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# Elevation has contrasting effects on avian and mammalian nest traits in the Andean temperate mountains

TOMÁS A. ALTAMIRANO,[1,2]* MARÍA TERESA HONORATO,[2] JOSÉ TOMÁS IBARRA,[2,3,4] MARIANO DE LA MAZA,[2,5] DEVIN R. DE ZWAAN,[1] CRISTIÁN BONACIC[2] AND KATHY MARTIN[1,6]

[1]*Department of Forest and Conservation Sciences, University of British Columbia, 2424 Main Mall, Vancouver, British Columbia V6T 1Z4, Canada (Email: tomas.altamirano@ubc.ca);* [2]*Fauna Australis Wildlife Laboratory, Department of Ecosystems and The Environment, School of Agriculture and Forest Sciences, Pontificia Universidad Católica de Chile, Macul, Santiago;* [3]*Centre for Local Development (CEDEL), Villarrica Campus, Pontificia Universidad Católica de Chile, Villarrica, La Araucanía Region;* [4]*Millennium Nucleus Centre for the Socioeconomic Impact of Environmental Policies (CESIEP), Pontificia Universidad Católica de Chile;* [5]*Department of Biodiversity Conservation, National Forestry Service (CONAF), Santiago, Chile; and* [6]*Pacific Wildlife Research Centre, Environment and Climate Change Canada, Delta, British Columbia, Canada*

**Abstract** Nest building is a widespread breeding strategy across taxa. Nest composition and structure can play a critical role in the breeding success and/or adult survival of nest-building vertebrates. Although nest traits are expected to vary adaptively across elevational gradients, few studies address this relationship. We studied the variation in nest traits (composition and structure) across elevation for two taxa with two different functions in the Andean temperate forests of southern Chile: a bird (*Aphrastura spinicauda*, Furnariidae, 170 breeding nests) and a marsupial mammal (*Dromiciops gliroides*, Microbiotheriidae, 91 winter torpor nests). For *A. spinicauda*, we further assessed how nest traits influenced clutch size and hatching success. Both species used fewer types of nest materials (items) with increasing elevation, and a greater proportion of leaves were used in highland compared to lowland forests. *Aphrastura spinicauda* used feathers and hair, and *D. gliroides* used bryophytes more frequently in lowland forests. The mass and volume of nests decreased with increasing elevation for *A. spinicauda* and increased for *D. gliroides*. Nest traits had subsequent fitness consequences for *A. spinicauda*, such that: (i) greater cup volume and depth were associated with larger clutch sizes, (ii) more items used during nest building were linked to improved clutch size at high elevation only, and (iii) nest wall thickness was negatively associated with hatching success. Thus, in temperate mountain ecosystems, elevation may be an important factor influencing nest-building behaviour for cavity-using vertebrates. However, the direction of the elevational effects may vary among taxa and nest functions in these ecosystems.

Abstract in Spanish is available with online material.

**Key words:** altitude, Austral Opossum, breeding, Chile, Thorn-Tailed Rayadito.

## INTRODUCTION

Across taxa, nest building is an important activity during the breeding and/or non-breeding seasons (Hansell 2000). The ecological function of nests extends far beyond simply being a receptacle for eggs and offspring (Mainwaring *et al.* 2014; de Zwaan & Martin 2018), or adults in the case of nests used for winter torpor (i.e. natural hypothermia, Bozinovic *et al.* 2004; Celis-Diez *et al.* 2012). For birds, nests play a critical role in the regulation of temperature, humidity, and pH for developing offspring, and can provide protection against potential predators (Collias & Collias 1984; Álvarez & Barba 2009; Mainwaring *et al.* 2014; de Zwaan & Martin,2018). Nest materials and structure can therefore be important factors influencing the breeding success of many bird species (Webb 1987; Álvarez *et al.* 2013). For mammals, nest traits are likely to influence reproductive success and/or adult survival in the case of roosting mammals that build nests for winter torpor, although this has yet to be assessed.

A broad spectrum of materials is used in avian and mammalian nests, and the use of specific materials can vary within and among species based on their function (Biddle *et al.* 2018a,2018b). Green nest materials such as leaves, vines, and bryophytes can

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*Corresponding author.

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contain volatile secondary compounds and a pH that restricts the development of pathogens in the nest (Wimberger 1984; Clark & Mason 1985; Dubiec *et al.* 2013; Honorato *et al.* 2016). Also, nest materials can have different insulation capacities depending on the prevailing environmental conditions (Schöll & Hille 2014). For example, feathers are a more effective insulation material than grass in dry environments (Windsor *et al.* 2013), but this relationship is reversed under wet conditions (Hilton *et al.* 2004), while leaves are a semi-insulative nest material regardless of environmental conditions (Reid *et al.* 2002). Therefore, local environmental conditions could produce a trade-off between the quality and quantity of materials incorporated into the nest structure (Crossman *et al.* 2011).

