The Auk
Ornithological Advances

AmericanOrnithology.org

Volume 132, 2015, pp. 826–835
DOI: 10.1642/AUK-15-28.1

RESEARCH ARTICLE

Reproductive life-history variation in a secondary cavity-nester across an elevational gradient in Andean temperate ecosystems

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Submitted January 29, 2015; Accepted June 23, 2015; Published September 2, 2015

ABSTRACT

Avian reproductive strategies have been hypothesized to vary with elevation. Shorter breeding seasons due to harsh environmental conditions, and potentially higher predation risks, may reduce clutch sizes at higher elevations, which in some species leads to increased parental care and offspring survival. However, this phenotypically plastic and potentially adaptive response has been documented only in a handful of species in the Northern Hemisphere. For the first time in a southern temperate ecosystem, we studied whether the breeding strategy of a secondary cavity-nester varied along an elevational gradient in Andean temperate forests, Chile. We installed 240 nest-boxes at 260–1,115 m elevation and monitored the breeding activity of 162 nests of Thorn-tailed Rayaditos (*Aphrastura spinicauda*) over 2 seasons (2010–2012). We included 50 nests from a third season only for recording clutch size and nestlings per clutch. As predicted, the breeding season was shorter in highland forests than in lower elevations, by 28% and 55% over the 2 successive seasons. Although timing of egg laying (1 egg every second day) and incubation period (average = 15 days) did not vary with elevation, we found smaller clutch sizes (average = 4.1 vs. 4.5) and fewer nestlings per clutch (average = 3.5 vs. 4.2) at higher elevations. The extent of parental care, expressed as the duration of the nestling period, was slightly but significantly greater in highland than in lowland forests (22.2 vs. 21.6 days). Despite the longer nestling period at higher elevations, nesting success was lower at high elevations, mainly because of nest predation. Our findings suggest that Thorn-tailed Rayaditos may change to a slower reproductive strategy along elevational gradients. Yet these changes do not appear to compensate for the increased predation rates at higher elevations, calling into question the potential adaptive significance of this strategy.

Keywords: Andean forest, cavity-nesting, environmental gradient, fast–slow continuum, life-history traits, montane, Thorn-tailed Rayadito

Variación de los rasgos reproductivos en la historia de vida de un nidificador secundario de cavidades a través de un gradiente altitudinal en ecosistemas templados andinos

RESUMEN

Los gradientes altitudinales han sido propuestos como impulsores de cambio en la estrategia reproductiva de las aves. Temporadas reproductivas más cortas, debido a las severas condiciones ambientales, y el potencial mayor riesgo de depredación en zonas altas pueden producir una reducción en los tamaños de puesta. Ésto, en algunas especies conduce lo que en algunas especies conduce a un incremento en el cuidado parental y en la sobrevivencia de los polluelos. Sin embargo, esta respuesta plástica y potencialmente adaptativa ha sido sólo documentada en algunas especies del hemisferio norte. Por primera vez en el ecosistema templado de Sudamérica, estudiamos si la estrategia reproductiva de un nidificador secundario de cavidades varía a lo largo de un gradiente altitudinal en el bosque templado andino, Chile. Instalamos 240 cajas-nido entre los 260 y 1.115 m de elevación, y monitoreamos la actividad reproductiva en 162 nidos de *Aphrastura spinicauda* durante dos temporadas reproductivas (2010–2012). Incluimos 50 nidos de una tercera temporada sólo para datos de tamaño de puesta y número de polluelos por nido. La temporada reproductiva fue un 28% y un 55% más corta en bosques de zonas altas durante las dos temporadas. Aunque el momento de puesta de cada huevo (1 huevo cada dos días) y el periodo de incubación (15 días) no variaron con la

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altitud, encontramos tamaños de puesta más pequeños (promedio 4,1 vs. 4,5) y un menor número de polluelos por nido (promedio 3,5 vs. 4,2) en zonas altas. El periodo de cría fue levemente más largo (22,2 vs. 21,6 días) en bosques de zonas altas. A pesar del aumento en el periodo de cría, el éxito reproductivo fue menor en zonas altas, principalmente debido a la depredación. Nuestros resultados sugieren que *Aphrastura spinicauda* podría cambiar hacia una estrategia reproductiva más lenta a lo largo de gradientes altitudinales. Sin embargo, este cambio no parece compensar el aumento en las tasas de depredación en bosques de zonas altas, cuestionando el carácter adaptativo de esta estrategia.

