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Size of nest-cavity entrance influences male attractiveness and paternal provisioning in house wrens

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Abstract

In altricial birds, parental provisioning is plastic and can respond to a variety of environmental stimuli. In this study, we manipulated the size of entrances into artificial nest cavities (i.e., nestboxes) in a population of house wrens (*Troglodytes aedon*) as a means of manipulating a male's sexual attractiveness, and examined changes in parental provisioning. Nest cavities with large entrances are less desirable as nesting sites, and the males at these sites are less attractive to females. Therefore, we predicted that males at boxes that had large entrances would invest more in parental care (i.e., those that succeeded in finding a mate would provision their offspring at a higher rate) than males at nestboxes with small entrances. As predicted, males provisioned their offspring with food at the highest rates at nestboxes with enlarged entrances, and male provisioning effort positively predicted the number of fledglings they produced per egg. Males at these boxes provisioned more than their mates and more than females and males at nestboxes with small entrances. At nestboxes with small entrances, males provisioned at the same rate as females, and female provisioning did not differ significantly between treatments, on average. Male and female provisioning rates were negatively correlated, such that the increase in provisioning by males at nestboxes with enlarged entrances did not enhance nestling condition, likely because food delivery by females declined with increased provisioning by males. However, the amount of time females spent providing warmth for their ectothermic young increased with increases in male provisioning, suggesting that levels of male parental care altered the mode, not necessarily the extent, of care provided by females. These findings suggest that male provisioning is related to sexual attractiveness, and that sexual conflict over biparental care may not be as simple as the assessment of food provisioning might otherwise suggest.

Graphical abstract

Abbreviated summary for graphical TOC: In biparental species in which males provide care for offspring, theory predicts that the effort put forth by males should vary inversely with their sexual attractiveness. We tested this, and found that unattractive males provided an increased level of care for offspring, but that male and female food-provisioning effort was negatively correlated. Although females provisioned less food to offspring as their mates delivered more food, these

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females also spent more time brooding their nestlings, thereby altering the mode of parental care they provided. These findings suggest that sexual conflict over biparental care may not be as simple as the assessment of food provisioning alone might suggest.

Keywords

parental care; paternal care; provisioning; sexual conflict; altricial; sexual selection; *Troglodytes aedon*; nest cavities

Introduction

Varying environmental conditions often generate variation in the fitness benefits associated with any behavior. For example, a given unit of parental investment in offspring is expected to yield different fitness returns for parents depending on changes in population size and resource availability (e.g., Pianka 1978). Because environmental changes generate variance in fitness, plasticity in behavior that reduces the variance in fitness attributable to short-term environmental variation should increase an individual's fitness in the long term (e.g., Kaplan & Cooper, 1984; West-Eberhard, 1989; Gamelon *et al.*, 2013). Thus, selection should favor plasticity in the expression of behavior according to environmental conditions, thereby allowing individuals to adjust to changes in their social and abiotic environment, and should generally be favored over the canalization to fixed, invariant behavioral responses (Kaplan & Cooper, 1984; Gamelon *et al.*, 2013). This should especially be the case when rearing altricial young, as different circumstances may influence the value of a given brood of offspring to an individual parent, including the extent to which it is likely to transmit copies of a parent's genes to future populations (e.g., Trivers, 1972; Queller, 1997; Parker, Royle & Hartley, 2002; Bowers *et al.*, 2014a, 2015b). In species with biparental care, females often copulate with males other than the one with which they form a social bond, and the cuckolded males often respond by reducing their parental investment commensurate with their decreased confidence of paternity in the brood (Matysioková & Remeš 2013; Schroeder *et al.*, 2016). Indeed, selection should favor plasticity that allows individuals to recognize the optimal behavioral strategy in any given context.

