

**UNIVERSIDAD NACIONAL DE SAN AGUSTÍN DE AREQUIPA**

**FACULTAD DE CIENCIAS BIOLÓGICAS**

**ESCUELA PROFESIONAL DE BIOLOGÍA**



Building multiple nests is associated with reduced breeding performance in  
a south temperate population of Grass Wrens *Cistothorus platensis*  
*platensis*

**Tesis Formato Artículo presentada por el**

**Bachiller:**

**Daniel Pascual Caceres Apaza**

**Para optar el título Profesional de: Biólogo**

**Asesor:**

**Dr. López Tejeda, Evaristo Luciano**

**Arequipa – Perú**

**2019**

## **AGRADECIMIENTOS**

Al CONICET (D1791, PIP 11220100100039 y 11220130100198) y al FONCYT (PICT 2010-1033) del país de Argentina, por la subvención recibida. A Dr. Paulo Emilio Llambías por la asesoría y acogida en el laboratorio de biología de aves, del IADIZA-CONICET.

## TIPO DE PARTICIPACIÓN EN LA INVESTIGACIÓN

- **Autor:** PAULO EMILIO LLAMB\_ÍAS,<sup>1,2\*</sup>
- **Co-Autor:** DANIEL PASCUAL CACERES APAZA,<sup>1</sup>
- **Co-autores:** MAR\_ÍA MILAGROS JEFFERIES,<sup>1</sup> † PAULA SABRINA GARRIDO,<sup>1</sup> AGUST\_IN ZARCO,<sup>1,3</sup>  
RAMIRO SANTIAGO ARRIETA<sup>1</sup> & JOSÉ BENJAMIN BENDER<sup>1,2</sup>

<sup>1</sup>Biología de Aves – IADIZA-CONICET, Av. Ruiz Leal s/n, Parque General San Martín, 5500 Mendoza, Argentina

<sup>2</sup>Colección de Ornitología IADIZA-CONICET, Av. Ruiz Leal s/n, Parque General San Martín, 5500 Mendoza, Argentina

<sup>3</sup>Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Cuyo, Padre Jorge Contreras 1300,

5500 Mendoza, Argentina. †Present address: Museo de Historia Natural, Universidad Nacional

de San Agustín de Arequipa, Av. Daniel Alcides Carrión s/n, Arequipa, Perú.

**Building multiple nests is associated with reduced breeding performance in a south temperate population of Grass Wrens**

*Cistothorus platensis platensis*

PAULO EMILIO LLAMBÍAS,<sup>1,2,\*</sup> MARÍA MILAGROS JEFFERIES,<sup>1</sup> DANIEL PASCUAL CÁCERES APAZA,<sup>1,3</sup> PAULA SABRINA GARRIDO,<sup>1</sup> AGUSTÍN ZARCO,<sup>1,4</sup> RAMIRO SANTIAGO ARRIETA<sup>1</sup> & JOSÉ BENJAMIN BENDER<sup>1,2</sup>

<sup>1</sup>*Biología de Aves – IADIZA-CONICET, Av. Ruiz Leal s/n, Parque General San Martín, 5500 Mendoza, Argentina*

<sup>2</sup>*Colección de Ornitología IADIZA-CONICET, Av. Ruiz Leal s/n, Parque General San Martín, 5500 Mendoza, Argentina*

<sup>3</sup>*Present address: Museo de Historia Natural, Universidad Nacional de San Agustín de Arequipa, Av. Daniel Alcides Carrión s/n, Arequipa, Perú*

<sup>4</sup>*Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Cuyo. Mendoza, Argentina*

\*Corresponding author.

Email: [pllambias@mendoza-conicet.gob.ar](mailto:pllambias@mendoza-conicet.gob.ar)

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/ibi.12722 This article is protected by copyright. All rights reserved.

**ABSTRACT.-** Grass Wrens *Cistothorus platensis* build two types of non-breeding nest structures: platforms and dummy nests. Platforms are rudimentary accumulations of grasses concealed between vegetation. Dummy and breeding nests are dome-shaped with a similar structural layer. We used a nest-removal experiment and observational data to evaluate several hypotheses regarding the adaptive significance of building multiple nests in a south temperate population of Grass Wrens. Building non-breeding nests was not a strategy of males to attract additional females as most of these nests were built after pair formation and both sexes collaborated during building. Building non-breeding nests was not a post-pairing display as the presence of multiple nests did not increase female investment in the breeding attempt: clutch size and female provisioning to nestlings did not differ between experimental and control territories where no non-breeding nests were removed. Similarly, in non-manipulated territories, clutch size and female provisioning were not correlated with the number of non-breeding nests or with males' nest building effort. Contrary to this hypothesis, the number of non-breeding nests was associated with delayed clutch initiation and reduced hatching success. The presence of non-breeding nests did not reduce nest predation and brood parasitism, which did not differ between experimental and control territories. We did not detect differences in concealment between non-breeding and breeding nests, suggesting that non-breeding nests were not the result of abandonment before egg-laying to reduce subsequent nest predation. Dummy nests did not provide shelter; they were not frequently used for roosting over the breeding season and were not maintained during the non-breeding season. We suggest that building non-breeding nests may be attempts by males to manipulate the decision of females to breed with a mate they might otherwise reject or to start reproduction earlier than optimal for them.

**Keywords:** breeding biology, nest building, nest predation, nest concealment, roosting behaviour, sexual conflict

**RESUMEN.** - El Cucarachero de los Pastizales *Cistothorus platensis* construye dos tipos de estructuras de nidos no reproductivos: plataformas y nidos ficticios. Las plataformas son acumulaciones rudimentarias de pastos ocultos entre la vegetación. Los nidos ficticios y reproductivos tienen forma de cúpula con una capa estructural similar. Utilizamos un experimento de remoción de nidos y datos de observacionales para evaluar varias hipótesis con respecto a la importancia adaptativa de la construcción de múltiples nidos en una población del Cucarachero de los Pastizales en el sur templado. La construcción de nidos no reproductivos no fue una estrategia de los machos para atraer hembras adicionales, ya que la mayoría de estos nidos se construyeron después de la formación de parejas y ambos sexos colaboraron durante la construcción. La construcción de nidos no reproductivos no fue un despliegue posterior al emparejamiento, ya que la presencia de múltiples nidos no aumentó la inversión de la hembra en el intento de reproducción: el tamaño de la nidada y el aprovisionamiento de la madre a los pichones no difirieron entre los territorios experimentales y de control donde no se removieron nidos no reproductivos. Del mismo modo, en territorios no manipulados, el tamaño de las nidadas y el aprovisionamiento de la hembra no se correlacionaron con el número de nidos no reproductores o con el esfuerzo de construcción de nidos de los machos. En oposición a esta hipótesis, el número de nidos no reproductivos se asoció con un inicio tardío de la nidada y un menor éxito de eclosión. La presencia de nidos no reproductivos no redujo la depredación de nidos y ni el parasitismo de cría, que no difirió entre los territorios experimentales y de control. No detectamos diferencias en el ocultamiento entre los nidos no reproductivos y reproductivos, lo que sugiere que los nidos no reproductivos no fueron el resultado del abandono antes de la puesta de huevos para reducir la posterior depredación de nidos. Los nidos ficticios no proporcionaron refugio; no se utilizaron con frecuencia para descansar durante la temporada de reproducción y no se mantuvieron durante la temporada de no reproducción. Sugerimos que la construcción de nidos no reproductivos puede ser un intento de los machos para manipular la decisión de las hembras de reproducirse con una pareja que de otro modo podrían rechazar o comenzar la reproducción antes de lo óptimo para ellas.

**Palabras clave:** biología reproductiva, construcción de nido, depredación de nido, ocultamiento de nido, comportamiento de descanso, conflicto de sexos

## INTRODUCTION

Nests are structures built by breeding birds for tending eggs and, in many altricial and semi-altricial species, developing young (Hansell 2000, Winkler 2016). Nests provide shelter from adverse environmental conditions and protection from predators (Soler *et al.* 1998, Hansell 2000, Hansell & Deeming 2002). Nest building is a demanding behaviour that in most species requires considerable investments of time and energy (Berg *et al.* 2006, Moreno 2012, Mainwaring & Hartley 2013). Both experimental and observational studies suggest a trade-off between the costs of nest building and subsequent parental effort (Hansell 2000, Moreno 2012, Mainwaring & Hartley 2013). Furthermore, nest building can reduce adult survival by increasing exposure to predators (Collias & Collias 1984, Soler *et al.* 1998). Accordingly, some species reduce the costs of nest building by usurping nests, stealing nest material, or re-using old nests (Hansell 2000, Winkler 2001, Mainwaring & Hartley 2013). In contrast, other species may increase the costs by building additional nest structures that are not used for breeding (e.g. Ueda 1984, Evans & Burns 1996, Friedl & Klump 1999, Berg *et al.* 2006, Beckmann & Martin 2016).

Sexual selection before and after pair formation may play an important role in the evolution of multiple nest building behaviour. Prior to pairing, males of socially polygynous species may display non-breeding nests to attract females. The female attraction hypothesis proposes that females preferentially pair with males that build the largest number of non-breeding nests on their territories (Verner & Engelsen 1970, Garson 1980, Soler *et al.* 1998).

Males that build nests to attract more than one female usually provide reduced parental care as they keep building non-breeding nests during their social mate's incubation and nestling stages (Verner & Engelsen 1970, Burns 1982, Evans 1997). In Eurasian Wrens *Troglodytes troglodytes* and Southern Red Bishops *Euplectes orix*, the number of empty nests on a territory increases the probability of attracting more females (Garson 1980, Evans & Burn 1996, Friedl & Klump 1999). However, there is no clear relationship between building multiple nests and mate attraction in other socially polygynous species (e.g. Sedge Wren *Cistothorus stellaris*; Burns 1982, Marsh Wren *Cistothorus palustris*; Metz 1991).