Palabras clave: Aphrastura spinicauda, bosque andino, nidificador de cavidades, estrategia reproductiva rápida-lenta, gradiente ambiental, montano, rasgos de historia de vida

INTRODUCTION

Worldwide, there is a vast diversity of life-history traits across co-occurring species within a given taxon, but also within the same species along environmental gradients (Roff 1992). Elevation is an environmental gradient that has been considered an important factor in the evolution of life-history traits (Badyaev 1997, Badyaev and Ghalambor 2001, Camfield et al. 2010, Evans Ogden et al. 2012, Boyle et al. 2015, Hille and Cooper 2015). Indeed, extreme conditions encountered at high elevations—such as cold temperatures, prolonged snow cover, variable weather, and shorter warm seasons—have been shown to influence most of the life-history traits associated with avian reproduction (Perfito et al. 2004, Martin 2013). Within a fast–slow continuum gradient of reproductive strategies (Sæther 1987), an expected adaptation to harsher conditions is a shift to a "slow reproductive strategy," in which lower breeding outputs (e.g., clutch size and number of nestlings per clutch) and fewer nesting attempts are compensated by increased offspring survival from increased parental care while nesting (Badyaev and Ghalambor 2001, Boyle et al. 2015, Hille and Cooper 2015). This general response has been observed in both interspecific (Badyaev 1997, Sandercock et al. 2005) and intraspecific comparisons (Bears et al. 2009, Martin et al. 2009, Boyle et al. 2015), mainly in the Northern Hemisphere. However, very few studies have evaluated direct and indirect effects of the environmental stress gradient, plastic behavioral responses, and consequent offspring survival during the nestling period and postfledging.

Although few studies have quantified changes in birds' life-history traits across elevational gradients (Martin 2001, Boyle et al. 2015), and even fewer in cavity-nesting species, some patterns emerge from the small number of studies in montane systems. For example, within an assemblage of 84 cardueline species, clutch size decreased and incubation period significantly increased with increasing elevations occupied by different species (Badyaev 1997). These changes can be understood as consequences of decreased energy availability for reproduction in highlands, due to harsh environmental conditions. It is unclear, however, whether nestling period is significantly longer in higher-elevation species, which would indicate a change in reproductive strategy. Intraspecific variation in reproductive traits across elevation has also been documented. For instance, Dark-eyed Juncos (*Junco hyemalis*, ground-nesters) show a shift in their reproductive life-history traits with elevation, reducing their breeding period and decreasing the number of nestlings per nest (Bears et al. 2009). Pacific Wrens (*Troglodytes pacificus*, cavity-nesters) reduce their annual nesting success with increasing elevation, possibly in response to a 61% shorter breeding season at higher elevations; however, there is no evidence of a shift in breeding parameters and behavioral attributes that could increase offspring survival in highlands (as a shift to a slower reproductive strategy; Evans Ogden et al. 2012).

Reproductive life-history traits of temperate forest birds have been poorly studied in south-temperate systems (Martin 2004). In the temperate forest of southern Chile, most birds species inhabit and breed across wide elevational gradients (Vuilleumier 1985). However, life-history variation along this gradient remains unknown because most studies have focused on coastal areas (e.g., Cornelius et al. 2000, Estades and Tomasevic 2004, Tomasevic and Estades 2006, Vergara and Marquet 2007, Quilodrán et al. 2012) and island ecosystems (e.g., Willson et al. 1994, 2005, Rozzi et al. 1996, Reid et al. 2004, Vergara and Schlatter 2004, Díaz et al. 2005, 2006, Moreno et al. 2005, Ippi et al. 2009).

The Thorn-tailed Rayadito (*Aphrastura spinicauda*) is a small furnariid species endemic to South American temperate forests (Martínez and González 2004). The breeding biology of this species has been studied only in coastal temperate forests at <100 m elevation. In one of these studies, Moreno et al. (2005) described clutch sizes of 3–6 eggs (mode = 4 eggs), broods of 2–5 nestlings (mode = 3 chicks), an incubation period of 9–16 days (mode = 14 days), and a nestling period of 16–23 days (Moreno et al. 2005). Furthermore, Quilodrán et al. (2012) reported clutch sizes of 2–4 eggs (mode = 3 eggs), broods of 1–4 nestlings (mode = 3 chicks), an incubation period of 14–18 days (mode = 16 days), and a nestling period of 21 days. Thorn-tailed Rayaditos inhabit areas from sea level up to 2,400 m in the Andes (Housse 1945) and are therefore a good model species for examining

