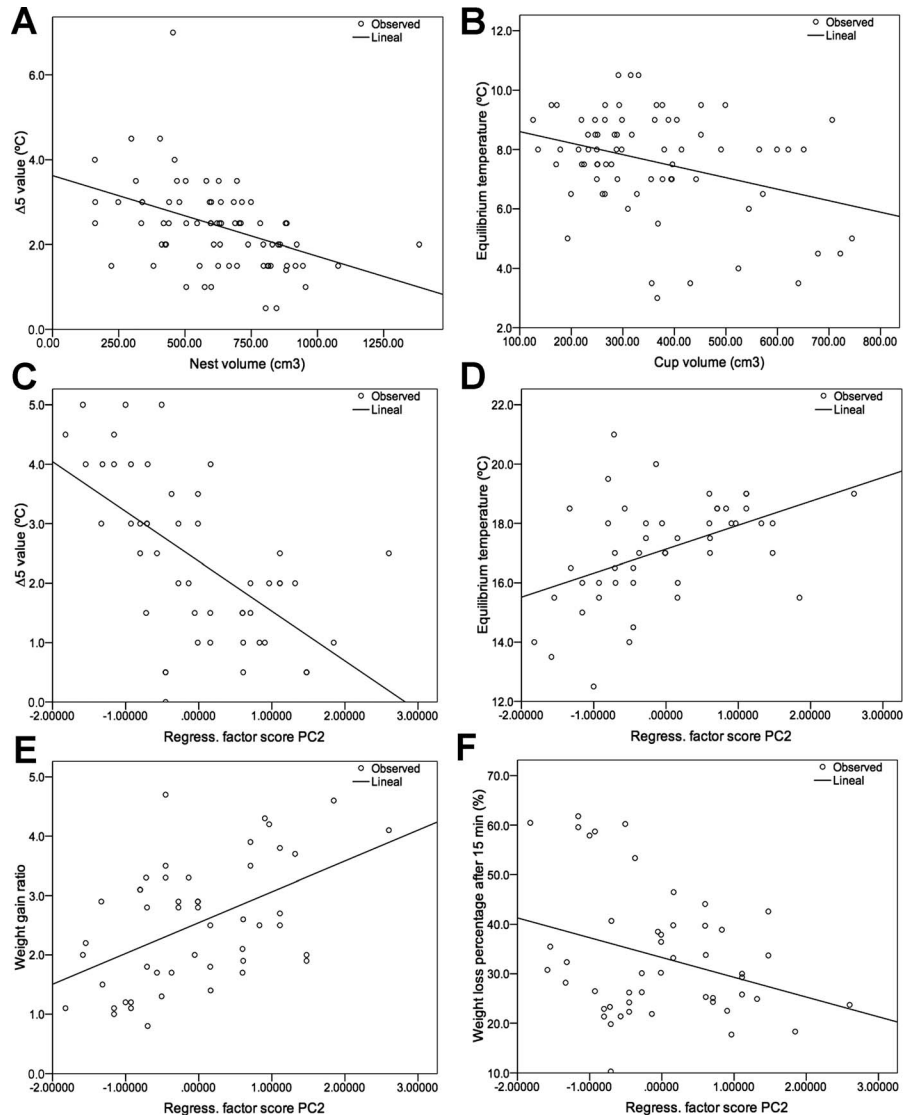


FIGURE 3. Multiple regression models testing the functional relationship between nest architecture and thermal-hygroscopic properties in Fray Jorge National Park and Isla Navarino, Chile. Dependent variables for regression models were obtained from (A, B) a test simulating the effects of heat loss by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

using feathers for the nest's internal lining, birds can increase insulation by modifying the nest structure (see Mainwaring et al. 2014). Wider and less porous nest walls have lower thermal conductivity (Kern 1984), and larger nests can retain more heat than smaller structures (White et al. 1975, Skowron and Kern 1980, Liljeström et al. 2009; but see Szentirmai et al. 2005). Additionally, nests with deeper and/or narrower cups can better protect the eggs and nestlings than nests with shallower and wider cups (Windsor et al. 2013).

Extremely low temperatures and strong winds are the main pressures that Thorn-tailed Rayaditos experience in

Navarino during the breeding season (Figure 1), and this probably explains why they build highly insulated nests. The high abundance of feathers and the lower relative humidity would allow birds to use more hygroscopic materials for the nest lining (see Hilton et al. 2004), which in turn would reduce heat loss by conduction (Figure 3). The first 2 mo of the breeding season in Navarino can present a challenge to Thorn-tailed Rayaditos, because October and November are very windy, and temperatures frequently drop below 3°C during the first hours of daylight (<http://www.meteochile.gob.cl>). Nest-box walls and probably cavities' inner surfaces were very cold during

the mornings, so nests could easily lose heat through contact with these surfaces (E. Botero-Delgadillo personal observation). Unless birds were not using large amounts of feathers and hairs, nests would be losing heat at faster rates because of their greater surface area and shallower and wider cups compared to nests from Fray Jorge (Table 1).

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

Concluding Remarks

Following previous studies, we tried to simulate the effects of weather conditions on the nests of a cavity-nesting bird (e.g., Mainwaring et al. 2012). In addition, we analyzed the roles of convection, conduction, and humidity separately, which indicated that potential trade-offs (insulation–humidity) could be differently affecting the nest-building behavior of 2 populations that occur near the limits of the distribution of the Thorn-tailed Rayadito. We are aware that including more populations in further studies will be essential to understanding how nest morphology varies throughout the latitudinal range occupied by this species, as well as to evaluating how nesting behavior is affected by local variations in the availability of nesting materials and biotic interactions. For instance, assessing the role of social and interspecific interactions in Thorn-tailed

Rayadito nest construction can help determine to what extent climatic regimes are affecting nest morphology, and whether biotic and abiotic factors are exerting agonistic selective pressures (Rohwer et al. 2015). Unlike in open-nesting birds, the influence of competition or predation on differences in nest design is likely negligible in cavity-nesting birds, compared to the effects of climate; hence, future work could also focus on the effects of extreme weather conditions, in order to predict how bird populations would respond to the marked environmental variation potentially triggered by climate change (Møller et al. 2010).

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Author contributions: E.B.-D. conceived the idea, conducted the research, analyzed data, and wrote the paper. N.O. and D.S. performed part of the experiments and helped during data analysis. Y.P. helped collect data and edited the paper. R.A.V. supervised research, edited the paper, and contributed substantial resources.

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APPENDIX

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

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

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

Variable	Regression coefficient <i>B</i>	Standardized <i>B</i>	<i>t</i>	<i>P</i>
(A) Convection test				
Independent variables for analysis on Δ_5 value ^a				
Nest volume	-0.02 ± 0.00	-0.44	-4.18	0.000
Independent variables for analysis on equilibrium temperature ^b				
Cup volume	-0.04 ± 0.01	-0.36	-3.04	0.004
(B) Conduction test				
Independent variables for analysis on Δ_5 value ^d				
PC2 ^c	-0.84 ± 0.16	-0.61	-5.16	0.000
Independent variables for analysis on equilibrium temperature ^d				
PC2 ^c	0.81 ± 0.23	0.46	3.55	0.001
(C) Hygroscopic properties				
Independent variables for analysis on gain ratio ^d				
PC2 ^c	0.52 ± 0.13	0.49	3.92	0.000
Independent variables for analysis on percent weight loss ^d				
PC2 ^c	-4.00 ± 1.82	-0.31	-2.20	0.030

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