Additionally, for birds, nest structure may also have consequences for breeding success (Mainwaring *et al.* 2014). Larger nests or nest cups have been linked with increased clutch size (Soler *et al.* 2001; Alabrudzinska *et al.* 2003; Álvarez & Barba 2008). For example, in southern Spain, Soler *et al.* (2001) found that *Pica pica* (Magpie) females, which build domed nests, reduced their clutch sizes when nest size was experimentally reduced. However, this pattern is not ubiquitous, as cup characteristics and clutch size were not associated with the open-cup nesting *Setophaga discolour* (Prairie warbler) in the north-eastern United States (Akresh *et al.* 2017). Hatching success has also been linked to nest traits (Lombardo 1994; Álvarez & Barba 2011; Glądalski *et al.* 2016), where structural properties of a nest can improve the micro-environment, and subsequently increase hatching success by reducing heat loss and regulating humidity (Deeming 2011; Deeming & Mainwaring 2015). In eastern Spain and Poland, two cavity nesters, *Parus major* (Great tit) and *Cyanistes caeroleus* (Blue tit), had greater hatching success with deeper nest cups and larger nests (Álvarez & Barba 2011; Glądalski *et al.* 2016). These variable results among species from different nesting guilds indicate that the type of nest (open cup, domed, cavity) may further contribute to the strength of the association between nest traits and fitness correlates (Alabrudzinska *et al.* 2003; Álvarez & Barba 2008; Akresh *et al.* 2017). Despite the importance and currently inconclusive role of nest composition and structure, the number of detailed studies on nest traits among different populations in the southern hemisphere is limited (e.g. Honorato *et al.* 2016; Botero-Delgadillo *et al.* 2017).

Elevation is an important factor influencing life-history traits in birds (Badyaev & Ghalambor 2001; Boyle *et al.* 2016). At high elevations, animals must contend with lower temperatures and higher solar radiation than at low elevations, which may shape the reproductive life-history traits of animals inhabiting these environments (Luebert & Pliscoff 2006; Boyle *et al.* 2016). For example, many species reduce their clutch sizes and/or increase the time spent in parental care with increasing elevation (Badyaev & Ghalambor 2001), including cavity-using birds (Altamirano *et al.* 2015). However, studies addressing the variation in nest composition and structure across elevation have found consistent variation in nest composition (Kern & Van Riper 1984; Bears 2002), but not nest structure and insulation across elevation (Kern & Van Riper 1984; Heenan *et al.* 2015; Lee 2015; Table 1). While Kern and Van Riper (1984) found that nests of *Chlorodrepanis virens* (Hawaiian Honeycreeper, an open-cup nester) had greater insulation and denser nest walls at higher elevations in Hawaii, Heenan *et al.* (2015) found the opposite pattern for 36 bird species in Australia, and Schöll and Hille (2014) found no differences in nest insulation quality with elevation for *Parus major*. Along with limited research on this topic, our understanding of nest trait variation across elevation tends to be biased towards one taxa (i.e. birds) and one life-history stage (i.e. breeding; Table 1). More studies of nest composition and structure across elevation for other vertebrates are required to understand consistencies and variation of patterns within and among both different taxa and nest functions (e.g. breeding *vs.* winter torpor; Mainwaring *et al.* 2014).

South American temperate forests occur along a narrow strip (~180 km) of land between 35° and 55° south latitude (Armesto *et al.* 1998), which includes two mountain ranges with forests spanning 0 to ~1800 m in elevation. These mountain forests are highly threatened, with only 30% of the original vegetation cover remaining (Myers *et al.* 2000). These forests support a high degree of endemic bird (41%) and mammal (33%) (Vuilleumier 1985; Armesto *et al.* 1996), and one of the highest percentage of cavity nesting birds in the world (57% of whole bird community; Altamirano *et al.* 2017). For nests built for breeding by a furnariid bird *Aphrastura spinicauda* (thorn-tailed rayadito) and nests built for winter torpor by a microbiotheriid mammal *Dromiciops gliroides* (Austral Opossum), we studied the following: (i) described and compared the elevational variation in nest traits (i.e. composition and structure) for two cavity-using vertebrates in Andean forests, and (ii) addressed the fitness effects (i.e. clutch size and hatching success) of nest composition and structure for *A. spinicauda*. We predicted that nest composition and structure would vary with elevation for both species due to the harsh climatic conditions in highland forests (e.g. higher precipitation and lower temperatures compared to lowland forests; Luebert & Pliscoff 2006; Ibarra *et al.* 2010). Specifically, we predicted that high elevation nests would have greater: (i) proportions of more efficient insulation material (i.e.

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**Table 1.** Available studies addressing nest trait variation across elevation

| | | | | | | | Association with elevation[§] | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Location | Latitude | Elevation (m) | *n*[*] | Spp | Taxa[†] | Nest type[‡] | Composition | Structure | Insulation | Source[¶] |
| Alberta | 52° N | 1000–2114 | 57 | 1 | B | O | –/+ | + | na | 1[‖] |
| British Columbia | 50° N | 400–2340 | 42 | 1 | B | O | na | ns | na | 2[‖] |
| Austria | 48° N | 488–878 | 33 | 1 | B | C | na | na | ns | 3 |
| Hawaii | 20° N | 650–2600 | 90 | 1 | B | O | –/+ | + | + | 4 |
| Australia | 25° S | 4–667 | 201 | 36 | B | O | na | ns | – | 5 |
| Chile | 39° S | 260–1115 | 261 | 2 | B, M | C | –/+ | –/+ | na | 6 |

[*] Sample size (# nests). [†] B = bird; M = mammal. [‡] O = open-cup nesting birds; C = cavity-nesting animals. [§] Directional responses to increasing elevation are provided, indicating differences between taxa or among nesting materials (–/+ = significantly decreasing/increasing; na = variable not assessed; ns = no significant effects). Nest composition refers to the identity and proportion of nest materials. Nest structure refers to both nest mass and volume. [¶] Sources: 1. Bears (2002); 2. Lee (2015); 3. Schöll and Hille (2014); 4. Kern and Van Riper (1984); 5. Heenan *et al.* (2015); 6. This study. [‖] Thesis dissertation.

feathers and hair; Hilton *et al.* 2004), (ii) mass, and (iii) volume, than lowland forests (Kern & Van Riper 1984). Finally, based on previous results in cavity-nesting birds, we expected larger clutch size and higher hatching success of *A. spinicauda* nests with larger cup and nest dimensions (Lombardo 1994; Álvarez & Barba 2008; Glądalski *et al.* 2016).

