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

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ABSTRACT

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

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Nest composition; nest structure; intra-seasonal variation; southern Chile; sub-Antarctic forests

Introduction

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

Although environmental adjustment is the most invoked explanation for seasonal variation in nest

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

This study focuses on a secondary cavity-nesting furnariid, the Thorn-tailed Rayadito (*Aphrastura spinicauda*), in order to describe the seasonal variation in nest morphology during its breeding season in a sub-Antarctic population in southern Chile. We aimed to assess the temporal differences in nest building periods and nest architecture, and their relationship with the seasonal fluctuation of ambient temperature (an 'environmental adjustment' hypothesis; see Mainwaring *et al.* 2014) and time constraints (an 'optimal time frame'

hypothesis; see Mainwaring and Hartley 2008). If climate is the main cause of nest variation, we predicted (i) a decrease in nest size and a reduced use of insulating materials towards the end of the breeding season, but (ii) no seasonal trend in these variables once the effects of daily temperatures on nest morphology were statistically removed. In contrast, if time constraints are more relevant, we predicted (i) a decrease in nest building periods and nest size as the breeding season progresses, and (ii) the maintenance of such a trend after correcting for the effects of temperature variation.

Materials and methods

Study area and meteorological data

This study was carried out during September–December 2013 on Isla Navarino (55° 4' S, 67° 40' W), located in the Magallanes y Antártica Chilena Region, southern Chile (Figure 1(A)). This locality is part of the southern distributional range of the Thorn-tailed Rayadito, where its breeding season usually extends from October to January (Remsen 2003; Quirici *et al.* 2014). Despite daily fluctuations of temperature during this period, monthly mean temperature tends to increase towards the end of the year

(Figure 1(B, C)). Meteorological data used for description and subsequent analyses were obtained from the ‘Guardia Marina Zañartu’ meteorological station (<http://www.meteochile.goc.cl/>), located in the study area.

Nest collection and measuring

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

Nests were collected from nest boxes a month after the end of the breeding season. During nest collection, we measured the nest depth (i.e. from top of the nest to bottom of the box) in each of its four sides and the

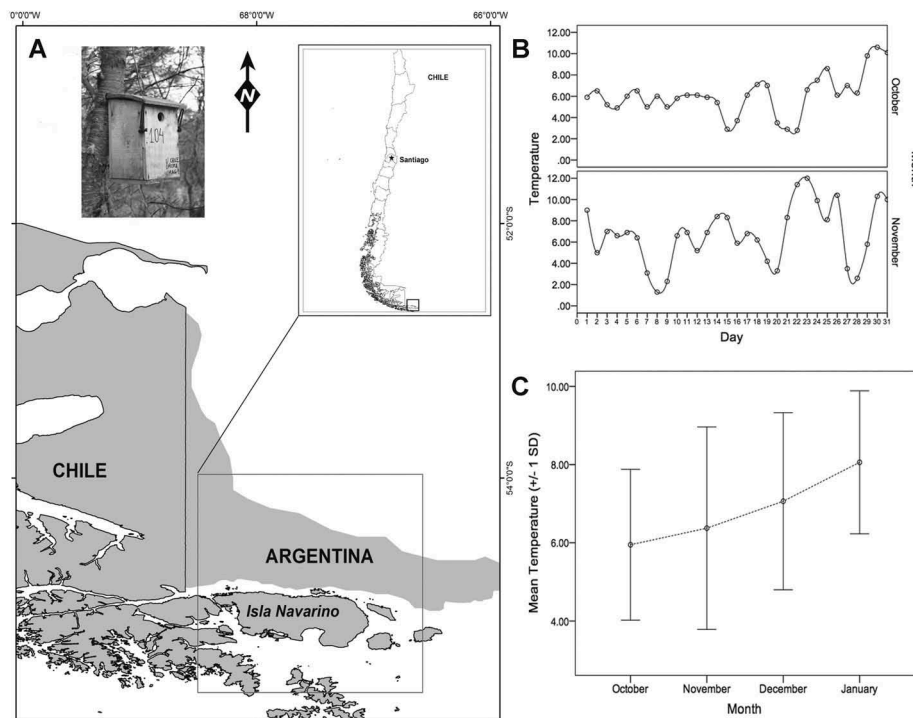


Figure 1. Location of the study area and values of daily/monthly temperature during the 2013 breeding season of the Thorn-tailed Rayadito. (A) A total of 201 nest boxes were offered to a southern population of rayaditos at Isla Navarino, southern Chile. (B) Fluctuation of daily temperature during October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

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

Data analyses

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

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

daily mean temperature as the predictor variable. Temperature values were defined as the mean temperature recorded during each nest building start day. Finally, residuals from these analyses were used for testing whether seasonal trends remained after removing the effects of temperature, regressing the residuals against building start dates.