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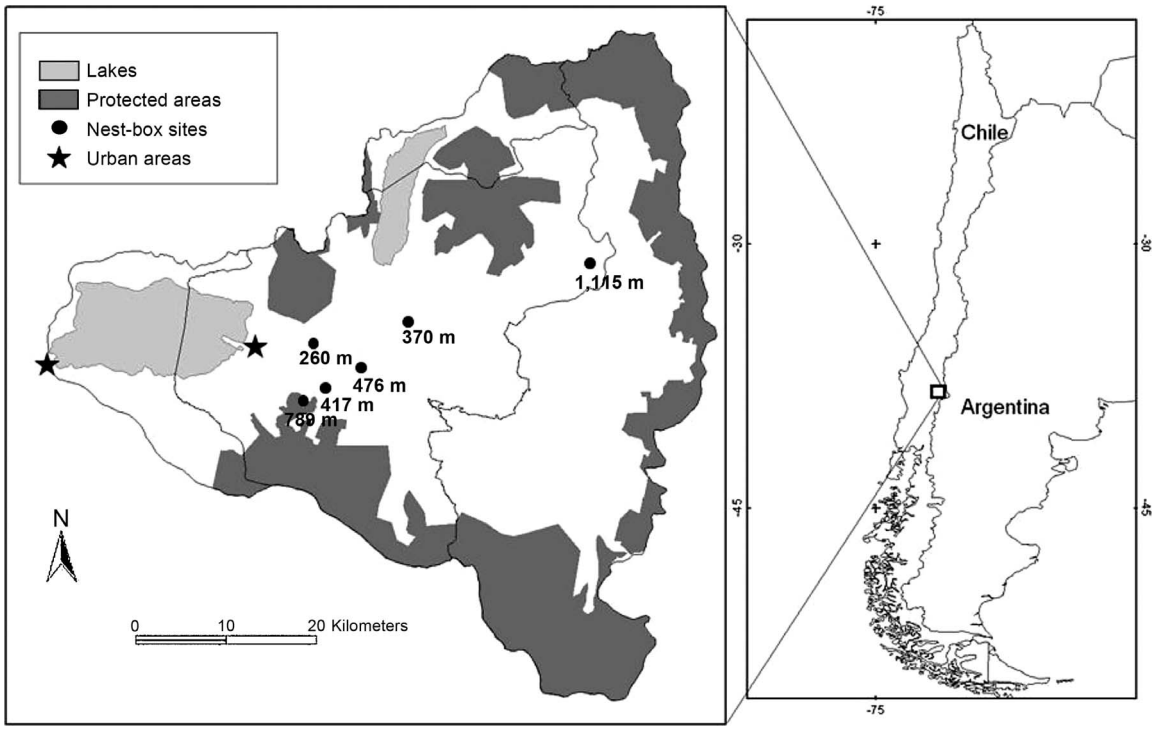

FIGURE 1. Location of 6 forest sites, including the specific elevation for each, where a total of 240 nest-boxes were deployed during 3 breeding seasons (October 2010–December 2012) near the city of Pucón, La Araucanía region, Chile.

how reproductive life-history traits change across an elevational gradient.

Here, we investigate changes in reproductive life-history traits of this species by examining nesting birds across an elevational gradient over 2 consecutive breeding seasons. We explore whether changes in reproductive traits may be indicative of a plastic and potentially adaptive change in reproductive strategy. Specifically, we (1) provide a detailed description of the breeding biology of Thorn-tailed Rayaditos in Andean locations and (2) determine elevational differences in the length of the breeding season and reproductive life-history strategies, mainly in clutch size, incubation period, number of nestlings per clutch, nestling period, and nesting success. Because of harsh environmental conditions and the potentially high predation risk at high elevations, we predicted that (1) the breeding season of Thorn-tailed Rayaditos at high elevations is delayed and the length shorter in comparison to low elevations (Perfito et al. 2004, Boyle et al. 2015), and (2) Thorn-tailed Rayaditos shift toward a slower reproductive strategy at high elevations, producing smaller clutch sizes and fewer nestlings per clutch but investing more time in the development of broods (incubation and nestling period; Hille and Cooper 2015) in comparison to low elevations.

METHODS

Study Area and Species

The study was conducted in the Andes Mountains of southern Chile, within the La Araucanía region near the city of Pucón (39°16′S, 71°48′W; Figure 1). We selected 6 study sites in forests at the same latitudinal degree and along an elevational gradient from 260 to 1,115 m. A minimum linear distance of 1.6 km separated the sites. Four sites were dominated by broadleaf species such as *Lophozonia obliqua*, *Nothofagus dombeyi*, and *Laurelia sempervirens*. The other 2 sites were conifer–broadleaf mixed forests dominated by *Saxegothaea conspicua*, *Laureliopsis philippiana*, and *N. dombeyi*. The understory composition in both lowland and highland forests was dominated by bamboo species (*Chusquea* spp.), *Rhaphithamnus spinosus*, *Azara* spp., and tree saplings. Understory habitat conditions were similar in all the study sites.

Thorn-tailed Rayaditos are considered forest specialists and have been classified as large-tree users (Díaz et al. 2005). They are year-round residents in temperate forests of South America (Lencinas et al. 2005, Ippi et al. 2009). During the breeding season, they focus most of their activities in a 30-m radius from their nests (Van Dongen et al. 2009) and display high intraspecific and interspecific

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territoriality (Ippi 2009). Their diet consists mainly of insects (Martínez and González 2004), although there are incidental records of individuals feeding on plant seeds (Estades 2001, McGehee 2007). They are obligate cavity nesters, making their nests in tree cavities and, to a lesser extent, in bank cavities (Jaramillo 2003, Altamirano 2014). The nests are located 0–29 m above the ground (Cornelius 2008, McGehee et al. 2010, Altamirano et al. 2012). Breeding couples are commonly attracted to artificial cavities (i.e. nest-boxes; Moreno et al. 2005)