## METHODS

### Study area

We conducted this study in Andean temperate forests, Pucón Municipality (39° S), La Araucanía Region, Chile (for location details see Altamirano *et al.* 2015). Lowland forests (<700 m of elevation) are dominated by evergreen tree species of the genera *Nothofagus*, *Persea*, *Gevuina*, and *Laurelia* and one deciduous tree *Nothofagus obliqua*. Highland forests (>700 m of elevation) are dominated by evergreen tree species of the genera *Laureliopsis*, *Saxegothaea*, and *Araucaria*, and one deciduous tree *Nothofagus pumilio* (Rojas *et al.* 2011). The predominant understory across all elevations is bamboo (*Chusquea* spp), several ferns, and shrubs. The most common vine species include *Boquila trifololiata*, *Cissus striata*, *Muehlenbeckia hastulata*, *Lapageria rosea*, *Hydrangea serratifolia* and *Mitraria coccinea*.

### Study species

We selected two contrasting cavity-using vertebrate species from South American temperate forests. *Aphrastura spinicauda* is an endemic songbird (11.7 g) inhabiting forested areas from 0 to 2400 m of elevation in the temperate Andes (Housse 1945; Martínez & González 2004). Between October and February (austral breeding season), this species builds their nests in both tree cavities and nest-boxes ranging from ground level to 29 m of height (Cornelius 2008; McGehee *et al.* 2010; Altamirano *et al.* 2012). Clutch size ranges from 2 to 7 eggs, with decreasing clutch sizes in highland forests (Altamirano *et al.* 2015). *Dromiciops gliroides*, the only living member of the order Microbiotheria, is a small endemic marsupial (30.5 g; Celis-Diez *et al.* 2012) that inhabits forests from 0 to 1600 m of elevation (Martin 2010). This species builds nests for breeding in the austral summer and also between May and September for winter torpor during the austral winter (Mann 1978; Celis-Diez *et al.* 2012). A winter torpor nest is likely different from the breeding nest because it contains between 1 and 14 individuals, including females and males of different ages (Celis-Diez *et al.* 2012; T.A. Altamirano, pers. obs., 2013).

### Nest collection and treatment

In September 2010, we deployed 240 nest boxes which remained in the field for three breeding seasons and occupied six forest stands, covering an elevational gradient from 260 to 1115 m above sea level (a.s.l). Each forest stand contained 40 nest boxes hung from tree branches 1.5 m above-ground and distributed evenly in a grid consisting of five transects with eight nest boxes each, such that each nest box was separated by 25 m (Altamirano *et al.* 2015; Honorato *et al.* 2016). The nest boxes were made using the same wood type and thickness, with consistent inner dimensions (length = 16.5 cm, width = 13.2 cm, depth from entrance to base = 17.1 cm), and an entrance-hole diameter of 3.1 cm. After each breeding season (February–March), we collected all nests built by *A. spinicauda*. All nests built for winter torpor by *D. gliroides* (Bozinovic *et al.* 2004) were collected following the end of the winter torpor period (September). We found no breeding nests for this mammal species.

Nests were stored in the laboratory at ambient temperature and then dried in a convection oven at 105 °C for five hours. We measured nest mass and nest volume for both species. Additionally, for *A. spinicauda*, we measured cup depth, cup volume and nest wall thickness. We recorded the nest mass (±0.1 g), using an electronic balance (Hansell 2000). Using a non-digital dial calliper (±0.05 mm), we measured cup depth ($C_d$, from the top of the nest to the bottom of the nest cup), cup diameter ($C_w$, the largest diameter), nest wall thickness (the average between the thickest and thinnest section of the nest wall), nest length ($N_l$), nest width ($N_w$), and nest height ($N_h$, from the top of

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the nest to the bottom of the nest-box). With these metrics, and using half of an ellipsoid equation (Lombardo 1994; Botero-Delgadillo *et al.* 2017), we calculated cup volume as follows:

$$\text{cup volume (cm}^3) = \frac{\frac{4}{3}\left[\pi\left(\frac{C_w}{2}\right)^2 C_d\right]}{2}$$

Nest volume was calculated as follows for *A. spinicauda* (Lombardo 1994; Honorato *et al.* 2016) and *D. gliroides*:

$$\text{nest volume}_{A.\ spinicauda}(\text{cm}^3) = (N_l N_w N_h) - \text{cup volume}$$

$$\text{nest volume}_{D.\ gliroides}(\text{cm}^3) = (N_l N_w N_h)$$

For nest composition, each material type was classified as one of the following items: feathers, hair, bryophytes (mainly mosses and liverworts), lichens, leaves, tree and shrub twigs (hereafter twigs), vines, seeds, bark, wood chips, mud, spider web, and artificial material (e.g. nylon, plastic and thread; Atienzar *et al.* 2010). We dissected each nest on a grid which allowed us to estimate the relative proportion of the nest volume for each nesting material (±5%; Honorato *et al.* 2016). This estimation was conducted by M.T. Honorato to ensure consistency. All leaves were identified to the species level.