In a recent study, Dorset (2015) manipulated the size of nest entrances in a population of house wrens (*Troglodytes aedon*), an obligate secondary-cavity-nesting bird. As secondary cavity nesters, house wrens cannot excavate their own nest cavities, but readily use human-made nestboxes for nesting. Dorset (2015) detected behavioral plasticity in the effect of this treatment on parental behavior, finding that nestboxes with small entrances were strongly preferred over those with large entrances (see also Pribil & Picman, 1997 for a similar result). House wrens typically exhibit protandrous settlement on breeding sites, whereby a male selects a breeding site and defends it from rivals while attempting to attract a mate. Both males and females preferred nesting cavities with small entrances. Males took longer to settle on a site with a large entrance and the males that settled on these sites were much less likely to pair with a female, and, if they did attract a mate, took longer to do so than males on territories with small entrances (Dorset, 2015). These nesting sites act as part of a male's phenotype, and indeed his sexual attractiveness is determined, in part, by the quality of his breeding territory (Belles-Isles & Picman, 1986; Eckerle & Thompson, 2006; Grana *et al.*, 2012); in fact, the quality of a male's breeding territory appears to be an even stronger determinant of his attractiveness than components of his morphology (Eckerle & Thompson, 2006) or song (Cramer, 2013). Therefore, the manipulation of nestbox-entrance size makes it possible to manipulate a male's sexual attractiveness.

Here, we assessed whether a male's attractiveness to females, as influenced by manipulating the size of nestbox entrances, was associated with male parental behavior. Because entrance size affects between-male differences in sexual attractiveness (Pribil & Picman, 1997; Dorset, 2015), we predicted that food-provisioning rates would differ between males at boxes with large and small entrances. In the indigo bunting (*Passerina cyanea*), for example, males that are more attractive to females spend less time providing parental care than males that are less sexually attractive (Ritchison & Little, 2014; see also Smith, 1995; Qvarnström, 1997; Sanz, 2001 for similar examples in other species). Indeed, an unattractive male, with few chances for procreation, may maximize his fitness by investing heavily in any offspring he manages to produce, whereas more attractive males may not invest as heavily into any one brood, as this time and energy could better be spent seeking additional mates. In other words, investing heavily into paternal care may allow unattractive males to produce a higher number of fledglings than they otherwise would if they did not increase their level of care. Thus, we predicted that males breeding on sites with large nest entrances would provision their offspring at a higher rate than those with small nest entrances. For females, however, we predicted no difference in provisioning rates with respect to entrance size. Finally, we expected that provisioning rates by male and female parents would be negatively correlated, as an increase in provisioning effort by males may be met with a decrease in provisioning effort by females, regardless of the size of their nest entrance. Moreover, because females, but not males, brood the young, ectothermic nestlings, we predicted that male provisioning would also be positively correlated with the time that females spent on the nest brooding their nestlings.

Materials and Methods

The study was conducted in McLean County, Illinois, at the Mackinaw Study Area (40.665°N, 88.89°W) from May-August of 2015, during the breeding season of the

migratory northern house wren, a widely distributed passerine in the United States (Johnson, 2014). The local population has been under study since the 1980 breeding season. The section of the study area used is an open woodland savannah with 115 nestboxes arranged along transects (see Fig. 1, DeMory et al. 2010). Transects run north to south, with 30 m between each nestbox and 60 m between transects. Nestboxes were constructed of 1.9-cm-thick wooden boards with an interior volume (height $\times$ width $\times$ depth) of 22 cm $\times$ 8.8 cm $\times$ 9 cm mounted on 1.5-m metal poles equipped with an aluminum disk (48.3 cm in diameter) serving as a predator baffle mounted underneath the nestboxes. Lambrechts *et al.* (2010) provide further details on nestboxes. During incubation or early in the nestling-rearing stage, we captured adults inside nestboxes or by using mist nets near the box ($N=51$ females and 48 attendant males in the current study; there were 3 additional males who provisioned food to their young, but we could not identify them). We measured their body mass (± 0.1 g) and tarsus length (± 0.1 mm), and banded them with a uniquely numbered U. S. Geological Survey leg band; males received three additional colored bands in a unique combination so that they could be identified using binoculars (males are more difficult to capture than females).