After pair formation, males may benefit from building multiple nests through differential allocation of their mates (Soler *et al.* 1998, Moreno 2012, Mainwaring *et al.* 2014). The post-pairing display hypothesis proposes that males build nests as displays directed to their social partners to increase female investment in the brood (Moreno *et al.* 1994, Moreno 2012). Several studies have reported that females adjust parental investment to male effort during nest building (reviewed by Soler *et al.* 1998, Moreno 2012, Mainwaring *et al.* 2014). In

Eurasian Penduline Tits *Remiz pendulinus*, females are more likely to provide parental care for the nestlings of males that build larger nests and invest more time in nest building (Szentirmai *et al.* 2005). In Black Wheatears *Oenanthe leucura*, mated males carry stones to potential breeding cavities during the pre-laying period (Moreno *et al.* 1994). When the stone carrying activity was increased by removing stones from active sites, females advanced egg laying and increased the total number of eggs produced in a season (Soler *et al.* 1996). However, in Australian Reed Warblers *Acrocephalus australis*, although food supplementation increased the number of non-breeding nests built by males, females did not adjust clutch size to the number of non-breeding nests (Berg *et al.* 2006).

The nest predation avoidance hypothesis proposes that empty nests may serve as decoys that reduce both the reward per unit time of nest searching and the probability that a predator will find a nest in which a breeding attempt is underway (Leonard & Picman 1987, Watts 1987, Noske *et al.* 2013). In Large-billed Gerygones *Gerygone magnirostris*, nests that are closer to non-active nests have lower predation probability than nests located at greater distances (Noske *et al.* 2013). In Marsh Wrens, a greater number of empty nests on a territory increased the probability of breeding success in one study in Manitoba (Leonard & Picman 1987). However, in another study, in Ontario, the total number of non-breeding nests within a territory did not affect nest predation (Metz 1991). Empty nests may also serve as decoys to reduce brood parasitism, although we are not aware that this hypothesis has been examined to date. The deficient concealment hypothesis proposes that to minimize nest predation risk, adults should abandon the nests that are not well-concealed by surrounding vegetation prior to egg laying (Beckmann & Martin 2016). In contrast to other hypotheses that assume that non-breeding nests are supplementary functional structures, the deficient concealment hypothesis simply proposes that 'non-breeding' nests are those that have been abandoned. Accordingly, in Grey Fantails *Rhipidura albiscapa*, nests that are not used for reproduction have less vegetation concealment than those that are (Beckmann & Martin 2016). However, a later experimental study showed that artificial nests placed at previously abandoned nest sites had similar risk of predation as nests placed at sites where nests were predated or successful (Flegeltaub *et al.* 2017).

Finally, some species build additional nests to provide shelter for adults and fledglings. Several species build dormitory nests that are used for roosting at night (e.g. Song Wrens *Cyphorhinus phaeocephalus*; Robinson *et al.* 2000, Buff-breasted Wrens *Cantorchilus leucotis*; Ahumada 2000, Gill & Stutchbury 2005). However, in Rufous-and-white Wrens

*Thryophilus rufalbus*, monitoring so-called dormitory nests at dusk could not confirm the use of these nests for roosting (Ahumada 2000).

There is still no consensus on the adaptive significance of building multiple nests and its effects on breeding success. For a better understanding of this rare and yet unique aspect of nest-building behaviour in birds, there is a need for more experimental studies that combine the removal of non-breeding nests with detailed field observations.

Grass Wrens *Cistothorus platensis* build two types of non-breeding nest structures: platform nests and dummy nests (Fig. 1). Platform nests are rudimentary accumulations of grasses concealed between vegetation (Fig. 1A). Dummy and breeding nests are dome-shaped with a similar structural layer (Fig. 1B and 1C). However, dummy nests usually lack an internal cup lining. In this study, we performed a nest-removal experiment and used observational data to test five hypotheses explaining the function of non-breeding nests in a south temperate population of Grass Wrens in Argentina. Although social polygyny is rare in our population (3%; Llambías *et al.* 2018), a high incidence of polygyny (i.e. 60% of the males bred polygynously) in 2015 allowed us to evaluate the role of non-breeding nests in female attraction. If non-breeding nests are used by males to attract females (female attraction hypothesis) we predict that: (1) males will build non-breeding nests before pair formation, (2) paired males will build non-breeding nests to attract additional females while their social partners are tending eggs and nestlings, and (3) polygynous males will have more non-breeding nests on their territories than monogamous males. If building multiple nests is a post-pairing display (post-pairing display hypothesis), building non-breeding nests should be associated with increased female parental investment and breeding performance. Specifically, we predict that: (1) building multiple nests will occur after pair formation and before egg laying both in monogamous and polygynous associations, (2) females will produce smaller clutches, lay later and/or feed nestlings less on experimental territories where non-breeding nests were removed than on control territories where no non-breeding nests were removed, and (3) in non-manipulated territories, females of pairs that build more non-breeding nests will lay earlier, produce larger clutches and will provide more food to nestlings than females of pairs that build fewer non-breeding nests. If non-breeding nests are built as decoys to reduce nest predation and or brood parasitism (predation avoidance hypothesis), we predict that: (1) nest predation and or brood parasitism will be greater on experimental territories than on control territories, and (2) non-breeding nests will be re-built after removal. If building multiple nests is a consequence of nest abandonment caused by inappropriate nest concealment (inefficient concealment hypothesis), we predict differences in nest location, nest concealment and vegetation structure between breeding and non-breeding nests. Finally,

if dummy nests are used as dormitories (roosting hypothesis) we predict that: (1) wrens will build new non-breeding nests after removal, (2) non-breeding nests will be maintained by adults during the year, and (3) adults and/or fledglings will roost inside dummy nests at night.

## **METHODS**

### **Study species**

The Grass Wren is a small insectivorous passerine that inhabits dry and inundated grasslands from Mexico to Tierra del Fuego (Ridgely and Tudor 1989, Gill and Donsker 2018, but see Remsen *et al.* 2018 for a different taxonomic status). Grass Wrens are year-round residents and predominantly socially monogamous (Kroodsmma *et al.* 1999, Brewer 2001, de la Peña & Salvador 2016, Llambías *et al.* 2018). Males sing and defend breeding territories, but only females incubate the eggs and brood the nestlings (Herkert *et al.* 2001, Llambías *et al.* 2018). In our study population, both sexes provide food to nestlings in similar proportions (Llambías *et al.* 2018).

### **Study site**

We studied Grass Wrens in the flood plain of the Uspallata Stream and Mendoza River (32° 38' S, 69° 22' W, 1800 m asl), Mendoza Province, Argentina. Although mean annual precipitation is low (~100 mm), the stream forms a fertile corridor with small swamps and riparian grasslands dominated by Pampas Grass *Cortaderia selloana* (Carretero 2000). Seasonality is pronounced, with temperatures below freezing and occasional snowfall during the austral winter (mean temperature = 6.88°C) and warmer temperatures in the austral summer (mean temperature = 13.78°C; Carretero 2000).

### **Field methods**

Over seven breeding seasons (October-February, 2010-2016) we monitored Grass Wren territories on a daily basis. The number of territories varied between 14 and 49 per breeding season as some were lost to flooding events or fire, and because we expanded the study area in 2011, 2012 and 2015.

We followed the breeding activities of 147 males and 153 females (95.2% of the males and 64.7% of the females were colour-ringed). We captured most unringed adults at the beginning of the breeding season, either driving pairs into mist-nets or attracting males into mist-nets with playback within the territories. We also captured some unringed individuals at the nest when nestlings were 7-14 days old.

### **Classification of nests**

We located 665 nest structures and recorded the location of each with hand-held GPS units (Garmin Etrex 20, KS, USA). We classified a nest as 'platform' (grass accumulation which

did not change in structure for at least four days), as 'dummy' (dome nest with a defined entrance with no eggs being present for at least two weeks), and as 'breeding' (dome nest with at least one egg present; Fig. 1). All nests are started as platforms, and may develop into dummy or breeding nests if adults then build the dome-shaped structural layer. We considered a nest status as unknown if after initiating a nest, the adults were not observed again on the territory.

Based on daily observations of nests that we found during nest-building initiation, we assumed that it requires one day to build a platform (mean  $\pm$  1 sd:  $1.33 \pm 0.50$  d,  $n = 76$ ), three days to build an early dome (adults building the structural layer of the dome;  $2.76 \pm 0.78$  d,  $n = 76$ ) and five days to build an advanced dome (adult building the interior of the dome;  $5.27 \pm 0.80$  d,  $n = 56$ ). We calculated nest initiation date for all nests that we found during the building stage and considered the day that the first nest was initiated (day one) as a reference date and sequentially assigned initiation dates for all nests for each breeding season from it.

### **Social mating system**

We used behavioural observations of males and females during nest searching and nest monitoring to determine the boundaries of territories and establish the socio-spatial association between males and females. For this purpose, we opportunistically re-sighted ringed individuals and recorded singing perches and agonistic interactions between neighbours. We transcribed these observations on to satellite images to delineate territories. We recorded a male and a female as paired if for at least four consecutive days we observed on a territory the male following the female at close distance (0.5-2.0 m) in the presence of no additional males. We recorded a male as socially polygynous if it was associated with more than one female with overlapping reproductive activity (from nest building until nutritional independence of young). We classified females associated with a polygynous male as 'primary' (first female to initiate egg laying) and 'secondary' (second female to initiate egg laying). Females associated with polygynous males seldom interact with each other, but forage and breed on sub-territories within the territory of their social mate (Llambías *et al.* 2018).