## Breeding monitoring

During each breeding season, nest boxes used by *A. spinicauda* were monitored every 3–4 days to determine clutch size, and daily near expected hatch date to determine the hatching success (i.e. number of hatched eggs; for more details see Altamirano *et al.* 2015). We were unable to assess fitness correlates for *D. gliroides* as all nests located were used for winter torpor (non-breeding season).

## Data analysis

We analysed the data for both species separately given that each species used their nests for different life history stages. For nest composition, we pooled lichens, seeds, bark, wood chips, mud, spider web and artificial materials into an 'other' category due to an overall minimal presence of these materials in the nests. The variable 'number of items' did not have a normal distribution (Lilliefors's tests, $P < 0.01$), and the relative proportions of each material were zero-truncated, making it difficult to test relationships between nest composition and elevation (i.e. most elevations were associated with a zero for certain relative proportions). Therefore, in this case only, we addressed associations between nest composition and elevation by categorising nests as occupying either a lowland (<700 m a.s.l) or highland forest (>700 m a.s.l) and tested compositional differences between these elevation categories, using univariate t-tests (relative proportions) and Mann–Whitney *U* Tests for the non-normal 'number of items.' We used 700 m a.s.l. as an inflection point between lowland and highland elevation categories because it approximates the snow line in the Andean temperate forests, above which the majority of precipitation in winter and early spring falls as snow (Ibarra *et al.* 2010), and subsequently the breeding season is delayed by an average of 36 days and the duration shortened by 31 days (Altamirano *et al.* 2015). To address associations between nest structure (i.e. nest mass, nest volume, cup volume) and elevation, we fit linear models with elevation as a continuous variable to better represent the data.

For fitness correlates, we addressed clutch size and hatching success for *A. spinicauda*. Hatching success was calculated as the proportion of eggs hatched with respect to the clutch size. We removed six nests from the analysis where none of the eggs hatched because it is likely that this complete clutch failure was caused by something unrelated to nest structure (e.g. infertility). We fit clutch size and hatching success to generalised linear models with a Gaussian and Binomial distribution (logistic regression), respectively. Each nest trait (i.e. nest mass, nest volume, cup depth, cup volume, nest wall thickness, and number of items) was included as the explanatory variable in separate models to test their influence on clutch size and hatching success for a total of six models for each response variable (Table 3). We included elevation (continuous) as an interaction term in each model to test for different slopes between the nest structure variables and fitness correlates across elevations. We centred each explanatory variable (i.e. subtracting the mean from each observation) to reduce the correlation between the additive and the interaction terms, as well as to allow interpretation of additive effects in the presence of a significant interaction (Quinn & Keough 2002). If the interaction term was not significant, we only included elevation as an additive control because fitness correlates have been shown to decrease across elevation for this species (Altamirano *et al.* 2015). See Table 3 for a list of all final models.

Since we measured the nest traits after the breeding season, associations between hatching success and cup dimensions may be confounded by the stage at which the nest was terminated (i.e. eggs, nestlings). After hatching, the cup diameter may become stretched, altering both the cup volume and nest wall thickness, particularly for nests that successfully fledged or were depredated close to when they might have fledged because of the increasing size and activity of the nestlings. To determine if nest stretching was a factor in our analyses, we fit two linear models testing cup volume and nest wall thickness as the dependent variables, with clutch fate (failed prior to hatch = 0, successfully hatched = 1) and nestling age (days, hatch day = 0) as the explanatory variables. Both cup volume and nest wall thickness were unrelated to clutch fate (cup volume: $t = 0.03$, $P = 0.98$, nest wall thickness: $t = 0.04$, $P = 0.97$) or nestling age (cup volume: $t = 0.68$, $P = 0.50$, nest wall thickness: $t = -0.75$, $P = 0.46$). Thus, we assume that nest stretching is not a confounding factor in our analyses of clutch size and hatching success with respect to nest size. All data are presented as means ± standard error (SE), and statistical tests were considered significant with $P < 0.05$. Analyses were conducted using JMP 9 and R 3.4.3 (R Development Core Team, 2015).

## RESULTS

We analysed a total of 261 nests; 170 belonging to *A. spinicauda* (32 highland and 138 lowland) and 91 belonging to *D. gliroides* (50 highland and 41 lowland).

### Elevational effects on nest composition

*Aphrastura spinicauda* built their nests with fewer items in highland forests than in lowland forests (5.59 ± 0.25 *vs.* 6.51 ± 0.09 number of items; $U = 1377.5$; $P < 0.01$). This species used mainly leaves, twigs and vines in both highland and lowland forests (Fig. 1). However, the proportional volume of feathers ($t = 4.47$, $P < 0.01$), hair ($t = 3.45$, $P < 0.001$), and leaves ($t = 3.39$, $P < 0.01$) varied significantly between elevations (Figs 1, 2a), with a lower proportion of feathers and hair in highland (feathers: 2.5 ± 0.5; hair: 1.9 ± 1.0) than in lowland forests (feathers: 5.6 ± 0.4; hair: 6.4 ± 0.6). In contrast, leaves were used more often by *A. spinicauda* in highland (23.4 ± 3.8) than in lowland forests (9.4 ± 3.1).