In the current study, nestboxes with entrance diameters of 5.0 cm (large-entrance diameter; $N=58$) and 3.2 cm (small-entrance diameter; $N=57$) were alternated along the north-south transects. There were 72 total nests initiated in these nestboxes during this time (46 with small entrances and 26 with large entrances). Overall, success rates of nests in large-entrance nestboxes, assessed as the percentage of nests fledging at least one young (the typical measure of avian nest success; e.g., Johnson 2014), was lower than those built in small-entrance nestboxes (50.0 ± 9.8 % of nests in large-entrance nestboxes fledged at least one young [least-squares mean $\pm$ SE] vs. 73.9 ± 6.5 % of nests produced in small-entrance nestboxes; $F_{1,70} = 4.07$, $P = 0.048$). This sample includes nests in which the identity of the female producing the clutch was unknown. Analyzing the success (percentage of nests that fledged at least one young) of only those nests at which the identity of the female was known ($N=63$ nests), and with the inclusion of maternal identity as a random effect to account for non-independence of nests produced by the same female (four of these females were known to produce a replacement nest after having a previous attempt fail), reveals a non-significant effect of entrance size on nest success ($F_{1,30.7} = 2.59$, $P = 0.118$; success rate of large-entrance nests: 61.9 ± 10.6 %, success rate of small-entrance nests: 81.0 ± 6.1 %, least-squares mean $\pm$ SE). Thus, these data suggest an effect of nest-entrance size on the probability of nest failure, but this effect primarily occurred prior to hatching (see Results). We were able to record parental provisioning behavior for fifty-one nests (35 with small entrances and 16 with large entrances).

Parental provisioning behavior was recorded using digital video cameras 4–5 d after hatching began within a nest. This is the age at which nestling growth is most rapid, and previous work has found that the amount of food delivered by parents at this age positively predicts nestling growth and the recruitment of offspring as breeders into the local population (Bowers *et al.*, 2014b, 2015a). One to two days before filming, dummy poles were set up to acclimate the birds to the presence of the camera near their nest (parental behavior is generally unaffected by the presence of these cameras; see Bowers *et al.*, 2014a). We recorded at least one hour of provisioning behavior between 0600–1100 CDT (time of

day has no effect on provisioning rate, Bowers *et al.*, 2015a), and analyzed provisioning rates as the number of food items delivered to the nest per hour once the birds resumed provisioning (i.e., the first hour of provisioning was scored). When females are flushed from the nestbox, their young are always warm to the touch. Thus, because brooding females represent the offspring's only source of heat, we also used the amount of time females spent in the nestbox during these observations as a measure of the time they spent brooding their young. Results of previous studies suggest that hour-long observations are generally reflective of parental behavior over longer periods of time (e.g., Bowers *et al.*, 2014a; Murphy *et al.*, 2015). House wrens are typically "single-load" provisioners, bringing only one prey item at a time back to the nest. Approximately one week later, 11 days after hatching began within nests, we banded, weighed (± 0.1 g), and measured the tarsus length (± 0.1 mm) of nestlings to estimate their body condition (body mass adjusted for body size) prior to fledging, a trait that positively predicts the probability of recruitment and longevity of these recruited offspring within the breeding population (Bowers *et al.*, 2014b).

Statistical analyses were conducted with SAS (ver. 9.4), all tests are two-tailed, and we converted data to z-scores prior to analysis to obtain standardized parameter estimates reflective of effect size (Schielzeth 2010). We also used Satterthwaite's degrees of freedom estimation, which can result in non-integer degrees of freedom. We first tested whether nestboxes of varying entrance size differed in their occupancy based on their availability using a generalized linear model (PROC GLIMMIX) with a binary response (i.e., occupied or not) and logit link function. We then tested for differences in the body condition (i.e., body mass with tarsus length as a covariate to control for skeletal size) and age of males nesting at the two types of nests using a general linear model (GLM, PROC MIXED). Data for male age reflect minimum ages (average age = 1.9 ± 1.1 yrs [mean $\pm$ SD], min = 1 yr, max = 5 yrs, $N = 42$ males), as many adults breeding in the population were captured for the first time as breeding adults and were not produced as offspring on the study area. Nonetheless, minimum ages are reflective of relative differences in age among individuals. We then tested for an effect of nestbox-entrance size on the number of eggs per clutch and the number of offspring fledged per brood using a GLM, with entrance size as a fixed effect and clutch-initiation date as a covariate. We also analyzed clutch-initiation dates using a Cox regression (survival analysis, PROC PHREG) to analyze the day of the year on which clutches were initiated in relation to nestbox-entrance size. We analyzed parental provisioning rates using a GLM with entrance size and parental sex as crossed fixed effects to test for an interaction between entrance size and sex in their effect on provisioning rate, and we included brood size and day of the year as covariates. We then analyzed the pre-fledging body condition (mass adjusted for body size) of nestlings in relation to the size of nestbox entrances using a linear mixed model with nest as a random effect to account for the non-independence of nestlings within broods, and we included brood size and hatching date as covariates. We also assessed the number of fledglings produced per egg laid by using a linear model to analyze the number of young fledged from a given nest in relation to parental provisioning rates with clutch size as a covariate. Finally, we predicted that male provisioning would (i) negatively predict the rate at which females provisioned their young with food, and (ii) positively predict the amount of time females spent brooding their young during our observations of provisioning, each of which we assessed using linear models.