### **Nest-building and nestling-provisioning behaviour**

Over four breeding seasons (2013-2016), we filmed dummy and breeding nests during the building stage to assess: (1) sexual roles during nest building, and (2) the relationship between the relative contributions of birds to the building of dummy nests and female parental investment in the brood. We only filmed dummy and breeding nests as we assumed that filming the nests during the early platform stage may cause nest desertion. Building behaviour was filmed for at least four continuous hours with micro-cameras (Mini 550 resolution button

screw micro-camera, Stuntcams, MI, USA) connected to a portable mini DVR (PV500 LITE, Stuntcams, MI, USA). We set the cameras 15-20 cm from the nests, concealed with small pieces of camouflage netting and grass stems. We filmed nests only once, between three and six days after nest-building initiation.

To explore the relationship between building non-breeding nests and nestling provisioning effort we filmed nests when nestlings were 2-4, 7-8 and 11-12 days (day 0 = the day on which most nestlings had hatched) for approximately 4 h with the same technique and equipment as above.

During video analysis, we determined male and female building effort (number of building trips/h) and provisioning effort (number of trips to feed the nestlings/h/nestling). Adults did not show obvious signs of abnormal behaviour in the presence of cameras and they returned to the nest within five minutes after disturbance in setting them up (Llambías *et al.* 2018).

### **Female investment and breeding performance**

To evaluate the relationship between building multiple nests, female parental investment in the brood and breeding performance we checked breeding nests every 2–3 days, and daily when eggs were close to hatching and nestlings close to fledging (incubation period = 14-18 d, fledging period = 13-16 d; Llambías *et al.* 2018). We recorded a breeding attempt if the female laid at least one egg. We determined clutch size only for nests that survived throughout the egg-laying stage and where there was no evidence of interference (e.g. pecked eggs, brood parasite eggs, enlarged dome entrance).

For each nest we recorded clutch initiation date, clutch size, brood size (maximum number of nestlings observed during the hatching stage) and the number of nestlings 10 days after hatching (3-6 days before fledging). To standardize clutch initiation date we designated the day that we observed the first egg laid in the population in a given breeding season as day one and sequentially assigned initiation days for each nest over the breeding season.

We deemed a nest as successful if at least one nestling fledged. We considered a nest to be depredated if eggs or young disappeared before fledging and as deserted if both adults were observed alive and eggs were cold or nestlings were dead. We considered a nest as interfered with by Shiny Cowbirds *Molothrus bonariensis* if we observed cowbird eggs or pecked Grass Wren eggs inside the nest. Eggs pecked by cowbirds and wrens show a different pattern of egg punctures; the former generally inflict one puncture hole while the latter inflict two (P.E.L. pers. obs.).

We calculated hatching success (brood size/clutch size) for nests where at least one nestling hatched or contained eggs for at least 20 days and nestling survival (number of nestlings 10

days after hatching/brood size) for successful nests. We used the number of nestlings that we observed in the nest 3-6 days before fledging as a proxy of the number for nestlings fledged.

### **Nest-removal experiment**

We removed platform and dummy nests on experimental territories to test whether the presence of non-breeding nests: (1) reduces nest predation or Shiny Cowbird parasitism probability, or (2) increases female investment and breeding performance.

Between November-January 2013-2015, we randomly selected 25 experimental and 25 control territories where at least one dummy nest was present. On experimental territories, we removed  $2.22 \pm 1.19$  dummy nests per breeding nest. On control territories  $2.06 \pm 0.86$  dummy nests were present per breeding nest. We arbitrarily considered that empty nests on neighbouring territories that were in a radius of 50 m from an experimental nest could act as decoys to predators. Hence, we removed five abandoned breeding nests and one dummy nest from territories adjacent to focal breeding nests on experimental territories. We removed from the analyses seven experimental territories (two burned and five flooded) and two control territories (flooded). As a result, we report data from 27 breeding nests on 18 experimental territories and 35 breeding nests on 23 control territories.

### **Nest site characteristics**

To evaluate differences between nest types in nest site selection, we quantified vegetation at the nest site. We measured nest sites approximately  $40 (\pm 7)$  days after nest initiation to avoid disturbing the adults and to control for vegetation growth throughout the breeding season.

To compare nest site selection between nest types, we collected data on seven variables on the plant supporting the nest (nest substrate). We measured nest height (distance from the ground to the base of the nest), nest distance to plant edge (distance from the nest to nearest edge of the substrate) and nest distance to plant centre (distance from the nest to the centre of the substrate).

At four points in each cardinal direction at 50 cm from the centre of the nest we quantified plant density (number of  $1 \times 1$  cm squares that were not hidden by vegetation in a 50 cm tape oriented horizontally), vegetation maximum height (height of the highest plant stem) and vegetation effective height (height that was 90 percent obscured by the vegetation in a 5 cm wide board placed vertically; Wiens 1969). We then calculated mean plant density, mean vegetation maximum height and mean vegetation effective height respectively. We calculated mean nest concealment by visually estimating the percentage (0, 25, 50, 75 or 100) of the nest that was covered by vegetation when facing the nest 50 cm from entrance, roof, sides and back. All metric measurements were made to the nearest 0.1 cm.

### **Use of dummy nests for roosting**

We used temperature data loggers (Onset Hobo Pro V2, No U23-001, Onset Computer, Pocasset, MA, USA) to determine whether adults or fledglings roost inside dummy nests during the breeding season. We inserted the external sensor through the nest so it was placed within the surface of the nest cup. The body of the device was hidden in grasses close to the nest to record external temperatures. The data logger took a temperature reading ( $\pm 0.21^{\circ}\text{C}$ ) inside the nest and recorded ambient temperature every 30 s. We registered temperature for at least seven days in nine dummy nests without fledglings on the territory and in eight dummy nests with young fledglings present on the territory. We later compared the internal and external temperature profiles to detect the presence of individuals inside the nest.

### **Statistical analyses**

We performed all statistical modelling in R software (version 3.4.1, R Core Team 2017). We used lme4 (Bates *et al.* 2015), glmmTMB (Brooks *et al.* 2017), lsmeans (Lenth 2016), visreg (Breheny & Burchett 2017) and ggplot2 (Wickham 2009) packages. We carried out multivariate analyses in InfoStat (Di Rienzo *et al.* 2017). We conducted stepwise model simplification of non-significant ( $P > 0.05$ ) terms to obtain a minimal adequate model (Crawley 2007). We conducted *post hoc* analyses between specified factor combinations of significant fixed effects in the models. All means are presented  $\pm 1$  s.e.

We assessed whether the number of non-breeding nests (platforms + dummies) built before a breeding attempt varied with the breeding attempt number (e.g. 1<sup>st</sup>, 2<sup>nd</sup>, etc.) with a negative binomial generalized linear mixed model (GLMM) with log link. The response variable was the number of non-breeding nests built between breeding attempts and the fixed effect were the breeding attempt number and the nest initiation day. We included year and pair identity as crossed random intercept effects to account for unpredicted variance from year differences and for statistical non-independence as some individuals bred in more than one breeding season.

### *Female attraction hypothesis*

We evaluated sexual differences in the contribution to building dummy and breeding nests with a negative binomial GLMM and log link function. The response variable was the number of building trips and the fixed effects were sex, nest type, social mating status (monogamous or polygynous) and the interactions between sex and social mating status and nest type. We considered the duration of building behaviour recordings as an offset in the model (in log (h)) to account for differences in exposure periods of each nest. The crossed random intercept effects were year and sex nested in pair identity.

We tested if the number of non-breeding nests present on the territories was related with male social mating status (unpaired, monogamous or polygynous) and non-breeding nest type (platform or dummy). The response variable was the number of non-breeding nests and the fixed effects were the interaction between male social status and nest type in a negative binomial GLMM with log link function. Year and male identity were the crossed random intercept effects.

#### *Post-pairing display hypothesis*

We tested with GLMMs and a linear mixed model (LMM) if female investment and breeding performance (1) differed between control and experimental territories and (2) varied with the number of non-breeding nests built on non-manipulated territories. We considered female investment (clutch size and female provisioning effort to feed nestlings) and breeding performance (standardized clutch initiation day, hatching success, nestling survival and number of nestlings present before fledging) as response variables. We used a Conway-Maxwell-Poisson distribution with a log link function for clutch size and number of nestlings present before fledging, a negative binomial distribution with log link function for female provisioning effort, a normal distribution for standardized clutch initiation day and a binomial distribution with logit link function for hatching success and nestling survival. The fixed effects were territory type (treatment or control) or the number of non-breeding nests. Pair identity and year were the crossed random intercept effects.

To assess the effect of male and female building effort on female investment and breeding performance we considered male and female provisioning effort per nestling, clutch size and hatching success as response variables of three generalized linear models (GLMs). We used a normal distribution for provisioning effort, a Conway-Maxwell-Poisson distribution with a log link function for clutch size and a binomial distribution with logit link function for hatching success. The fixed effect was the number of building trips per adult/h for each model.

#### *Predation avoidance hypothesis*

We compared nest predation and cowbird parasitism between experimental and control territories using binomial GLMMs with a logit link. Predation or cowbird parasitism were binomial response variables, territory type (experimental or control) was the categorical fixed effect and year and couple identity were the crossed random intercept effects in the models.