*Dromiciops gliroides* also built their winter torpor nests with fewer items in highland than in lowland forests (4.14 ± 0.22 *vs.* 5.29 ± 0.28 items; $U = 667.5$; $P < 0.01$), and used mainly leaves at both elevations (Fig. 2b). However, the proportional volume of bryophytes ($t = 5.37$, $P < 0.01$) and leaves ($t = 4.45$, $P < 0.01$) differed between elevations (Figs 1, 2b). A higher proportion of leaves and a lower proportion of bryophytes were used in highland (leaves: 79.2 ± 3.8; bryophytes: 5.6 ± 2.5) than in lowland forests (leaves: 51.8 ± 5.8; bryophytes: 32.8 ± 3.0).

**Fig. 1.** Representative nests constructed by two cavity-using vertebrates in Andean temperate forests.

### Elevational effects on nest structure

For *Aphrastura spinicauda*, nest mass was negatively associated with elevation ($F_{1,168} = 7.96$, $P < 0.01$; Fig. 3a), while both nest volume ($F_{1,168} = 1.46$, $P = 0.23$; Fig. 3c) and cup volume ($F_{1,156} = 0.45$, $P = 0.50$) did not vary. In contrast, for *Dromiciops gliroides*, nest mass and nest volume increased with elevation ($F_{1,89} = 30.03$, $P < 0.01$; Fig. 3b; $F_{1,89} = 15.52$, $P < 0.01$; Fig. 3d respectively). We provide mean ± SE values of these nest structure variables for high and low elevation as a reference in Table 2.

### Fitness correlates

For *A. spinicauda*, pooling nests from high and lowland forests, clutch size was positively associated with cup volume and depth (Table 3). There was also a significant interaction between number of items and elevation, such that the number of items used to build a nest were positively associated with clutch size, but only at high elevations (Table 3, Fig. 4). Nest mass, nest volume and nest wall thickness were unrelated to clutch size. Greater hatching success was associated with decreased nest wall thickness. All other associations between hatching success and nest traits were inconclusive. Larger cup volumes and greater number of items, as well as, smaller nest volumes, were marginally associated with improved hatching success. Nest mass and cup depth were unrelated to hatching success (see Table 3).

## DISCUSSION

Nest traits, including composition and structure, are expected to vary adaptively across different environmental conditions (Mainwaring *et al.* 2014). We demonstrate differing effects of elevation on nest composition and structure for two cavity-using vertebrates from southern temperate ecosystems. Contrary to our prediction based on the pattern found for other avian species (Kern & Van Riper 1984; Bears 2002), elevation was negatively associated with nest structure for *A. spinicauda* (nest mass), but in agreement with our expectations, elevation was positively associated with nest structure for *D. gliroides* (nest mass and volume). Our findings contribute to the limited knowledge on effects of elevation on nest traits and are consistent with our hypothesis that nest composition and structure vary across elevation. Furthermore, to our knowledge, this is the first study addressing this topic of using nests built by a mammalian species.

The number of items utilised by both species decreased with elevation. This result may be

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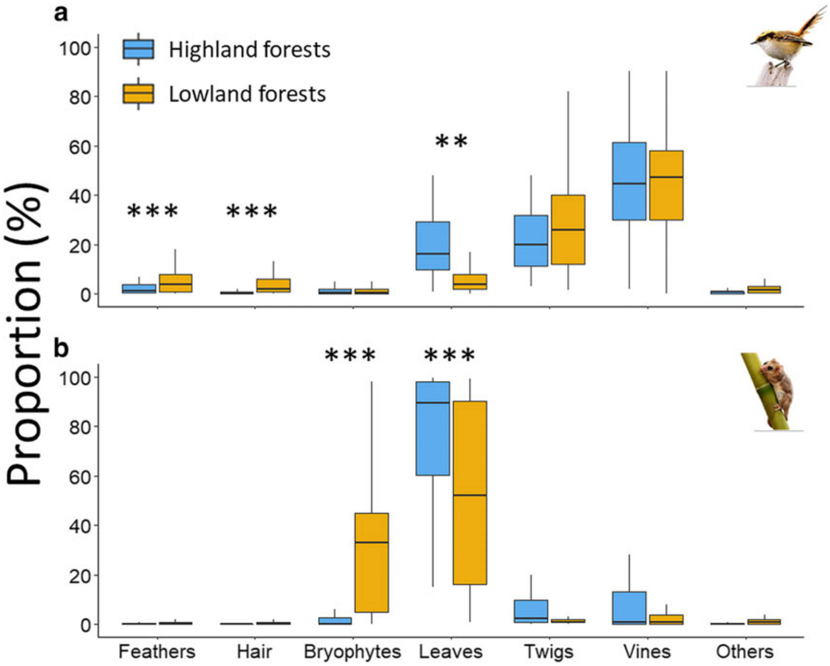

**Fig. 2.** Proportion of nest volume consisting of each material type for *Aphrastura spinicauda* (a, top) and *Dromiciops gliroides* (b, bottom) in Andean temperate forests. Horizontal lines show the median, the central box spans the first quartile to the third quartile and the bars represent the complete range of the data. Asterisks show statistical significance between the two elevations for each material type: ** = $P < 0.01$; *** = $P < 0.001$.