Results

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

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

Table 1. External measurements describing the variation in structure and composition of Thorn-tailed Rayadito nests. For descriptive purposes, nests were grouped as 'early' and 'late' nests depending on the building start date (before/after the mid-part of the breeding season: 25 October). Data shown are mean \pm SD

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

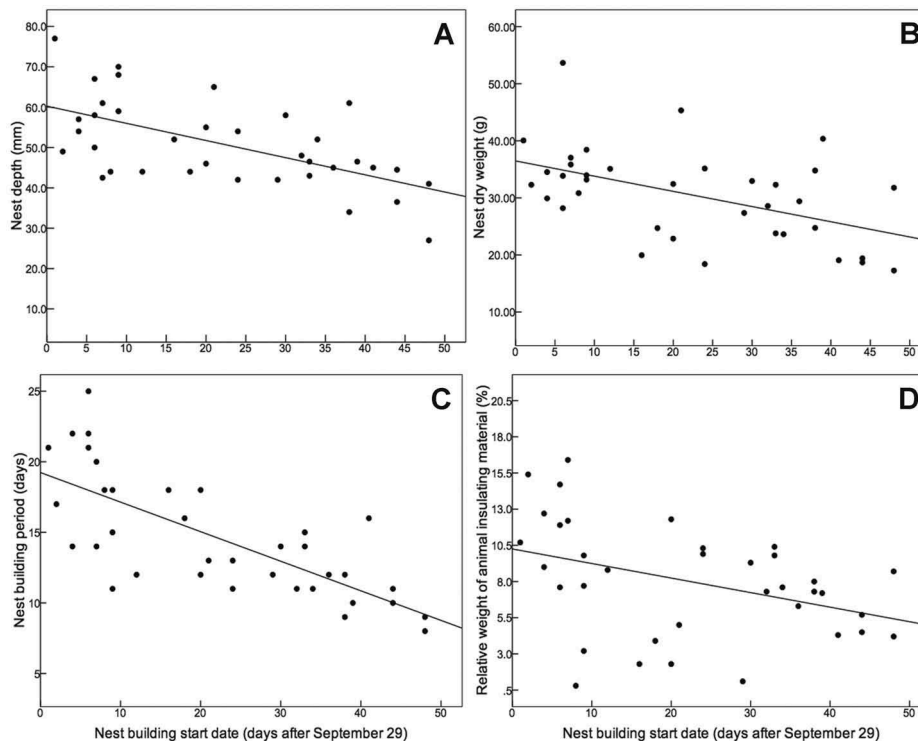


Figure 2. Linear regression models showing significant seasonal trends in the nest building behaviour and nest morphology of the Thorn-tailed Rayadito. (A) Mean nest depth values regressed against nest building start dates for the 2013 breeding season ($y = -0.45 * x + 60.24$). (B) Values of nest dry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

relative weight of plant-derived insulation ($r^2 = 0.01$, $F_{1,34} = 0.15$, $P = 0.703$).

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

Discussion

Our results showed that in this population, nest building periods and nest structure/composition changed throughout the breeding season. Although not all measurements of nest architecture varied temporally, we

observed that as the breeding season progressed rayaditos spent fewer days building their nests, built smaller nests, and used smaller amounts of animal-derived insulating material.

The observed decrease in nest size and the use of insulating material were related to the increase in temperatures towards the end of the year, as expected under an ‘environmental adjustment’ explanation. However, only the amount of insulating material was completely explained by temperature increase (Figure 3), implying that birds may adjust their nest to the prevailing conditions by only changing its composition, and that apparently co-varying changes in nest size are not a necessary consequence of the variation in environmental temperature. In fact, studies on intra-seasonal variation of nest morphology show that nest composition, but not nest dimensions, is related to the seasonal trends of ambient temperature (e.g. Blue Tit (*Cyanistes caeruleus*); Mainwaring and Hartley 2008), even though nest size and structure can have important consequences on the insulation quality of nests (White *et al.* 1975; Liljeström *et al.* 2009). Hence, our results support the idea that birds can assess the environmental conditions and adjust the frequency of use of some building materials (Bullitt