Experimental Design and Reproductive Monitoring

In the winter of 2010, we deployed 240 wooden nest-boxes (40 nest-boxes site^{-1}), following the design used successfully by Moreno et al. (2005). The nest-boxes (inner space $= 16.5 \times 13.2$ cm, depth $= 17.1$ cm from entrance to base, and entrance-hole diameter $= 3.1$ cm) were hung 1.5 m above ground from a tree branch (random entrance aspect) and were systematically separated by 25 m. All nest-boxes were placed $\geq$15 m from the forest edge, to reduce edge effects. During 2 breeding seasons (October 2010–February 2011, October 2011–February 2012), nest-boxes were monitored by direct observations and by camera traps (Reconyx RC 55; Reconyx, Holmen, Wisconsin, USA) to examine when nest-boxes were first used, record fledging dates, monitor nesting success, and identify any potential nest predators (Altamirano et al. 2013). Thus, camera traps allowed us to determine the exact moment when nestlings fledged or when a predation attempt occurred. For clutch size and number of nestlings per clutch, we included nest data from a third breeding season (October–December 2012). A nest-box was considered occupied when it had $\geq$1 egg or chick. Nest-boxes were checked weekly to determine the initial date birds started using them. The status of each nest-box (adult activity, clutch size, egg temperature, and number of nestlings per clutch) was monitored every 2–3 days, or every day when near the hatching or fledging dates. The latter was done in order to obtain the exact dates of these processes and accurately calculate egg laying, incubation period, nestling period, and nesting success.

The variables recorded for each nest-box were laying date of each egg, incubation period, clutch size, hatching date, number of nestlings per clutch, breeding period, and fledging date. "Incubation period" was defined as the duration of time from when eggs were warm for the first time until completion of hatching (Magrath et al. 2000). "Length of breeding season" was defined as the number of days elapsed between the date when the first egg in the first recorded nest was laid until the date that the last nestling from the last nest fledged, for lowland and highland forests separately. To calculate nestling period, hatching day was considered day 0 (Moreno et al. 2005), until the first nestling fledged. We considered a nest unsuccessful (value $= 0$) when no nestling fledged, partially successful (value $= 1$) when at least 1 chick fledged, and successful (value $= 2$) when all eggs resulted in fledglings.

Data Analysis

All reproductive data were $\log_{10}$ transformed before statistical comparison to improve normality and homogeneity of variances. Using Levene's test, we found that variances were homogeneous ($P > 0.05$) for all dependent variables (clutch size, number of nestlings per clutch, number of fledglings per nest, incubation period, nestling period, and nesting success). Nests that were not being incubated by the end of the observation were excluded from clutch-size analysis, because we were not sure whether the laying period had ended. Linear regression models were used to assess the association of elevation with clutch size, number of nestlings per clutch, incubation period, and nestling period. F values are presented as $F_{\text{df(effect)},\text{df(error)}}$. At elevations >700 m above sea level (a.s.l.), most precipitation falls as snow during Andean winters and remains in highland sites when the breeding season starts (Ibarra et al. 2010). Above 700 m a.s.l. the environment provides a shorter period of food availability, and the advantageous climatic conditions suitable for breeding are delayed and shortened (Bears et al. 2009). Therefore, we used an inflection point of 700 m a.s.l. between 2 elevation categories. To be conservative, we did not deploy nest-boxes between 476 and 789 m a.s.l. (a range of 313 m; Figure 1), in order to make sure that we were comparing populations breeding at either high or low elevations. Differences in reproductive parameters between lowland (<700 m a.s.l.) and highland (>700 m a.s.l.) forests were assessed using univariate t-tests, or rank-based Mann-Whitney U-tests when data were not normally distributed (Quinn and Keough 2002). We calculated nesting success as the proportion of successful nests between the 2 elevation categories and breeding seasons. This is a valid approach in a study of nest-boxes with known locations, because all nests had the same probability of being found, independent of nest stage (Mayfield 1961, 1975, Cooch and White 2014). All reproductive parameters are presented as means $\pm$ SD, except for nesting success, which was considered as a categorical variable and is presented as the median of values. Statistical tests were considered significant with $P < 0.05$.

RESULTS

Life-history Traits of Thorn-tailed Rayaditos

We monitored 162 nests and also include 50 additional nests (only for analyzing clutch size and number of nestlings per clutch) monitored for a third breeding season (October–December 2012). Nest-box use rates were higher in the second year (55 vs. 107 nests). Considering all nesting attempts, clutch size ranged from 2 to 7 eggs, with a mode of 5 (41.8% of 158); 32.9% contained 4 eggs,

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TABLE 1. Thorn-tailed Rayadito breeding outputs at low and high elevations in Andean temperate forests. Values are means ± SD, except for nesting-success category, which is presented as the median of values.

	Low elevation (260–476 m a.s.l.)		High elevation (789–1,115 m a.s.l.)	
	2010–2011	2011–2012	2010–2011	2011–2012
(A) Breeding parameter				
Clutch size (*n*)	4.2 ± 0.7	4.7 ± 0.9	4.1 ± 0.9	4.2 ± 0.8
Nestlings per clutch (*n*)	4.1 ± 0.8	4.3 ± 1.1	3.5 ± 0.9	3.7 ± 1.2
Fledglings per nest (*n*)	4.0 ± 0.8	4.2 ± 1.2	3.4 ± 0.9	4.0 ± 1.4
Laying period (days)	6.4 ± 1.5	7.7 ± 1.5	6.3 ± 2.0	7.0 ± 1.2
Incubation period (days)	15.0 ± 0.3	15.9 ± 1.3	15.0 ± 0.0	16.0 ± 1.0
Nestling period (days)	22.1 ± 0.8	21.4 ± 0.8	22.3 ± 0.5	22.0 ± 0.0
(B) Nesting success				
Nesting-success category [a]	2.0	1.0	1.0	0.0
Nests with fledglings (%)	79.1	54.5	66.7	10.5
Predated (%)	7.0	36.4	25.0	84.2
Abandoned (%) [b]	13.9	9.1	8.3	5.3

[a] Categorical variable: 0 = completely unsuccessful nests, 1 = at least 1 chick fledged, and 2 = completely successful nests.
[b] Nests were recorded as abandoned when eggs were cold or nestlings were dead without signs of predation. The latter may be associated with adult death and/or unviable eggs. See text for details of statistical analysis.