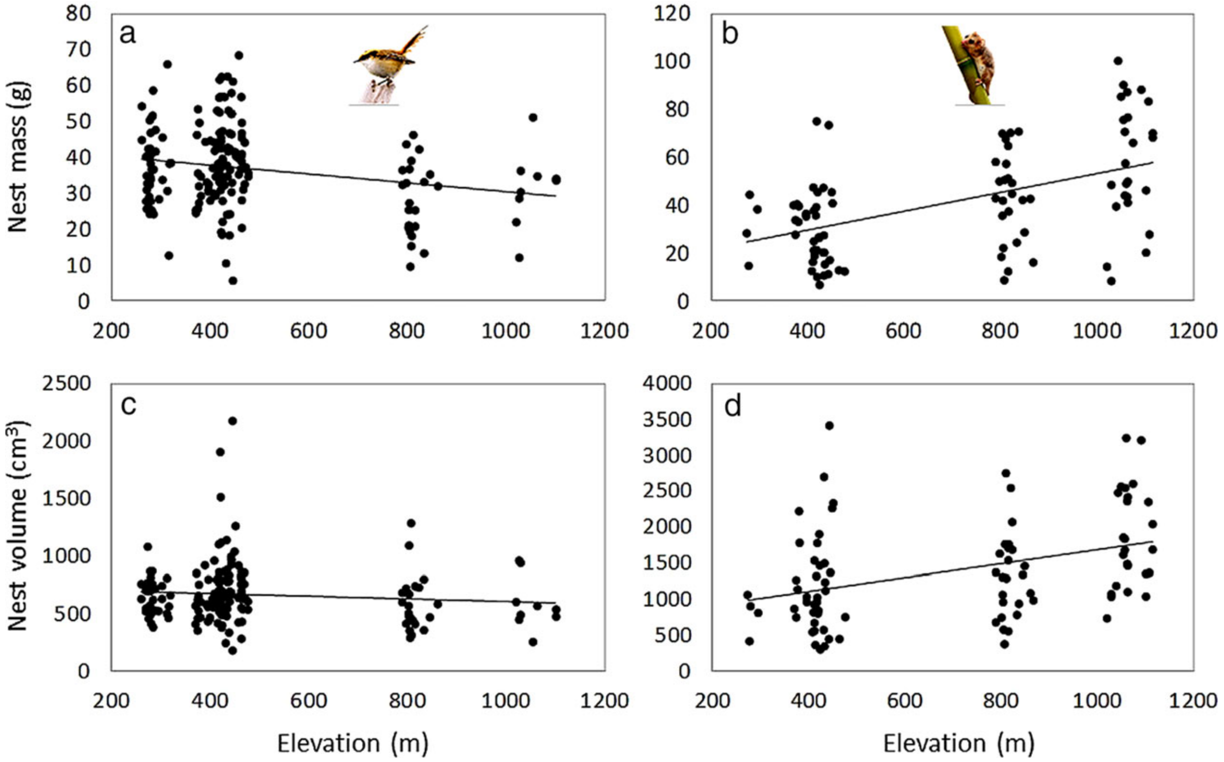

**Fig. 3.** Association between nest structure (nest mass and volume) and elevation (260–1150 m a.s.l.) in Andean temperate forests. Regression plots show weight (a) and volume (c) of nests built by *Aphrastura spinicauda* ($n$ = 170 nests), and weight (b) and volume (d) of nests built by *Dromiciops gliroides* ($n$ = 91 nests) during three breeding seasons (2010–2013).

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explained by a lower number of vascular plants and bryophyte species available at higher elevations in southern temperate forests (Smith-Ramírez *et al.* 2007). Contrary to our expectations, *A. spinicauda* used a lower proportion of hair and feathers in highland compared to lowland forests. This result differs from the previous studies assessing the effects of elevation on nest composition and structure. Kern and Van Riper (1984) found that nests of *C. virens* had higher insulation at higher elevations on the island of Hawaii, while Bears (2002) found that high elevation populations of *Junco hyemalis* used a greater overall mass of hair, lichens and moss. These differences, in our study system, may be explained by the following: (i) the relative availability of hair between elevations, and/or (ii) greater precipitation in highland forests (Luebert & Pliscoff 2006; Nagy & Grabherr 2009). Although hair is a better insulating material (Hilton *et al.* 2004), most hair present in *A. spinicauda* nests belonged to *Equus caballus* (Domestic horse), which are more abundant in lowland forests (CONAF, CONAMA & BIRF 1999). Further, precipitation could be an important driver of nest composition, since wet environments can change the insulation capacity of nest materials (Hilton *et al.* 2004; Heenan *et al.* 2015). Greater precipitation at high elevations in temperate ecosystems (Luebert & Pliscoff 2006; Nagy & Grabherr 2009), may cause hair and feathers to be avoided due to reduced insulation capacity (Hilton *et al.* 2004). In contrast, the proportion of leaves in nests increased with elevation, potentially because they act as an efficient insulation material in wet environments (Reid *et al.* 2002; Hilton *et al.* 2004). This could be a compensatory measure to regulate the insulation level for eggs and nestlings in