#### *Inefficient concealment hypothesis*

To test for differences between nest types in nest placement and vegetation structure, we performed a canonical discriminant analysis (CDA). We used leave-one-out cross-validation tests to obtain estimators of accurate classification probability by classifying unsorted vegetation structure data files in nest type groups (platform, dummy and breeding) from the

discriminant function. Classifiers with an error rate  $> 25\%$  were not accepted. We used a total of five non-correlated vegetation structure variables: nest height, nest distance to plant edge, nest distance to plant centre, mean plant density and mean nest concealment. We considered nest height in the discriminant analyses and excluded mean vegetation maximum height and mean vegetation effective height because they were correlated (correlation coefficient:  $r_2 = 0.82$ ,  $P < 0.01$ ).

## RESULTS

Over seven breeding seasons we located 665 nests, 139 platforms (20.9%), 156 dummies (23.5%) and 367 breeding nests (55.2%). We were unable to classify the status of three nests (0.4%). Wrens built 0-6 platforms ( $0.74 \pm 0.09$ ) and 0-5 dummy nests ( $0.85 \pm 0.08$ ) per territory ( $n = 187$ ). Platforms and dummy nests were present in 38.5% and 47.1% of the territories respectively. When wrens built platforms or dummy nests, they most frequently built one platform or one dummy per territory. The number of non-breeding nests (platforms + dummies) built before a breeding attempt decreased with the breeding attempt number both on monogamous and polygynous territories ( $X_2 = 8.77$ ,  $P < 0.01$ ; Fig. 2, Table 1).

### Female attraction hypothesis

Most non-breeding nests were built after social bond formation and before a breeding attempt in both monogamous and polygynous associations. Social mates were already established before the wrens started building non-breeding nests in 98.6% (145/147) of the monogamous pairs and 90.5% (19/21) of the polygynous associations. Monogamous males did not build non-breeding nests during the incubation and nestling stages of their social mates.

We observed both sexes building dummy nests. The contribution to building dummy or breeding nests differed between sexes (sex  $\times$  nest type:  $X_2 = 6.57$ ,  $P = 0.01$ ; Fig. 3, Table 1) but was not affected by the individual's social status ( $X_2 = 0.07$ ,  $P = 0.96$ ). Females contributed significantly more to building breeding than dummy nests (*lsmeans comparison*,  $Z = -2.98$ ;  $P < 0.01$ ; Fig. 3A). In contrast, male contribution did not significantly differ between breeding and dummy nests (*lsmeans comparison*,  $Z = 0.80$ ;  $P = 0.42$ ; Fig. 3B).

We found a significant interaction between male social status and non-breeding nest type ( $X_2 = 7.13$ ,  $P = 0.03$ ; Fig. 4, Table 1). Dummy nests were significantly more frequent on territories of polygynous males than on territories of monogamous (*lsmeans comparison*,  $Z \text{ ratio} = -3.51$ ,  $P < 0.01$ ) and unpaired males (*lsmeans comparison*,  $Z \text{ ratio} = -2.95$ ,  $P = 0.01$ ; Fig. 4A). However, we found no significant difference in the number of dummy nests in territories of monogamous and unpaired males (*lsmeans comparison*,  $Z \text{ ratio} = -0.37$ ,  $P = 0.93$ ; Fig. 4A).

Platform structures were more frequent on territories of monogamous and polygynous males than on territories of unpaired males (*lsmeans comparison*, Monogamous-Unpaired:  $Z$  ratio = -2.91,  $P = 0.01$ , Polygynous-Unpaired:  $Z$  ratio = -3.60,  $P < 0.01$ ; Fig. 4B). However, we did not find differences between the number of platforms in monogamous and polygynous territories (*lsmeans comparison*,  $Z$  ratio = -1.88,  $P = 0.14$ ; Fig. 4B).

### **Post-pairing display hypothesis**

Removal of non-breeding nests did not affect female investment and breeding performance. There were no significant differences between experimental and control territories in clutch size ( $X_2 = 0.80$ ,  $P = 0.42$ ), hatching success ( $X_2 < 0.01$ ,  $P = 0.97$ ), nestling survival ( $X_2 = 0.03$ ,  $P = 0.87$ ), number nestlings present before fledging ( $X_2 = 0.40$ ,  $P = 0.53$ ), and female provisioning effort (2-3 d nestlings:  $X_2 = 0.41$ ,  $P = 0.52$ , 7-8 d nestlings:  $X_2 = 0.26$ ,  $P = 0.61$ , 11-12 d nestlings:  $X_2 = 1.44$ ,  $P = 0.23$ ; Table S1).

In non-manipulated territories, building non-breeding nests was not associated with greater female investment. The number of non-breeding nests was not correlated with clutch size ( $X_2 = 0.66$ ,  $P = 0.42$ ; Table S2) nor with female provisioning effort (2-3 d nestlings:  $X_2 = 0.81$ ,  $P = 0.37$ , 7-8 d nestlings:  $X_2 = 0.05$ ,  $P = 0.83$ , 11-12 d nestlings:  $X_2 = 0.11$ ,  $P = 0.74$ ; Table S2). Similarly, male and female building efforts were not correlated with clutch size (male:  $X_2 = 1.32$ ,  $P = 0.25$ ; female:  $X_2 = 1.01$ ,  $P = 0.32$ ) nor with male and female provisioning efforts (male:  $F = 0.19$ ,  $P = 0.68$ , female:  $F = 0.26$ ,  $P = 0.63$ ; Table S3).

Building non-breeding nests was associated with reduced breeding performance. The number of non-breeding nests was associated with delayed clutch initiation of the first breeding attempt ( $F = 14.20$ ,  $P < 0.01$ ; Fig. 5, Table 2) and negatively correlated with hatching success ( $X_2 = 5.14$ ,  $P = 0.02$ ; Fig. 6, Table 2). However, nestling survival ( $X_2 = 0.30$ ,  $P = 0.58$ ) and the number of nestlings before fledging ( $X_2 = 0.02$ ,  $P = 0.98$ ; Table S2) were not correlated with the number of non-breeding nests. Male building effort was negatively correlated with hatching success ( $X_2 = -10.70$ ,  $P < 0.01$ ; Fig. 7, Table 2). A similar negative correlation between female building effort and hatching success was marginally significant ( $X_2 = -3.74$ ,  $P = 0.05$ ; Table 2).

### **Predation avoidance hypothesis**

After the removal of non-breeding nests, adults did not replace them while the breeding nest contained eggs or nestlings. We did not detect significant differences in the probability of nest predation ( $X_2 = 0.74$ ,  $P = 0.39$ ) nor in the probability of Shiny Cowbird parasitism ( $X_2 = 1.52$ ,  $P = 0.22$ ) between experimental and control territories (Table S1).

### **Inefficient concealment**

The CDA could not separate nest types based on vegetation variables (Fig. S1). The magnitude of cross classification percentage errors suggests that there were no differences in vegetation structure between platforms, dummy and breeding nests (Table S4 & S5).

### **Roosting hypothesis**

We detected higher nocturnal temperatures inside dummy nests compared to ambient temperatures (Fig. 8) on three territories (37.5%,  $n = 8$ ) where fledglings were present and in two territories (22.2%,  $n = 9$ ) with no fledglings present. We were able to confirm the presence of one individual inside the dummy nest on three occasions by inspecting the nest at dawn. Adults did not maintain the structures of dummy nests once the building process had finished. Thus, dummy nests gradually collapsed at later stages of the breeding season, suggesting that they are not used for roosting during the austral winter, once the breeding season is over.

## **DISCUSSION**

To the best of our knowledge, this is the first study demonstrating that building multiple nests is associated with reduced breeding performance. In our Grass Wren population, building non-breeding nests was associated with delayed clutch initiation and reduced hatching success (Fig. 5 & 6). Furthermore, building effort was negatively correlated to hatching success (Fig. 7). The presence of non-breeding nests did not affect breeding performance as we did not observe differences in performance between experimental territories where non-breeding nests were removed and control territories where no non-breeding nests were removed. Our results did not support any of the present hypotheses on the adaptive significance of building multiple nests.

It is unlikely that Grass Wren males build non-breeding nests to attract females. In species where nests are used to attract mates, only males are involved in nest building (Moreno 2012). However, Grass Wren females contributed to building dummy nests. Also, building non-breeding nests occurred predominantly in established pairs and it was restricted to the period before the onset of a breeding attempt both in monogamous and polygynous associations. Hence, the greater proportion of non-breeding nests on territories of polygynous males was the result of polygynous males being associated with more females than monogamous males, rather than the result of females being attracted to territories with more non-breeding nests. Social polygyny is rare in our population (3%; Llambías *et al.* 2018); however during 2015 we observed an unusually high rate of polygyny (60%). The ecological variables that can affect social polygyny are still under study in our population. Preliminary results suggest that

a male biased sex ratio in 2015 may have obliged the females to breed polygynously. Due to the reduced incidence of social polygyny over seven breeding seasons and the unusual demographic conditions associated with its occurrence, males should not invest time and energy in building non-breeding nests to attract additional females. Accordingly, Grass Wrens build on average less than one dummy nest per territory whereas social polygynous Sedge Wrens and Marsh Wrens build 5 and 7 dummy nests per territory respectively (Burns 1982, Leonard & Picman 1987).