15.2% contained 6 eggs, 7.0% contained 3 eggs, 1.9% contained 2 eggs, and 1.2% contained 7 eggs. Mean clutch size was 4.65 ± 0.93 eggs. With the exception of 1 clutch, all eggs within a nest hatched synchronically on the same day (within a period of 24 hr). Number of nestlings per clutch ranged from 2 to 7 chicks, with a mode of 4 (36.2% of 105); 33.3% contained 5 nestlings, 17.1% contained 3 nestlings, 6.7% contained 6 nestlings, 5.7% contained 2 nestlings, and 1.0% contained 7 nestlings. The mean was 4.21 ± 1.03 nestlings. Birds laid eggs every 2 days during the laying period, with a maximum laying period of 13 days (mean = 7.2 ± 1.6 days, $n = 103$). Incubation period was 15.3 ± 1.0 days ($n = 92$), ranging from 14 to 18 days. Nestling period was 21.7 ± 0.8 days ($n = 85$), ranging from 19 to 23 days (Table 1).

Association between Elevation and Reproductive Strategy

Length of breeding season. Over 2 yr of monitoring, the breeding season was 28% (62 vs. 82 days) and 55% (35 vs. 77 days) shorter in highland forests than in low-elevation areas. Nesting birds in lowland forests showed 2 peaks in clutch initiation periods (bimodal distribution), whereas only 1 initiation period occurred in highland forests (unimodal distribution). The latter period was between the 2 peaks in lowlands in 2010–2011 (Figure 2A), and almost simultaneous with the second peak period in lowlands in 2011–2012 (Figure 2B). The second breeding season started and finished earlier than the first breeding season in lowland forests, whereas at high elevations the breeding phenology was almost identical (Figure 2). Birds started laying eggs in lowland forests on October 10, 2010, and October 3, 2011. At high elevations, birds started laying eggs ~1 mo later than in lowlands: November 22, 2010, and November 1, 2011. The last fledging dates for lowland forests were February 12, 2010, and January 26, 2011. In highland forests, the last fledging dates were almost 1 mo earlier than at low elevations: January 23 and

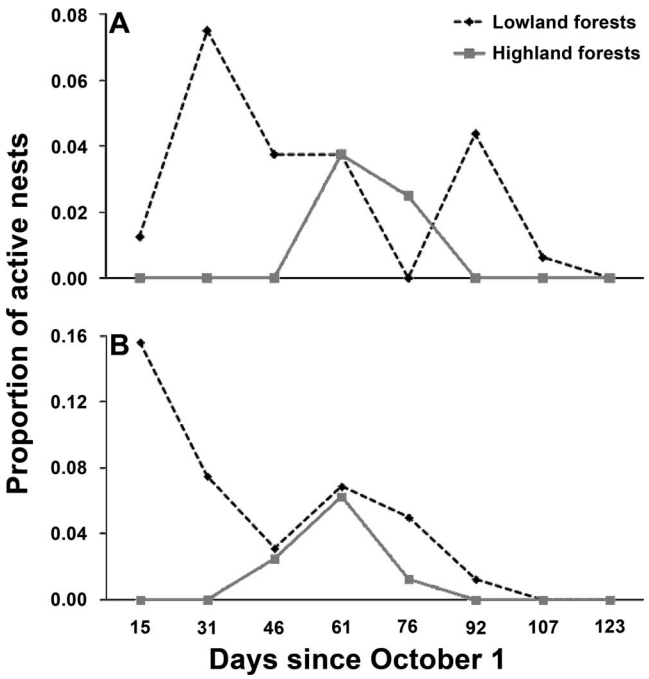

FIGURE 2. Thorn-tailed Rayadito breeding temporality in lowland and highland Andean temperate forests for each breeding season: (**A**) October 2010–February 2011 and (**B**) October 2011–February 2012. The *x*-axis shows the date of the first egg laid since October 1 (day 0) for all nesting attempts, and the *y*-axis shows the proportion of active nests per number of nest-boxes at each elevation.