**Table 2.** Structural characteristics of nests (mean ± SE) for two cavity-using vertebrates in the Andean temperate forests, Chile, subdivided into highland (789–1115 m a.s.l.) and lowland (260–476 m a.s.l.) forests

| | *n* | Highland forests | Lowland forests |
|---|---|---|---|
| *Aphrastura spinicauda* | | | |
| Nest mass (g) | 170 | 30.42 ± 2.20 | 38.31 ± 0.97 |
| Nest volume ($cm^3$) | 170 | 591.53 ± 41.23 | 683.70 ± 22.03 |
| Cup volume ($cm^3$) | 159 | 83.88 ± 12.90 | 77.83 ± 3.79 |
| *Dromiciops gliroides* | | | |
| Nest mass (g) | 91 | 50.42 ± 3.29 | 29.84 ± 2.45 |
| Nest volume ($cm^3$) | 91 | 1587.33 ± 98.35 | 1161.30 ± 107.48 |

**Table 3.** Final structure and results for models testing the influence of nest structure traits (nest mass, nest volume, nest wall thickness, cup volume, cup depth and number of items) on clutch size and hatching success. If the interaction term between a nest trait and elevation was not significant, it was excluded from the final model (i.e. additive model). Significant parameters are highlighted in bold

| Response | | Model parameters | | df |
|---|---|---|---|---|
| Clutch size ~ | Nest mass<br>$t = 1.09$, $P = 0.28$ | Elevation<br>**$t = -1.97$, $P = 0.05$** | | 4 |
| | Nest volume<br>$t = -0.03$, $P = 0.98$ | **Elevation**<br>**$t = -2.28$, $P = 0.02$** | | 4 |
| | Nest wall<br>$t = -0.26$, $P = 0.80$ | **Elevation**<br>**$t = -2.30$, $P = 0.02$** | | 4 |
| | **Cup volume**<br>**$t = 2.34$, $P = 0.02$** | **Elevation**<br>**$t = -2.27$, $P = 0.02$** | | 4 |
| | **Cup depth**<br>**$t = 2.71$, $P < 0.01$** | **Elevation**<br>**$t = -2.22$, $P = 0.03$** | | 4 |
| | Items<br>$t = 1.06$, $P = 0.29$ | Elevation<br>$t = -1.10$, $P = 0.27$ | **Items*Elevation**<br>**$t = 2.60$, $P = 0.01$** | 5 |
| Hatching success ~ | Nest mass<br>$t = -1.16$, $P = 0.25$ | Elevation$^{\dagger}$<br>$t = -1.81$, $P = 0.07$ | | 3 |
| | Nest volume$^{\dagger}$<br>$t = -1.74$, $P = 0.08$ | Elevation$^{\dagger}$<br>$t = -1.77$, $P = 0.08$ | | 3 |
| | **Nest wall**<br>**$t = -1.93$, $P = 0.05$** | Elevation<br>$t = -1.64$, $P = 0.10$ | | 3 |
| | Cup volume$^{\dagger}$<br>$t = 1.80$, $P = 0.07$ | Elevation<br>$t = -1.46$, $P = 0.14$ | | 3 |
| | Cup depth<br>$t = 0.20$, $P = 0.84$ | Elevation<br>$t = -1.53$, $P = 0.13$ | | 3 |
| | Items$^{\dagger}$<br>$t = 1.77$, $P = 0.08$ | Elevation<br>$t = -1.27$, $P = 0.21$ | | 4 |

$^{\dagger}$Marginally significant parameters ($0.05 < P < 0.10$).

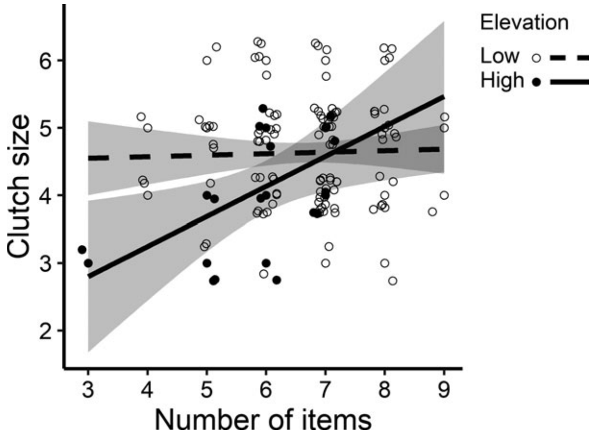

**Fig. 4.** The relationship between the number of items (material types) used to build the nest and clutch size for *A. spinicauda* in Andean temperate forests. The grey shaded area represents 95% confidence intervals of the raw data (points). Although the corresponding model was fit with elevation as a continuous variable, data points were categorised as high (>700 m a.s.l.) and low (<700 m a.s.l.) elevation for this figure to better visualise the items by elevation interaction.

*A. spinicauda* in order to reduce the thermodynamic costs of breeding (Hilton *et al.* 2004; Liljesthröm *et al.* 2009). We acknowledge that we did not explicitly test the insulation values of the specific nest materials and thus our ability to link our results to nest micro-climate benefits is based on results in the literature.