Our results did not support the post-pairing display hypothesis. We did not find an association between building non-breeding nests and clutch size or nestling provisioning effort by females. Contrary to predictions, the number of non-breeding nests built and building effort were inversely associated with hatching success. A reduction in hatching success can be caused by inbreeding depression, genetic incompatibility, lack of fertilization, inappropriate parental care, or from breeding with non-preferred mates (Morrow *et al.* 2002, Bluhm & Gowaty 2004, Gorman *et al.* 2005, Arnold *et al.* 2016). In birds, various external stimuli such as a singing behaviour and nest material can affect female sex hormone levels, stimulating ovarian development and inducing oviposition (Lehrman 1959, Arnqvist & Rowe 2005). In our population, the building of non-breeding nests may represent attempts by males to manipulate the decision of females to breed with a male they might otherwise reject or to start reproduction earlier than optimal for them. Under this scenario, the reduced female contribution to building dummy nests when compared to breeding nests (Fig. 3) may be the consequence of female resistance or reduced motivation to initiate egg laying. Indeed, building non-breeding nests was more frequent before the first breeding attempt than between subsequent breeding attempts (Fig. 2) and the females of pairs that built non-breeding nests started the first breeding attempt later than females of pairs who did not build them (Fig. 5). In this sense, non-breeding nests may not be different functional structures as previously thought (e.g. Llambías *et al.* 2018), but incomplete nest structures that were abandoned during different stages of nest building. Accordingly, all nests are initiated as platforms, however they may develop into dummy nests if wrens interlock grass stems to build a dome-shaped structure and into a breeding nests if they add an internal cup lining to the dome.

In our population, nest predation and Shiny Cowbird parasitism accounted for 60% of the breeding failures (Llambías *et al.* 2018). However, we did not find evidence that building multiple nests reduced nest predation or Shiny Cowbird brood parasitism because nest predation and cowbird brood parasitism rates did not significantly differ between experimental territories and control territories. Also, non-breeding nests were neither re-built after removal nor maintained during the breeding season. These results suggest that the

presence of non-breeding nests on the territory does not play a crucial role during subsequent breeding attempts. In Manitoba, Canada, where the presence of dummy nests on the territories of Marsh Wrens reduces the probability of nest predation, successful wrens build on average seven dummy nests per territory (Leonard & Picman 1987). Given that Grass Wrens built on average less than one dummy nest per territory in our population, it is unlikely that it can effectively reduce nest predation and cowbird parasitism.

We did not find significant differences in vegetation structure surrounding platform, dummy and breeding nests. Hence, it is unlikely that nests were deserted because the adults perceived a greater risk of nest predation. However, we cannot rule out the possibility that nests were deserted during building if adults encountered a predator.

Dummy nests were occasionally used for roosting at night during the breeding season (Fig. 8). However, this seems to be an opportunistic behaviour as dummy nests were not replaced by adults after removal. At our study site, Grass Wrens are sedentary even though seasonality is pronounced, with temperatures below freezing and occasional snowfall during the austral winter. If dummy nests were built as refuges during inclement weather, they should be built more frequently at the end of the austral summer to provide shelter during the austral winter. Contrary to this prediction, dummy nests were more frequently built before the first breeding attempt, early in the breeding season. Furthermore, as dummy nests were not maintained, none of them remained during the austral winter.

## **CONCLUSION**

Our results show that building multiple nests is associated with reduced hatching success and delayed clutch initiation. Under this scenario, non-breeding nests should not be considered as functional non-breeding nest structures but as incomplete nests. The proximate causes of reduced hatching success deserve further investigation. This study highlights the importance of considering both non-adaptive and adaptive hypotheses when evaluating the function of building of multiple nests.

We acknowledge detailed suggestions and helpful comments made by Jim Reynolds, and two anonymous reviewers, which greatly improved the manuscript. We thank Jacob Armiger, John Schoen, Sara Prussing and Lee Sutcliffe for help in the field and José D'Angelo for help with statistical analyses. Economic support was provided by CONICET (D1791, PIP 11220100100039 and 11220130100198), and FONCYT (PICT 2010-1033) grants.

### **Ethical approval**

All methods used in the present study meet the ethical requirements for science research and comply with the current laws of Argentina. Fieldwork permits were granted by Secretaría de Ambiente y Desarrollo Sustentable, Dirección de Recursos Naturales Renovables, Mendoza, Argentina.

## REFERENCES

- Ahumada, J.A.** 2000. Comparison of the reproductive biology of two Neotropical wrens in an unpredictable environment in Northeastern Colombia. *The Auk* **118**: 191-210.
- Arnold, K.E., Gilbert, L., Gorman, H.E., Griffiths, K.J., Adam, A. & Nager R.G.** 2016. Paternal attractiveness and the effects of differential allocation of parental investment. *Anim. Behav.* **113**: 69-78.
- Arnqvist, A. & Rowe, L.** 2005. Sexual conflict. Princeton, NJ: Princeton University Press.
- Bates, D., Machler, M., Bolker, B.M. & Walker, S.** 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**: 1-48.
- Beckmann, C. & Martin, K.** 2016. Testing hypotheses about the function of repeated nest abandonment as a life history strategy in a passerine bird. *Ibis* **158**: 335-342.
- Berg, M.L., Beintema, N.H., Welbergen, J.A. & Komdeur J.** 2006. The functional significance of multiple nest building in the Australian Reed Warbler *Acrocephalus australis*. *Ibis* **148**: 395-404.
- Bluhm, C.K. & Gowaty, P.A.** 2004. Social constraints on female mate preference in Mallards, *Anas platyrhynchos*, decrease offspring viability and mother productivity. *Anim. Behav.* **68**: 977-983
- Bolker, B.M.** 2007. Ecological models and data in R. Princeton, NJ: Princeton University Press.
- Breheny, P. & Burchett, W.** 2017. Visualization of regression models using visreg. *The R Journ.* **9**: 56-71.
- Brewer, D.** 2001. Wrens, dippers and thrashers. New Haven, CT: Yale University Press.
- Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M. & Bolker, B.M.** 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Jour.* **9**: 378-400.
- Burns, J.T.** 1982. Nests, territories, and reproduction of Sedge Wrens (*Cistothorus platensis*). *Wilson J. Ornithol.* **94**: 338-349.
- Carretero, E.M.** 2000. Vegetación de los Andes Centrales de la Argentina, el Valle de Uspallata, Mendoza. *Bol. Soc. Argent. Bot.* **34**: 127-148.
- Collias, N.E & Collias, E.C.** 1984. Nest building and bird behavior. Princeton, NJ: Princeton University Press.
- Crawford, R.D.** 1977. Polygynous breeding of Short-billed Marsh Wrens. *The Auk* **94**: 359-362
- Crawley, M.J.** 2007. The R book. John Wiley & Sons, Oxford, UK.

- de la Peña, M.R. & Salvador, S.** 2016. Aves Argentinas: descripción, comportamiento, reproducción y distribución. Tyrannidae a Turdidae. *Com. Mus. Prov. Cs. Nat. Florentino Ameghino*. **21**: 1-639.
- Di Rienzo, J.A., Casanoves, F., Balzarini, M.G., Gonzalez, L., Tablada, M. & Robledo, C.W.** 2017. InfoStat versión 2017. Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Argentina. <http://www.infostat.com.ar>.
- Evans, M.R.** 1997. Nest building signals male condition rather than age in wrens. *Anim. Behav.* **53**: 749-755.
- Evans, M.R. & Burn, J.L.** 1996. An experimental analysis of mate choice in the wren: A monomorphic, polygynous passerine. *Behav. Ecol.* **7**: 101-108.
- Flegeltaub, M., Biro, P.A. & Beckmann, C.** 2017. Avian nest abandonment prior to laying—a strategy to minimize predation risk? *J. Ornithol.* **158**: 1091–1098.
- Friedl, T.W.P. & Klump, G.M.** 1999. Determinants of male mating success in the Red Bishop (*Euplectes orix*). *Behav. Ecol. Sociobiol.* **46**: 387-399.
- Garson, P.J.** 1980. Male behavior and female choice: Mate selection in the wren? *Anim. Behav.* **28**: 491-502.
- Gill, S.A. & Stutchbury, B.J.M.** 2005. Nest building is an indicator of parental quality in the monogamous Neotropical Buff-Breasted Wren (*Thryothorus leucotis*). *The Auk* **122**: 1169-1181.
- Gorman, H.E., Arnold, K.E. & Nager, R.G.** 2005. Incubation effort in relation to male attractiveness in zebra finches *Taeniopygia guttata*. *J. Avian Biol.* **36**: 413-420.
- Hansell, M.H.** 2000. Bird nests and construction behaviour. Cambridge, UK.
- Hansell, M.H. & Deeming, D.C.** 2002. Location, structure and function of incubation sites. In Deeming, D.C. (ed) *Avian Incubation. Behavior, environment and evolution*. Oxford, UK.
- Herkert, J.R., Kroodsma, D.E. & Gibbs, J.P.** 2001. Sedge Wren (*Cistothorus platensis*). In Poole, A. (ed.) *The Birds of North America Online*. Ithaca, NY: Cornell Lab of Ornithology.
- Kroodsma, D.E., Sánchez, J., Stemple, D.W., Goodwin, E., Da Silva, M.L. & Vielliard, J.M.E.** 1999. Sedentary life style of Neotropical sedge wrens promotes song imitation. *Anim. Behav.* **57**: 855-863.
- Lehrman, D.** 1959. Hormonal responses to external stimuli in birds. *Ibis* **101**: 478-496.
- Lenth, R.V.** 2016. Least-Squares Means: The R Package lsmeans. *J. Stat. Softw.* **69**: 1-33.
- Leonard, M.L. & Picman, J.** 1987. The adaptive significance of multiple nest building by male marsh wrens. *Anim. Behav.* **35**: 271-277.