Results

Nests in small-entrance nestboxes occurred with a significantly greater frequency than those in large-entrance nestboxes ($F_{1, 113} = 14.72$, $P < 0.001$; Fig. 1). There were no differences in the body condition ($F_{1, 44} = 0.24$, $P = 0.625$) or age ($F_{1, 45} = 0.83$, $P = 0.366$) of males at either type of nest, nor did nests in boxes with large and small entrances differ in clutch size ($F_{1, 62} = 0.00$, $P = 0.986$) or the number of young fledged ($F_{1, 44} = 0.77$, $P = 0.385$). Moreover, once clutches of eggs hatched, parents rearing broods in small- and large-entrance nestboxes were equally likely to succeed in fledging at least one of their young ($F_{1, 52} = 0.63$, $P = 0.431$). However, clutches within large-entrance nestboxes were initiated significantly later than those within small-entrance nestboxes ($\chi^2_1 = 8.59$, $P = 0.003$).

While controlling for date and brood size, there was an interaction between nestbox-entrance size and parent sex in their effect on parental provisioning rates (Table 1, Fig. 2). Follow-up tests revealed that, at large-entrance nestboxes, males provisioned at a higher rate than their mates ($t_{1, 49} = 9.04$, $P = 0.004$; Fig. 2), and these males also provisioned food to their offspring at a higher rate than males at small-entrance nestboxes ($F_{1, 94.4} = 5.16$, $P = 0.025$; Fig. 2). At small-entrance nestboxes, males and females provisioned at a similar rate ($F_{1, 49} = 0.21$, $P = 0.650$), and there was no difference in average provisioning rate between females at the two types of nestbox ($F_{1, 94.4} = 1.25$, $P = 0.270$; Fig. 2). Parental provisioning also increased with brood size (Table 1; Fig. 3). Although males increased provisioning rate at large-entrance nesting sites, there was no effect of the treatment on nestling pre-fledging body condition (Table 2). There was, however, a positive effect of total provisioning rate (i.e., the sum of male and female deliveries per hour) on the number of fledglings produced, while controlling for clutch size (estimate $\pm$ SE = 0.233 ± 0.113 , $F_{1, 44} = 4.26$, $P = 0.045$; effect of clutch size: estimate $\pm$ SE = 0.560 ± 0.114 , $F_{1, 44} = 23.95$, $P < 0.001$). This effect appeared to be attributable primarily to male food deliveries, as analyzing this model with male and female provisioning rates as predictors revealed no effect of female provisioning rate (estimate $\pm$ SE = 0.016 ± 0.117 , $F_{1, 43} = 0.02$, $P = 0.889$), but an effect of male provisioning (estimate $\pm$ SE = 0.275 ± 0.116 , $F_{1, 43} = 5.59$, $P = 0.023$) on the number of fledglings produced per egg laid (analyzing the effect of male and female provisioning rate on number of fledglings produced independently produces qualitatively similar results; effect of male provisioning: estimate $\pm$ SE = 0.270 ± 0.109 , $F_{1, 44} = 6.15$, $P = 0.017$; effect of female provisioning: estimate $\pm$ SE = -0.073 ± 0.116 , $F_{1, 44} = 0.40$, $P = 0.532$).

The increase in male provisioning rate, and slight, albeit non-significant, reduction in female provisioning rate, at large-entrance nestboxes (Fig. 2) suggested that male and female provisioning rates may be negatively correlated, which was indeed the case (Pearson correlation: $r_{49} = -0.310$, $P = 0.027$; Fig. 4A). There was no interaction between entrance size and maternal provisioning rate in their effect on a male's provisioning ($F_{1, 47} = 1.81$, $P = 0.185$). We also quantified the amount of time females spent brooding their young during our observations. Although male and female provisioning rates were negatively correlated, the rate at which males delivered food to the nest positively predicted the amount of time their mates spent on the nest brooding (Table 3; Fig. 4B). There was no correlation within females between the amount of time spent inside the nestbox and the rate at which they delivered food to the nest ($r_{49} = -0.097$, $P = 0.497$).