*Dromiciops gliroides* used mainly bamboo species (*Chusquea* spp.) and bryophytes in lowland forests, similar to a study for Chiloé island in southern Chile (<150 m a.s.l.; Celis-Diez *et al.* 2012). At low elevations, bryophytes effectively regulate microclimate in cavities (Banbura *et al.* 1995). In highland forests, *D. gliroides* built nests mainly with bamboo leaves, probably in response to wet environmental conditions at high elevation (Luebert & Pliscoff 2006). This result might also be driven by the high availability of bamboo species above 600 m a.s.l. in the study area compared to low elevations (Veblen & Schlegel 1982), where bamboo is frequently removed by land owners (Ibarra & Martin 2015).

Nests built by *A. spinicauda* were lighter and smaller at high elevations (colder) compared to low elevations (warmer), contrasting with patterns observed for *C. virens* (Kern & Van Riper 1984) and *J. hyemalis* (Bears 2002). These results may be associated with nest type: *C. virens* and *J. hyemalis* are open cup nesters while *A. spinicauda* is an obligate cavity nester (Altamirano *et al.* 2012). Nesting inside tree cavities (or nest-boxes) might provide better insulation and protection against cold Andean temperatures compared to open-cup nesters (Mersten-Katz *et al.* 2012). Since nest building is an energetically demanding activity (Mainwaring & Hartley 2013), another plausible explanation could be a trade-off between the length of the breeding season and the amount of energy allocated to building a nest. In highland forests, harsher environmental conditions are coupled with a breeding season that is on average 31 days shorter than lowland forests (Altamirano *et al.* 2015). Thus, breeding birds in highland forests may be energy-constrained (i.e. investing more in self-maintenance) or time-constrained compared to parents in lowland forests, reducing the size of the nest. Interestingly, our result is consistent with the latitudinal pattern found for the same species (Botero-Delgadillo *et al.* 2017). Populations of *A. spinicauda* at lower latitudes (warmer) build larger nests compared to populations at higher latitudes (colder; Botero-Delgadillo *et al.* 2017), demonstrating a consistent response in nest-building behaviour to environmental gradients across elevation and latitude, where larger nests coincide with warmer ambient conditions. This contrasts with species studied in the northern hemisphere, where both higher elevations and latitudes are generally associated with heavier nests and larger cups, potentially to improve thermoregulation in colder ambient conditions (e.g. Rohwer & Law 2010; Crossman *et al.* 2011; Mainwaring *et al.* 2012).

Unlike *A. spinicauda*, nests of *D. gliroides* were 1.7 times heavier and 1.4 times larger in the highland than in lowland forests, similar to the previously documented patterns (Kern & Van Riper 1984; Bears 2002), as well as to the descriptive differences shown by *Phylloscopus* spp. in Tibet (Lu 2008). This contrasting result with respect to *A. spinicauda* nests may be expected since the nests are used for winter torpor rather than breeding (Bozinovic *et al.* 2004), and increasing the nest weight and volume presumably improves insulation to deal with the extreme low temperatures of winters in highland forests (Lu 2008; Martin 2013). The number of individuals in a winter torpor nest likely further influences the thermoregulatory capacity of a nest, but unfortunately, we did not have sufficient data to test the interaction between the number of marsupial occupants and nest traits.

*Aphrastura spinicauda* nest traits were positively associated with clutch size (cup depth and volume across all elevations, and number of items at high elevations only), while hatching success was negatively influenced by nest wall thickness. Several additional marginal associations reflect that nest traits likely work in combination with other factors (i.e. parental behaviour) to influence fitness correlates. For example, a marginally significant effect of cup volume on hatching success provides some support for the observation that increased nest capacity improves hatching success (Álvarez & Barba 2011; Glądalski *et al.* 2016), which may explain the negative association

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between hatching success and nest wall thickness (inversely related to cup volume). Thus, while nest structure may play a crucial role in the thermoregulation of eggs (Collias & Collias 1984), the relationship between nest structure and bird fitness may be mediated by parental quality (Vieyra *et al.* 2009; Álvarez & Barba 2014). Deeper nest cups may aid in heat retention when adults leave the nest, subsequently helping adults conserve energy during incubation (Glądalski *et al.* 2016). This could be especially true in highland locations of Andean temperate forests, where the mean day time temperature is 11.6 ± 0.06 °C during the breeding season (T.A. Altamirano, D.R. de Zwaan, J.T. Ibarra & K. Martin, unpubl. data, 2017). On the other hand, recent studies have found that nest size constitutes a signal of female quality, with males allocating more energy to reproduction when females build larger nests (Cantarero *et al.* 2016; Jelínek *et al.* 2016). Although we did not find any relation between fitness correlates and nest volume or mass, the fact that we found a positive relationship between the number of items and clutch size at high elevations only could be an honest signal of parental quality in a harsher environment (i.e. where nest material availability may be limited compared to low elevation). Future studies should empirically test the relationship between nest material choice and parental quality for *A. spinicauda*.

Andean temperate forests of South America are characterised by steep, mountainous topographies (Donoso 1993). In these mountain ecosystems, elevation may be an important factor influencing nest-building behaviour for cavity-using vertebrates (Altamirano *et al.* 2015; Boyle *et al.* 2016). Here, we have highlighted variation in compositional and structural nest traits across elevation for both breeding (*A. spinicauda*) and winter torpor (*D. gliroides*) nests, along with subsequent fitness effects for *A. spinicauda*. Our results also indicate that further experimental and comparative studies between nest boxes and natural cavities are required in order to understand the underlying mechanisms involved in the relationship between nest traits, elevation and avian fitness (Lambrechts *et al.* 2012; Heenan *et al.* 2015).

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