- Llambías, P.E., Garrido, P.S., Jefferies M.M. & Fernández G.J.** 2018. Social mating system, male parental care contribution and life history traits of a southern Sedge Wren (*Cistothorus platensis platensis*) population: A comparison with northern Sedge Wrens (*Cistothorus platensis stellaris*). *J. Ornithol.* **159**: 221-223.
- Mainwaring, M.C. & Hartley, I.R.** 2013. The energetic costs of nest building in birds. *Avian Biol. Res.* **6**: 12-16.
- Mainwaring, M.C., Hartley, I.R., Lambrechts, M.M. & Deeming, D.C.** 2014. The design and function of birds' nests. *Ecol. Evol.* **20**: 3909-3928.
- Metz, K.J.** 1991. The enigma of multiple nest building by male Marsh Wrens. *The Auk* **108**: 170-173.
- Moreno, J.** 2012. Avian nests and nest building as signals. *Avian Biol. Res.* **5**: 238-251.
- Moreno, J., Soler, M., Møller, A.P. & Lindén, M.** 1994. The function of stone carrying in the Black Wheatear, *Oenanthe leucura*. *Anim. Behav.* **47**: 1297-1309.
- Morrow, E.H., Arnqvist, G. & Pitcher, T.E.** 2002. The evolution of infertility: Does hatching rate in birds coevolve with female polyandry? *J. Evol. Biol.* **15**: 702-709.
- Noske, R.A., Mulyani, Y.A. & Lloyd P.** 2013. Besting beside old nests, but not over water, increases current nest survival in tropical mangrove-dwelling warbler. *J. Ornithol.* **154**: 517-523.
- R Core Team.** 2017. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna, Austria. <https://www.R-project.org/>
- Remsen, J.V. Jr, Areta, J.I., Cadena, C.D., Claramunt, S., Jaramillo, A., Pacheco, J.F., Pérez-Emán, J., Robbins, M.B., Stiles, F.G., Stotz, D.F. & Zimmer, K.J.** 2018. A classification of the bird species of South America. American Ornithologists' Union. [http://www.museum.lsu.edu/\\*Remsen/SACCBaseline.htm](http://www.museum.lsu.edu/*Remsen/SACCBaseline.htm).
- Ridgely, R.S. & Tudor, G.** 1989. The birds of South America. The Oscine Passerines. Austin, TX: University of Texas Press.
- Robinson, T.R., Robinson, W.D. & Edwards, E.C.** 2000. Breeding ecology and nest-site selection of Song Wrens in Central Panama. *The Auk* **117**: 345-354.
- Soler, J.J., Møller, A.P., & Soler, M.** 1998. Nest building, sexual selection and parental investment. *Evol Ecol.* **12**: 427-441.
- Soler, M., Soler, J.J., Møller, A.P., Moreno, J. & Lindén, M.** 1996. An experimental analysis of the functional significance of an extreme sexual displays: Stone-carrying in the Black Wheatear *Oenanthe leucura*. *Anim Behav.* **51**: 247-254.

- Szentirmai, I., Komdeur, J. & Székely T.** 2005. What makes a nest-building male successful? Male behaviour and female care in Penduline Tits. *Behav. Ecol.* **16**: 994-1000.
- Ueda, K.** 1984. Successive nest building and polygyny of Fan-tailed Warblers *Cisticola juncidis*. *The Ibis* **126**: 221-229.
- Verner, J. & Engelsens, G.H.** 1970. Territories, multiple nest building and polygyny in the Long-billed Marsh Wren. *The Auk* **87**: 557-567.
- Watts, B.D.** 1987. Old nests accumulation as a possible protection mechanism against search-strategy predators. *Anim. Behav.* **35**: 1566-1568.
- Wickham, H.** 2009. ggplot2: Elegant graphics for data analysis. Springer-Verlag New York, NY.
- Wiens, J.A.** 1969. An approach to the study of ecological relationships among grassland birds. *Ornithol. Monogr.* **8**: 1-93.
- Winkler, D.W.** 2001. Nests, eggs, and young: breeding biology of birds. In Podulka, S., Rohrbaugh, R.W. & Bonney, R. (eds.) *Handbook of Bird Biology*. Second Edition. Princeton, NJ: Princeton University Press.
- Winkler, D.W.** 2016. Breeding biology of birds. In Lovette, J.L & Fitzpatrick, J.W. (eds) *Handbook of Bird Biology*. Third edition. Wiley-Blackwell, Hoboken, NJ.

## FIGURE LEGENDS

**Figure 1.** (A) Platform nest, (B) dummy nest, and (C) breeding nest of Grass Wrens in Uspallata, Mendoza, Argentina. Photographs by: (A) and (B) Milagros M. Jefferies, (C) Paulo E. Llambías.

**Figure 2.** Relationship between the number of non-breeding nests (platform + dummies) built before a breeding attempt, and breeding attempt number in Grass Wrens. The black line and shading represents regression curve and 95% confidence interval predicted by GLMM, respectively. Note that some points overlap.

**Figure 3.** Number of building trips of (A) female and (B) male Grass Wrens to build dummy and breeding nests. Different lower case letters indicate that simple comparisons are statistically different. Box plots show the median and 25th to 75th percentile values fitted by GLMM. Whiskers show all data excluding values 1.5 times bigger than upper and lower box hinges. Dots represent outliers.

**Figure 4.** Number of (A) dummy and (B) platform nests built on territories of Grass Wren males of different social status. Different lower case letters indicate that simple comparisons are significantly different statistically. Box plots show the median and 25th to 75th percentile values fitted by GLMM. Whiskers show all data excluding values 1.5 times bigger than upper and lower box hinges. Dots represent outliers.

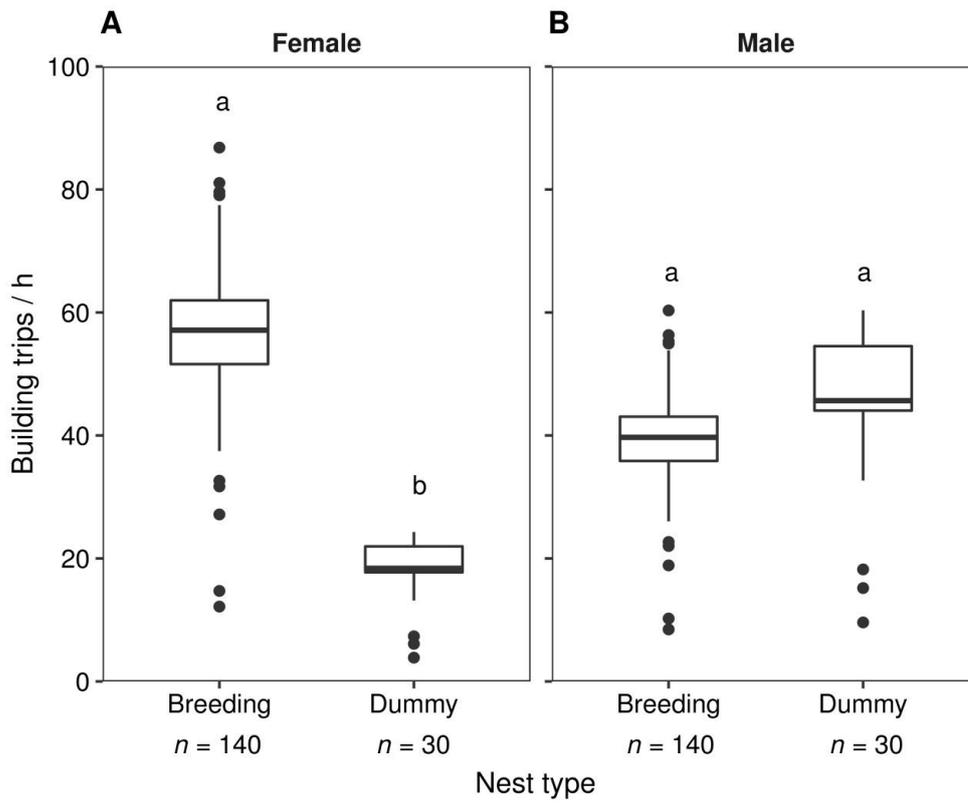
**Figure 5.** The relationship between clutch initiation date and number of non-breeding nests built before the first breeding attempt in Grass Wrens. Clutch initiation day was standardized by designating the day that the first egg was laid in the population in a given breeding season as day one and sequentially assigning initiation days for each nest over the breeding season. The black line and shading represents regression curve and 95% confidence interval predicted by GLMM, respectively. Note that some points overlap.

**Figure 6.** The relationship between hatching success (brood size/clutch size) and number of non-breeding nests built before a breeding attempt in Grass Wrens. The black line and shading represents regression curve and 95% confidence interval predicted by GLMM, respectively. Note that some points overlap.