Discussion

Neither clutch nor brood sizes differed between nests with respect to the size of the nestbox entrance. Thus, the total energetic requirements of nestlings between groups was likely similar, meaning parents experienced similar demand for feeding nestlings, and differences in male provisioning rates were not confounded by differences in the number of young within their broods. Given that the size of nestbox entrances has a strong effect on male attractiveness, the difference we observed in the rate at which males delivered food to the two types of nestbox suggests that males respond to inter-individual differences in their sexual attractiveness by modifying the effort they put forth in providing paternal care, consistent with previous studies on other species that found an effect of male attractiveness on male parental care (e.g., Smith, 1995; Qvarnström, 1997; Sanz, 2001; Ritchison & Little, 2014). Given the positive effect of male provisioning rate on the number of fledglings produced per egg laid, our data suggest that unattractive males can produce a higher number of fledglings than they otherwise would by increasing the level of paternal care that they provide. Although we do not know how males at the two types of nesting sites spend their time when not provisioning their offspring with food, the increase in male provisioning rate at large-entrance nestboxes may be a response to their reduced sexual attractiveness and associated reduction in opportunities to mate with multiple females. Future work determining the extent to which males of varying attractiveness seek to mate with females outside the pair bond may shed light on plasticity in male parental behavior in relation to their own attractiveness.

Our results appear somewhat inconsistent with those of a previous study on this population that experimentally altered a different aspect of male attractiveness (i.e., by manipulating the number of available nesting cavities on a male's territory after male settlement, DeMory, Thompson & Sakaluk, 2010; see also Eckerle & Thompson, 2006). In this earlier study, males with experimentally enhanced attractiveness did not differ from control males in provisioning rate, but, consistent with the current study, males settling on more-attractive territories (i.e., those with a greater number of available nest cavities) delivered food to the nest at a lower rate than males on less-attractive territories (DeMory, Thompson & Sakaluk, 2010). Although there is some evidence that males with more nestboxes on their territory are more attractive to females than males with fewer nestboxes (Eckerle & Thompson, 2006; Dubois, Kennedy & Getty, 2006), this trait was actually not associated with an effect on a male's ability to acquire a mate in the earlier study (DeMory, Thompson & Sakaluk, 2010). In contrast, the effect of nestbox-entrance size on male attractiveness (Pribil & Picman, 1986; Dorset, 2015) appears to be stronger than the effect that surplus nestboxes has on male attractiveness (Eckerle & Thompson, 2006; DeMory, Thompson & Sakaluk, 2010). Thus, the discrepancy in the effect of male attractiveness on provisioning rate may be attributable to the manner in which these manipulations of a male's territory influence his perception of his own sexual attractiveness.

Although males increased their provisioning rate at large-entrance nestboxes, there was no effect of entrance size on nestling body condition. The lack of an effect on nestling condition, despite the effect on male provisioning rate, may be a result of sexual conflict over biparental care (e.g., Wright & Cuthill, 1989; Sanz, Kranenbarg & Tinbergen, 2000;

Smiseth *et al.*, 2005; Harrison *et al.*, 2009), whereby the increase in paternal food deliveries at a given nest was met by a slight reduction in maternal provisioning rate. We cannot assess in the current study whether the negative correlation between male and female provisioning is attributable to male effort having a causal effect on female effort, or *vice versa*. However, the positive correlation between male provisioning and female time on the nest suggests that females may respond to the amount of food provided by their mate by simultaneously altering their provisioning rate and the effort they put forth in brooding their young. Although the negative correlation between maternal provisioning rate and brooding time was not statistically significant, a recent study conducted over multiple years suggests that females in the study population face a trade-off between the time they spend provisioning young and time spent brooding, and that this latter behavior also positively affects nestling growth (Bowers *et al.*, 2015a). Indeed, provisioning offspring with food is not the only form of care parents provide, and our data suggest that members of a pair may divide the work in an efficient way (see also Houston *et al.*, 2005; Bulla *et al.*, 2014; Parker *et al.*, 2014). Males neither incubate eggs nor brood nestlings, and, therefore, generally spend very little time inside the nest cavity. However, females spend considerable time within nest cavities through incubation and the rearing of nestlings. Only the female broods their ectothermic young, and males usually transfer prey items to females through the nest entrance, which the females then pass to nestlings. Females, therefore, have better information on the provisioning rate of their mate than do males, and may adjust their effort accordingly (Bowers *et al.*, 2014a). Although nestling condition did not differ significantly between the two types of nests, there was a non-significant trend for nestlings reared in large-entrance nestboxes to be lighter than those at small-entrance nests (Table 2), and the amount of food provided by parents positively predicted the number of fledglings produced per egg, suggesting that a potential conflict between male and female parents over care may, at least to some extent, entail negative consequences for nestlings (see also Royle, Hartley & Parker, 2002; McNamara *et al.*, 2003).