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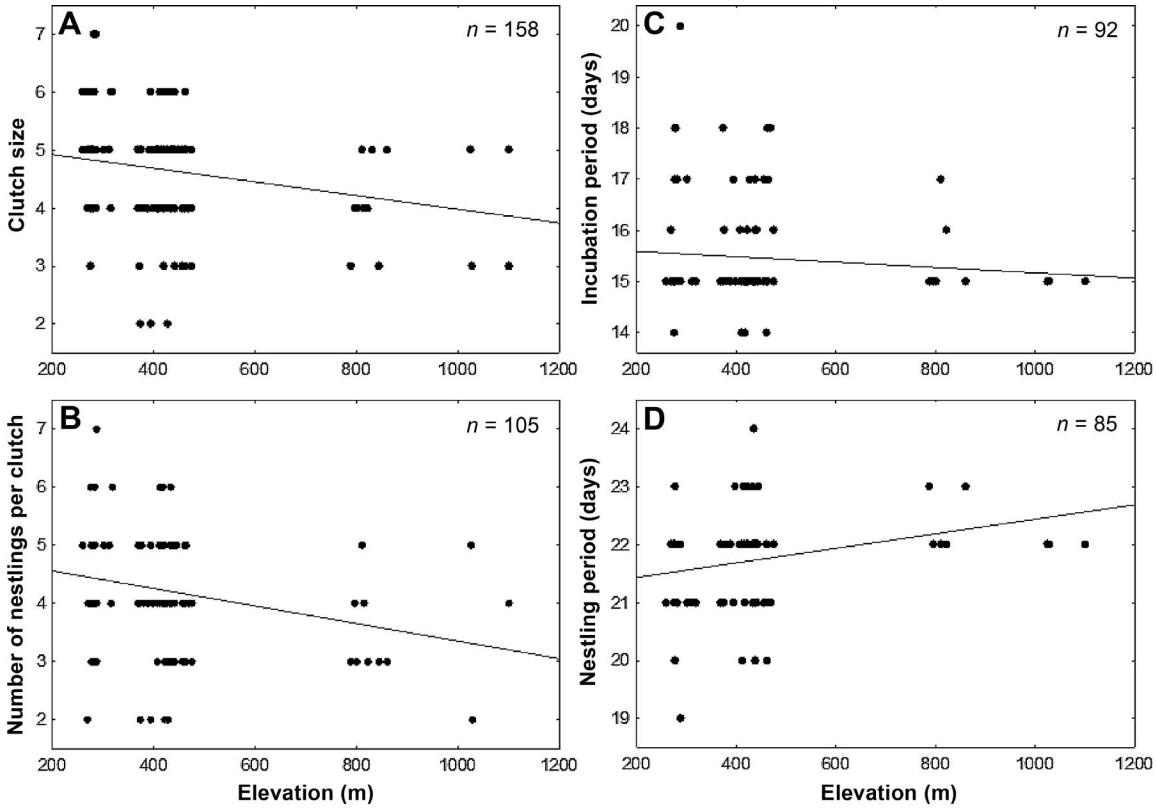

FIGURE 3. Association between breeding parameters (raw data) and an elevational gradient (260–1,115 m a.s.l.) in Andean temperate forests. Regression plots show (**A**) clutch size and (**B**) number of nestlings per clutch for 3 breeding seasons (October 2010–December 2012), and (**C**) incubation period and (**D**) nestling period for 2 breeding seasons (October 2010–February 2012).

January 2 for the first and second breeding seasons, respectively. Renesting attempts differed between elevations, with no second attempts in highlands and 17 in lowlands.

Clutch size, number of nestlings per clutch, and number of fledglings per nest. Elevation was negatively associated with both clutch size ($F_{1,156} = 6.64$, $P = 0.01$; Figure 3A) and number of nestlings per clutch ($F_{1,103} = 6.69$, $P = 0.01$; Figure 3B). Pairs breeding in highland forests had significantly smaller clutches than those in lowlands ($t = 2.18$, df = 156, $P = 0.03$), with mean clutch sizes of 4.1 ± 0.8 and 4.5 ± 0.9, respectively. We found fewer nestlings per clutch in highland forests than in lowlands (3.5 ± 0.9 and 4.2 ± 1.0, respectively; $t = 2.27$, df = 103, $P = 0.02$). Breeding at high elevations also resulted in fewer fledglings per nest compared with low elevations (3.5 ± 1.0 and 4.2 ± 1.0, respectively; $t = 2.08$, df = 87, $P = 0.04$; Figure 4A).

Incubation and nestling periods. Elevation was not significantly associated with incubation period ($F_{1,90} = 0.718$, $P = 0.39$; Figure 3C), but it did have a significant association with nestling period ($F_{1,83} = 7.658$, $P < 0.01$; Figure 3D). Furthermore, there was not a significant difference in incubation period between highland and lowland forests ($t = 0.36$, df = 90, $P = 0.71$), with an overall mean of 15.3 ± 0.7 days and 15.5 ± 1.1 days, respectively. Nestling period was marginally longer at high elevations ($t = -1.87$, df = 83, $P = 0.06$), with a mean of 22.3 ± 0.5 days in highlands and 21.7 ± 0.9 days in lowlands.

Nesting success. Breeding pairs had lower nesting success in highland than in lowland forests (Mann-Whitney U-test, $U = 1{,}344.5$, $P = 0.003$). At high elevations, 16% of nests were successful, 16% partially successful, and 68% unsuccessful (Figure 4B). By contrast, at low elevations, 42% of nests were successful, 21% partially successful, and 37% unsuccessful (Figure 4B). Most unsuccessful nests failed during the laying period in highlands (79%) and during the incubation period (45%) in lowlands. Predation accounted for 84% of nest failures in the second breeding season in highland forests (Table 1).