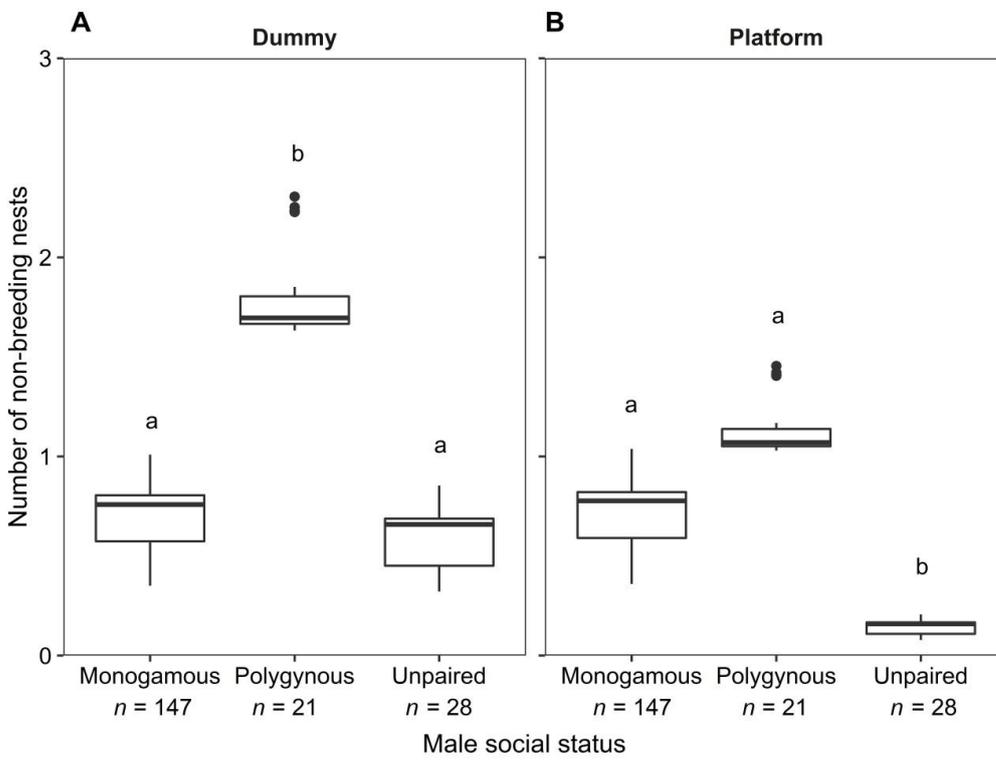
**Figure 7.** The relationship between hatching success (brood size/clutch size) in the subsequent breeding attempt and male effort in building dummy nests in Grass Wrens. The black line and shading represents regression curve and 95% confidence interval predicted by GLMM, respectively. Note that some points overlap.