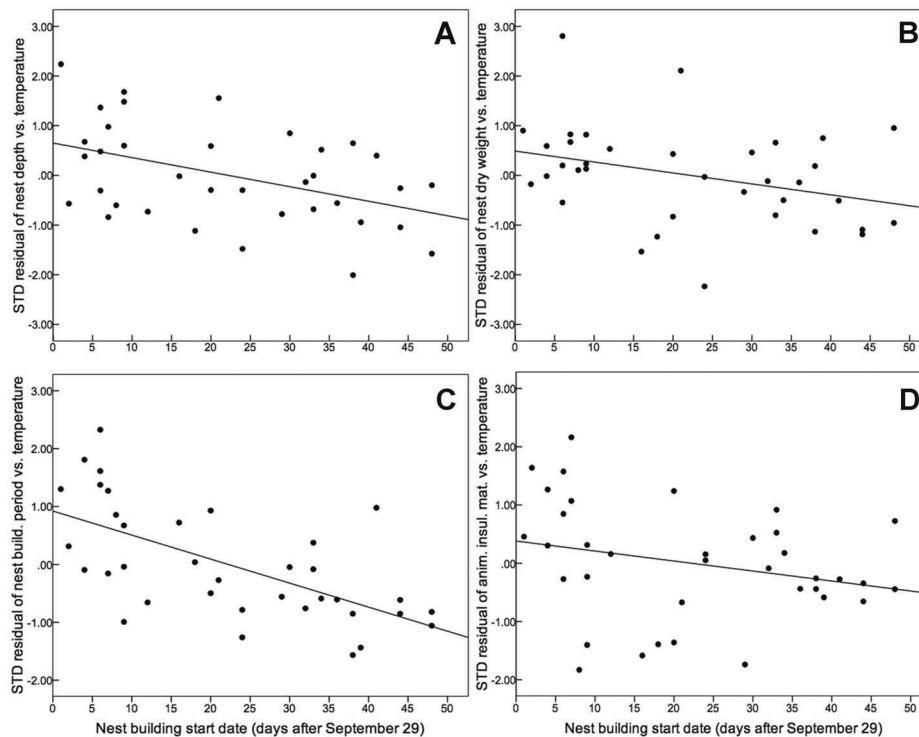


Figure 3. Linear regression models showing significant seasonal trends in the nest building behaviour and nest morphology of the Thorn-tailed Rayadito, after removing the potential effects of temperature increase during the breeding season (using linear regression). (A) Standardised (STD) residuals of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

and Massoni 2004; Mainwaring and Hartley 2008; Liljeström *et al.* 2009; Britt and Deeming 2011), possibly regulating nest microclimate for an optimal development of embryos and chicks (Webb 1987; Lombardo *et al.* 1995).

Variation in nest building periods was totally explained by the nest building start date, which agreed with the predictions of an ‘optimal time frame’ explanation. Nest depth and dry weight were partially explained by temperature increase, but after removing this effect we still detected a seasonal decline in both variables, further supporting the idea that time constraints can affect nest building behaviour and nest structure. Although some studies have failed to provide evidence of the potential relevance of time constraints (e.g. McGowan *et al.* 2004), others suggest it can cause birds to accelerate nest building, although this will not necessarily involve changes in nest structure (Mainwaring and Hartley 2008). Our results, however, point to a seasonal trend in nest building that has consequences for nest size for Thorn-tailed Rayaditos. Furthermore, a previous study carried out on Isla Grande de Chiloé, southern Chile, provided evidence on how other reproductive traits of rayaditos show a

seasonal trend that could be a consequence of time constraints (see Moreno *et al.* 2005). The authors not only observed that the period between laying of the first egg and hatching of the brood was negatively related to laying date but also that the duration of the nestling period was negatively associated with hatching date, indicating either that laying intervals were shortened or the embryonic development rate increased over the course of the season.

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

Despite the fact that our data did not account for some potential confounding factors, this study has shown that both environmental adjustment and time constraints can influence the nest building behaviour of this cavity-nesting bird, and consequently

the design of the nest structure (Mainwaring and Hartley 2008). We have also shown that diverse factors can affect different components of the nesting ecology of birds, and that the final product, i.e. the nest, can be the consequence of several non-mutually exclusive forces (Mainwaring and Hartley 2008). Given the need to provide a regulated environment for the development of their brood, breeding birds accordingly change the type and amount of insulating material as temperatures gradually increase throughout the breeding season (McGowan *et al.* 2004). On the other hand, the time invested in nest building and the dimensions of the resulting structure can be the consequence of birds synchronising the most critical stages of their breeding attempt with peaks of resource availability (Mainwaring and Hartley 2013).

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