DISCUSSION

We have provided the first assessment of the association between elevation and the reproductive strategy of a cavity-nesting bird, controlled for latitude (same latitudinal

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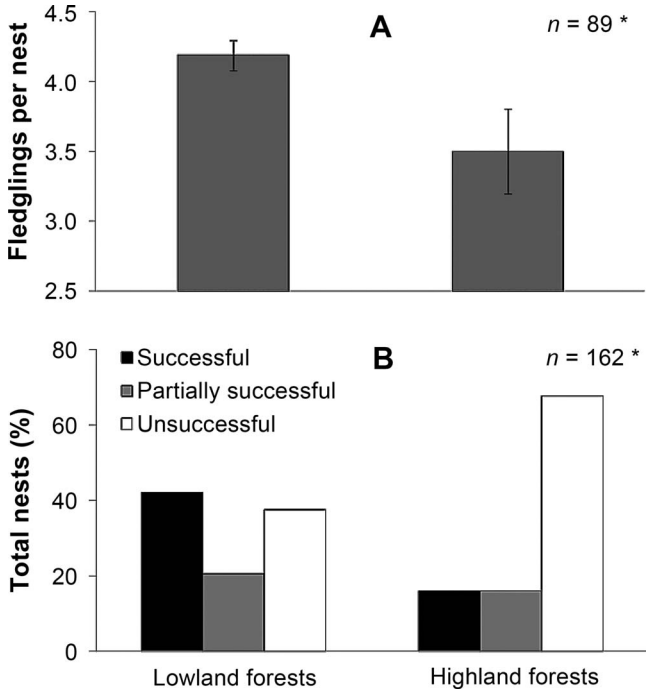

FIGURE 4. (**A**) Mean number of fledgling Thorn-tailed Rayaditos per nest and (**B**) percentage of nests in each nesting-success category (0 = unsuccessful nest, no nestling fledged; 1 = partially successful, ≥1 chick fledged; and 2 = successful, all eggs resulted in fledglings) for 2 breeding seasons (October 2010–February 2012) at high and low elevations in Andean temperate forests. Bars represent SE, and asterisk shows statistical significance (A: $t = 2.08$, $P = 0.04$; B: Mann-Whitney U-test, $U = 1{,}344.5$, $P = 0.003$).

degree), in temperate forests of South America. Across a fast–slow continuum gradient of reproductive strategies (Sæther 1987), we found a potential shift in reproductive life-history traits (i.e. clutch size, number of nestlings per clutch, and nestling period) from faster to slower reproductive strategy with increasing elevation in Thorn-tailed Rayaditos. This result is similar to the shift in reproductive strategy documented in northern temperate ecosystems—for example, in an open-cup nester (Dark-eyed Junco; Bears et al. 2009) and a ground-nester (Savannah Sparrow [*Passerculus sandwichensis*]; Martin et al. 2009). We also found a pronounced reduction in the length of the breeding season at high elevations (28% and 55% shorter than at low elevations for 2 breeding seasons). This reduction is comparable to the one found by Evans Ogden et al. (2012) in a cavity-nesting bird, the Pacific Wren, along an elevational gradient in British Columbia, Canada. Furthermore, patterns of clutch initiation dates for Thorn-tailed Rayaditos were similar to those of Pacific Wrens, which also show bimodal and unimodal distribution in lowland and highland forests, respectively. However, the outcomes for Thorn-tailed Rayaditos differed from those observed by Evans Ogden et al. (2012); the shorter breeding season at high elevations was related to smaller clutch sizes, fewer nestlings per clutch, and a longer nestling period. These results may be associated with fewer offspring per breeding season and apparently greater parental care at high elevations. The latter 2 shifts at high elevations agree with patterns found in both open- and cavity-nesting birds (Badyaev and Ghalambor 2001) and suggest a trade-off between parental care and number of offspring produced.

Our results are comparable to those of the few studies on life-history traits across elevations that have been conducted in tropical ecosystems. For example, Kleindorfer (2007) reported that Darwin's Small Ground Finch (*Geospiza fuliginosa*) had smaller clutch sizes and higher predation rates in highlands, compared with lowlands, on Santa Cruz Island in the Galápagos. However, comparisons between south temperate and tropical ecosystems must be considered carefully, because current knowledge of how reproductive life-history traits vary along elevational gradients in these 2 areas is rudimentary at best (Martin 1996, Boyle et al. 2015). Therefore, further studies in these areas are necessary to provide generalities of avian life-history traits in the fast–slow continuum along elevational gradients.

We assessed a set of specific reproductive life-history traits in Thorn-tailed Rayaditos, but we lack knowledge of other stages in their life cycle. In conjunction with the results we have presented, an examination of offspring and adult survival could provide a greater understanding of how their reproductive life-history traits are correlated with elevation. Our observed changes in reproductive life-history traits across elevations may be linked to habitat and food supply (Martin 1993, Zanette et al. 2006, Camfield et al. 2010); however, the latter 2 factors are also subordinated to environmental conditions (e.g., temperatures, variable weather) encountered across elevational gradients (Loiselle and Blake 1991, McCain 2009). Despite the lack of an overall picture, our results are consistent and suggest the potential presence of intraspecific variation of reproductive traits across elevational gradients in Andean forests.