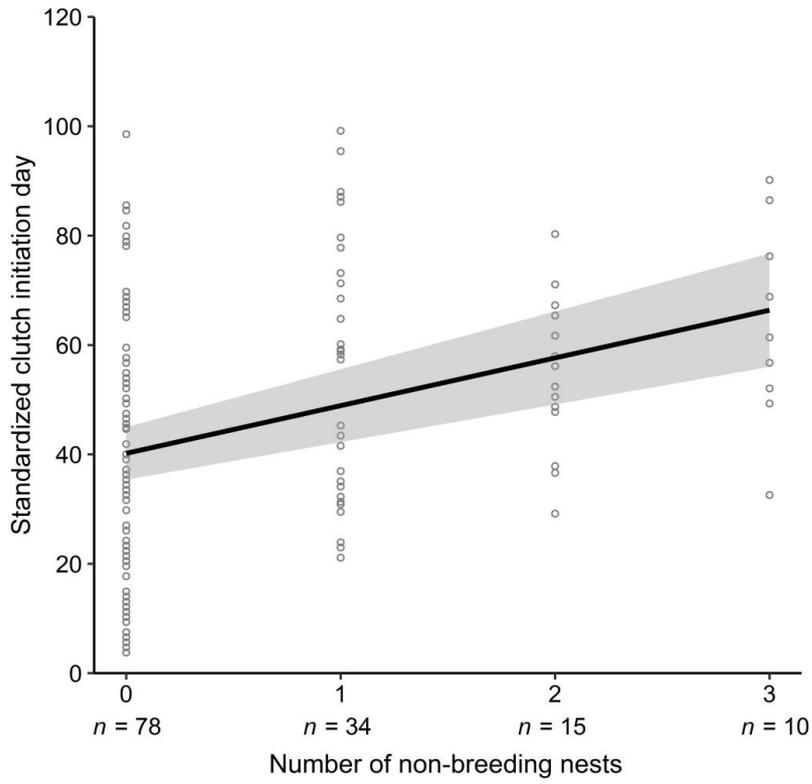
**Figure 3**



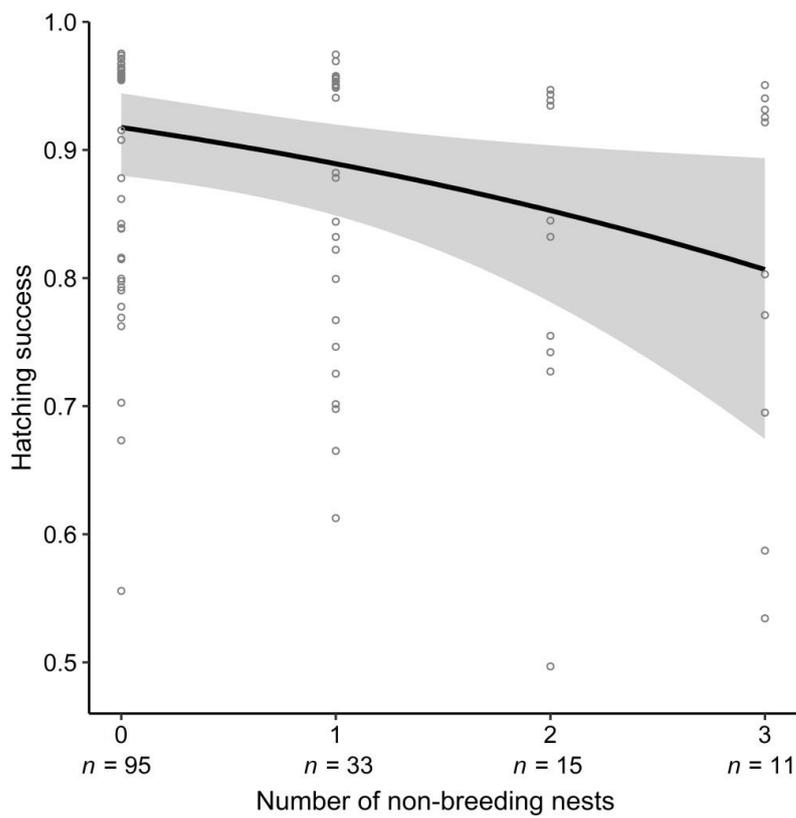
**Figure 4**



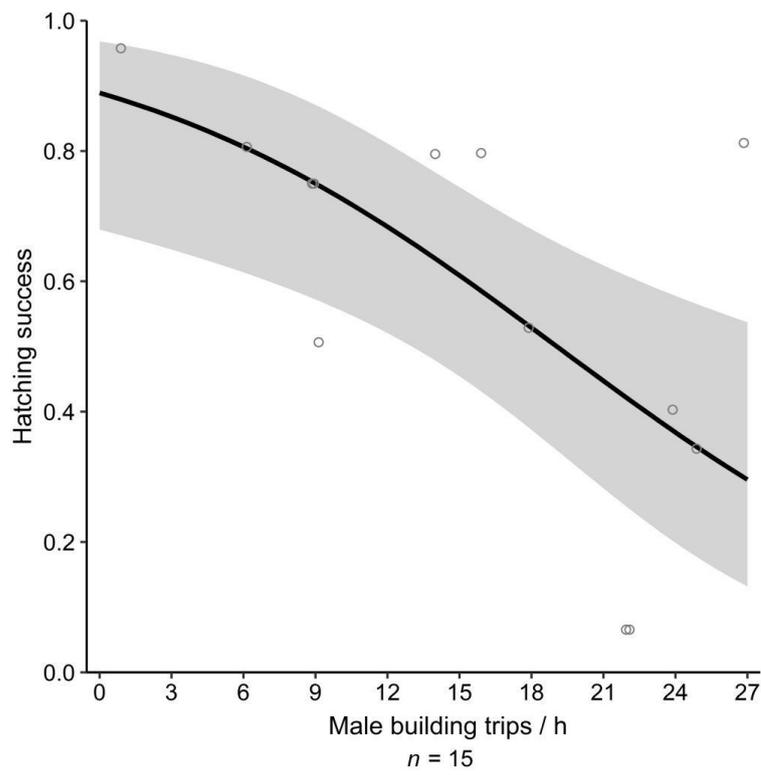
**Figure 5**



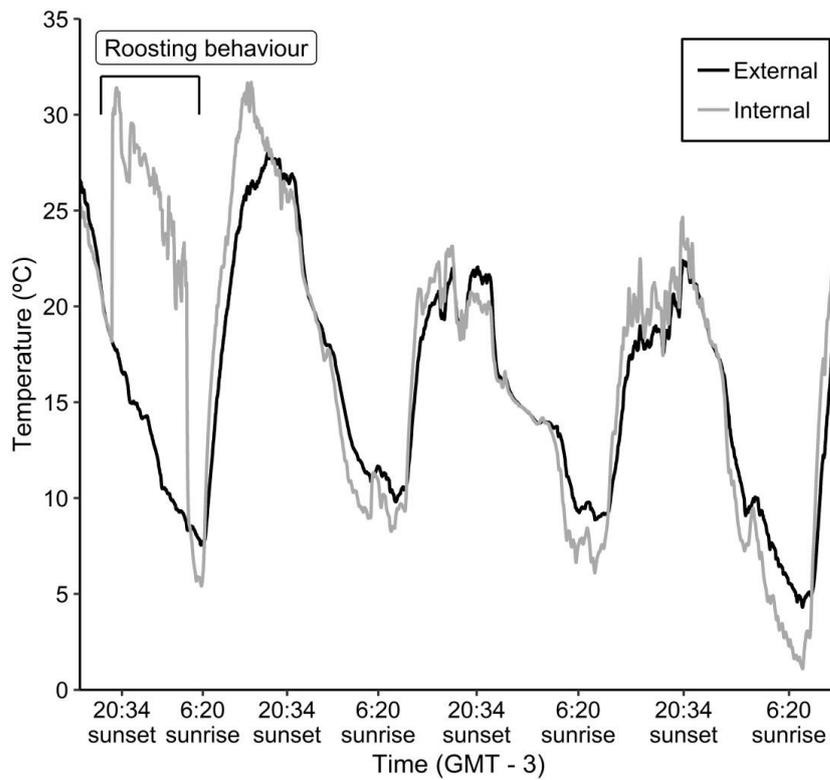
**Figure 6**



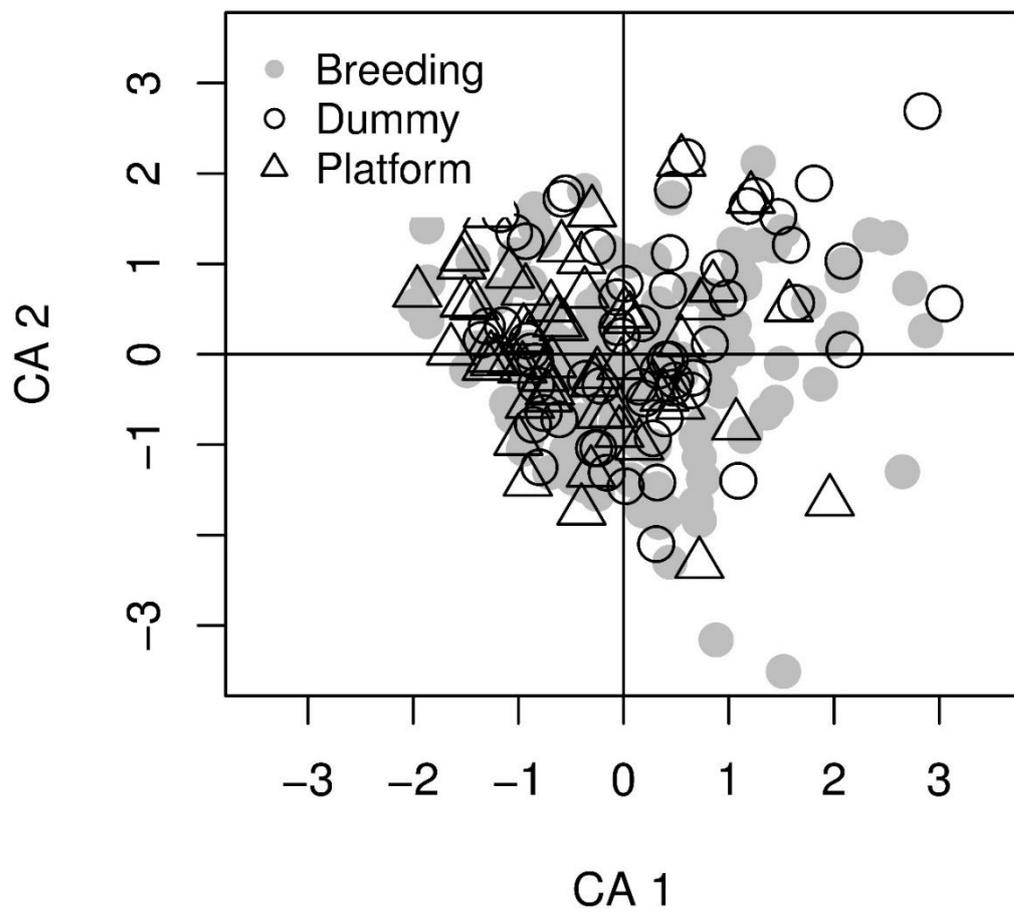
**Figure 7**



**Figure 8**



**Fig. S1.** Plot of the first (CA 1) and the second (CA 2) canonical axis from a Canonical Discriminant Analysis of five vegetation variables measured on the plant supporting platforms (n = 59), 60 dummies (n = 60) and 144 breeding nests (n = 44) of Grass Wrens.



**Table S1.** Summary outputs of the experimental removal of non-breeding nests and its effect on: probability of nest predation, Shiny Cowbird parasitism, clutch size, hatching success, number of nestling alive 10 days after hatching, nestling survival and female provisioning effort to feed nestlings of 2-3, 7-8 and 11-12 days old in Grass Wrens. Year and breeding couple were used as random crossed factors on each model. DU: Distribution used on the GLMM, link function in parenthesis. Int.: Intercept, CMP: Conway Maxwell Poisson. Neg. Bin.: Negative Binomial; Bin.: Binomial.

**Table S2.** Summary outputs describing the effects of the number of non-breeding nests (platforms + dummies) on clutch size, number of nestlings alive 10 days after hatching, nestling survival and female provisioning effort to feed nestlings of 2-3, 7-8 and 11-12 days old in non-manipulated territories of Grass Wrens. Year and breeding couple were used as random factors on each model. DU: Distribution used on the GLMM, link function in parenthesis. Int.: Intercept, Norm.: Gaussian, CMP: Conway Maxwell Poisson. Neg. Bin.: Negative Binomial; Bin.: Binomial.

**Table S3.** Summary outputs describing the effect of building effort on clutch size and male and female provisioning effort to feed nestlings on non-manipulated territories of Grass Wrens. DU: Distribution used on the GLM, link function in parenthesis. CMP: Conway Maxwell Poisson. Norm.: Gaussian; Bin.: Binomial.

**Table S4.** Discriminant loading of the canonical discriminant analyses comparing vegetation variables of platforms, dummy and breeding nests of Grass Wrens.

**Table S5.** Canonical Discriminant Analysis leave-one-out cross-validation tests for platform, dummy and breeding nests considering vegetation structure measurements in Grass Wrens.

**Table S1.**

Models	Estimate	SE	Z	P	DU
<b>a) Nest predation (Int.)</b>	-1.60	1.20	-1.34	0.18	Bin.
Nest removal	0.96	1.15	0.83	0.41	(logit)
<b>b) Shiny Cowbird parasitism (Int.)</b>	-0.26	0.61	-0.43	0.67	Bin.
Nest removal	-0.91	0.80	-1.14	0.25	(logit)
<b>c) Clutch size (Int.)</b>	1.58	0.02	64.30	<0.01	CMP
Nest removal	0.02	0.03	0.80	0.42	(log)
<b>d) Hatching success (Int.)</b>	2.06	0.45	4.54	<0.01	Bin.
Nest removal	0.02	0.56	0.04	0.97	(logit)
<b>e) Number of nestlings at day 10 (Int.)</b>	1.47	0.13	11.63	<0.01	CMP
Nest removal	-0.01	0.16	-0.64	0.52	(log)
<b>f) Nestling survival (Int.)</b>	6.49	4.16	1.56	0.12	Bin.
Nest removal	-0.45	2.78	-0.16	0.87	(logit)
<b>g) Female provisioning effort</b>					
<b>Nestling day 2-3 (Int.)</b>	-0.08	0.36	-0.23	0.82	Neg.
Nest removal	0.13	0.21	0.64	0.52	Bin.
<b>Nestling day 7-8 (Int.)</b>	-0.82	0.29	-2.87	<0.01	(log)
Nest removal	0.13	0.23	0.55	0.58	
<b>Nestling day 11-12 (Int.)</b>	0.32	0.19	1.65	0.10	
Nest removal	0.00	0.00	0.86	0.39	

**Table S2.**

Models	Estimate	SE	Z	P	DU
<b>a) Clutch size (Int.)</b>	1.55	0.01	117	<0.01	CMP
Non-breeding nests	0.00	0.00	0.00	0.97	(log)
<b>b) Number of nestlings at day 10 (Int.)</b>	1.28	0.06	21.71	<0.01	CMP
Non-breeding nests	0.00	0.03	0.14	0.89	(log)
<b>c) Nestling survival (Int.)</b>	9.11	1.83	4.96	<0.01	Bin.
Non-breeding nests	-0.44	0.63	-0.69	0.49	(logit)
<b>d) Female provisioning effort</b>					
<b>Nestling day 2-3 (Int.)</b>	0.06	0.14	0.45	0.65	Neg.
Non-breeding nests	-0.03	0.04	-0.90	0.37	Bin.
<b>Nestling day 7-8 (Int.)</b>	-0.19	0.15	-1.21	0.23	(log)
Non-breeding nests	0.01	0.05	0.23	0.82	
<b>Nestling day 11-12 (Int.)</b>	0.21	0.21	1.02	0.31	
Non-breeding nests	-0.02	0.07	-0.33	0.74	

**Table S3.**

Models	Estimate	SE	Z	P	DU
<b>a) Clutch size &amp; male building effort (Int.)</b>	1.24	0.33	3.74	<0.01	CMP
Male building trips per hour	0.01	0.20	0.02	0.98	(log)
<b>b) Clutch size &amp; female building effort (Int.)</b>	1.14	0.21	5.46	<0.01	CMP (log)
Female building trips per hour	0.02	0.01	1.05	0.29	
<b>c) Male provisioning effort to feed 2-3 d nestlings (Int.)</b>	1.08	0.44	2.44	0.05	Norm.
Male building trips per hour and per nestling	0.01	0.02	0.44	0.68	
<b>d) Female provisioning effort to feed 2-3 d nestlings (Int.)</b>	1.05	0.23	4.63	0.06	Norm.
Female building trips per hour and per nestling	-0.01	0.01	- 0.51	0.63	

**Table S4.**

Variables	Canonical axis 1	Canonical axis 2
Nest height	-0.29	0.16
Nest distance to plant edge	-0.34	0.74
Nest distance to plant centre	0.23	-0.40
Nest cover	-0.14	0.20
Density	0.71	0.78

**Table S5.**

Group	Platform	Dummy	Breeding	Total	Error (%)
Platform	30	10	14	54	44.44
Dummy	16	25	19	60	58.33
Breeding	48	37	59	144	59.03
Total	94	72	92	258	55.81