In conclusion, manipulating the attractiveness of nesting sites by varying the size of nestbox entrances was associated with inter-individual differences in the extent of parental care provided by male house wrens, as predicted. Rates of food delivery also generally increased with increases in brood size, and were negatively correlated between male and female parents. This negative correlation may reflect conflict between male and female parents over the optimal level of parental investment.

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Figure 1.

Probability of nestbox occupancy in relation to entrance size. Plotted are least-squares means $\pm$ SE; numbers reflect the number of nestboxes occupied (numerator) and the number available (denominator) for each group. Figure and analysis based on data in Dorset (2015).

Figure 2.

Provisioning rate by parents in relation to their sex and the size of the nestbox entrance. Plotted are least-squares means $\pm$ SE ($N=35$ small-entrance nests and 16 large-entrance nests).

Figure 3.

Total provisioning in relation to brood size. The dashed line represents the best-fit line from a linear model, and overlapping data for broods of similar size are jittered ($N=51$ nests).

Figure 4. Maternal provisioning rate (A) and time spent brooding young per hour (B) in relation to male provisioning rate. Dashed lines represent the best fit from a linear model; some datapoints are overlapping ($N = 51$ nests).

Table 1

Effects on parental provisioning. Data were analyzed using a linear mixed model with nest identity as a random effect to account for the potential non-independence of provisioning by males and females at the same nest ($N = 51$ nests).

	Estimate $\pm$ SE	F	df	P
Nest entrance size		0.79	1, 47	0.380
Large ^a	0.677 $\pm$ 0.298			
Parent sex		7.54	1, 49	0.008
Female ^b	-0.116 $\pm$ 0.253			
Date	0.027 $\pm$ 0.090	0.09	1, 47	0.766
Brood size	0.209 $\pm$ 0.080	6.81	1, 47	0.012
Entrance size $\times$ Sex	-1.010 $\pm$ 0.452	5.00	1, 49	0.030
Intercept	0.004 $\pm$ 0.161			

^a relative to small-entrance nestboxes,

^b relative to male parents

Table 2

Effects on nestling pre-fledging body mass. Data were analyzed using a linear mixed model with nest identity as a random effect to account for the potential non-independence of offspring within broods ($N = 290$ young from 47 nests).

	Estimate $\pm$ SE	F	df	P
Nest entrance size		1.92	1, 40.8	0.174
Large ^a	-0.321 $\pm$ 0.232			
Hatching date	0.159 $\pm$ 0.104	2.35	1, 42.2	0.133
Brood size	-0.156 $\pm$ 0.100	2.42	1, 47.9	0.126
Provisioning rate ^b	-0.115 $\pm$ 0.107	1.15	1, 40.4	0.291
Tarsus length	0.469 $\pm$ 0.025	356.39	1, 277	< 0.001
Intercept	0.043 $\pm$ 0.116			

^a relative to small-entrance nestboxes,

^b combined rate of food provisioning for both parents

Table 3

Effects on maternal time spent brooding. Data were analyzed using a linear model ($N = 51$ nests).

	Estimate $\pm$ SE	F	df	P
Nest entrance size		0.22	1, 46	0.645
Large ^a	-0.159 ± 0.342			
Male provisioning rate	0.368 ± 0.152	5.88	1, 46	0.019
Date	-0.178 ± 0.157	1.28	1, 46	0.264
Brood size	-0.109 ± 0.146	0.56	1, 46	0.458
Intercept	0.050 ± 0.173			

^a relative to small-entrance nestboxes