We found lower nesting success at high elevations, mainly associated with predation (Skutch 1985, Roper and Goldstein 1997, Kleindorfer 2007). This pattern is consistent with the hypothesis that greater parental care is related to higher predation risk, since the predators can use parental activity to find nests (Skutch 1949). In temperate forests of South America, the main cavity-nester predators, Austral Opossums (*Dromiciops gliroides*; Celis-Diez et al. 2012) and Güiña (*Leopardus guigna*; Altamirano et al. 2013), are nocturnal, whereas Thorn-tailed Rayaditos are active during the day. Therefore, predation rate is likely not influenced by the diurnal activity of birds. We suggest that the higher predation rates

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observed at high elevations are related to a higher density of native predators in highland forests due to lower habitat disruption in these areas (Ibarra et al. 2012, 2014). However, it is necessary to assess conjunct effects between nest sites and parental care to understand current patterns of nest predation (Martin et al. 2000).

Our results differ from the breeding biology of Thorn-tailed Rayaditos reported from coastal locations (Moreno et al. 2005, Quilodrán et al. 2012). Quilodrán et al. (2012) suggested that, consistent with the hypothesis proposed by Lack (1947), clutch size increases at higher latitudes, with mean clutch sizes of 3.3 at 35°S and 4.1 at 42°S. However, we found a larger clutch size (mean = 4.7) at an intermediate latitude (39°S). This suggests there might not be linear differences in reproductive life-history traits along a latitudinal gradient, even more so when contrasting breeding parameters at similar elevations (<500 m of elevation). Our findings also support the idea that differences in clutch sizes along elevational gradients may covary with latitude and are reflected in avian life histories (Camfield et al. 2010). However, potential interactions between elevation and latitude, as drivers behind these differences, are still unknown. To identify these drivers, we would have to assess differential effects across elevational gradients at different latitudes. Nevertheless, implementing such an experimental design is complex because many independent variables (e.g., weather, food availability, nest-site availability, predators) may interact with population life histories (Tieleman 2009).

Artificial cavities (nest-boxes) are useful for assessing the effects of environmental gradients on cavity-nesting birds (e.g., Johnson et al. 2006) because they allow the control of cavity-level conditions (i.e. entrance size, depth, internal volume, among others) that may interfere with breeding parameters, such as clutch size and nesting success (Karlsson and Nilsson 1977, Llambías and Fernández 2009). Nonetheless, nest-boxes are artificial tools and, as such, conclusions obtained from their utilization should be interpreted with caution. For example, results from nest-boxes on predation rates and nesting success do not necessarily reflect the real success of predation attempts (Altamirano et al. 2013).

We conclude that Thorn-tailed Rayaditos may have an adaptive response to shorter breeding seasons at higher elevations: They have smaller clutches and fewer nestlings per clutch, and they invest more time in taking care of nestlings (Badyaev and Ghalambor 2001, Hille and Cooper 2015). Furthermore, Thorn-tailed Rayaditos do not appear to make second nesting attempts at higher elevations (Boyle et al. 2015). However, these potential adaptations do not seem to compensate for the increased predation rates at higher elevations, which calls into question the adaptive significance of this strategy and suggests that individuals at higher elevations make only a marginal contribution to overall population abundance. Finally, the reproductive life-history traits of Thorn-tailed Rayaditos in Andean locations were different from those of coastal locations, resulting in a higher number of offspring per nest. Our results highlight the importance of studying the ecology of birds in southern Andean locations and examining the effects of elevational gradients on bird communities in temperate forests of South America.

ACKNOWLEDGMENTS

The Chilean Forest Service (CONAF), Kodkod: Lugar de Encuentros, M. Venegas, and R. Sanhueza (Lahuen Foundation and Guías–Cañe), Kawelluco Private Sanctuary, C. Délano, M. Sabugal, R. Timmerman, and many other landowners allowed us to work on their lands. Special thanks to A. Dittborn, J. Laker, K. Martin, T. Honorato, A. Vermehren, P. Corvalán, T. Tüchelmann, and M. I. Mujica for their great commitment to this research. Numerous friends, local inhabitants, and students provided priceless assistance in the field. Suggestions from two anonymous reviewers greatly enhanced the manuscript. T.A.A., J.T.I., and M.D.M. were supported by a grant from Comisión Nacional de Investigación Científica y Tecnológica (CONICYT).

Funding statement: We thank the Chilean Ministry of the Environment (FPA Project 09–078–2010, 9–I–009–12), Center for Local Development (especially G. Valdivieso and A. Hargreaves, CEDEL – Campus Villarrica, PUC), Idea Wild, Rufford Small Grants Foundation, The Peregrine Fund (especially F. H. Vargas), and the François Vuilleumier Fund for Research on Neotropical Birds (Neotropical Ornithological Society). None of our funders had any influence on the content of the submitted or published manuscript, and none required approval of the final manuscript.

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