



Original Article

Experimental cross-fostering of eggs reveals effects of territory quality on reproductive allocation

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Parental and territory quality are often correlated in territorial birds, and both factors influence the resources allocated to offspring. Surprisingly, the relative contribution of these two components of variation in parental investment remains obscure. We experimentally decoupled the normal covariation between parental quality and territory quality to test the hypothesis that territory quality influences female prenatal and postnatal reproductive allocation. Territories were categorized into low-, intermediate-, and high-quality based on fledging success of nests over the previous 6 years (nesting sites are fixed in space). To decouple covariation between territory quality and individual quality, nestbox entrance size was increased on high-quality territories and left small on poor-quality sites because house wrens (*Troglodytes aedon*) prefer small over large entrances to their nest sites. We found a significant prenatal effect of territory quality on nestling provisioning: when reared on intermediate-quality territories, nestlings hatching from eggs produced on low-quality territories were provisioned at a higher rate than those hatching from eggs produced on high-quality territories. We propose that the increased provisioning was brought about by increased nestling begging mediated by a maternally derived compound, such as corticosterone, transferred to the eggs of stressed females in poor-quality habitat.

Key words: postnatal effects, prenatal effects, provisioning, reproductive allocation, territory quality.

INTRODUCTION

The quality of breeding habitats for many species is likely to be heterogeneous over a range of spatial scales, with some areas of breeding habitat having greater resource availability than others (Sergio and Newton 2003; Janiszewski et al. 2013). In territorial species, such as many birds, individuals benefit from recognizing heterogeneity among habitats and identifying high-quality areas in which to settle (Hildén 1965; Lanyon and Thompson 1986; Orians and Wittenberger 1991). Thus, settlement of nesting sites in territorial species may be nonrandom with regard to territory quality (Fretwell and Lucas 1969), and, not surprisingly, patterns of nonrandom settlement have been observed in natural populations (Sergio and Newton 2003; Bowers et al. 2017a). In territorial species with extensive parental care, both quality of parents and breeding territory may influence quantity and timing of investment during the breeding cycle (Krist 2009). For altricial birds (i.e. those with offspring that are underdeveloped upon hatching, requiring

extensive parental care), variation in availability of food resources for reproduction across a heterogeneous landscape may differentially affect the allocation of resources during egg formation, incubation, and nestling care.

An important component of prenatal maternal allocation in birds is reflected by variation in egg size, which might also be affected by territory quality. In many species, there is significantly greater variation in egg size and composition among (70%), rather than within (30%), clutches (reviewed by Christians 2002), a pattern also documented in our house wren (*Troglodytes aedon*) study population (Styrsky et al. 1999; Styrsky et al. 2002). Additionally, the size of nestlings is strongly correlated with the size of the eggs from which they hatch, especially early in life (Styrsky et al. 1999, 2000; Christians 2002; Krist 2011). Egg size also is related to the survival rate of fledglings and juveniles, with nestlings hatching from larger eggs having a higher likelihood of survival (Krist 2011).

Variability in egg size among females is likely attributable to a combination of the effects of variation in territory quality and genetic differences among females (Styrsky et al. 2002; see also Christians 2002). In house wrens, egg size significantly affects the size of nestlings early in postnatal development during first broods

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early in the breeding season (May–June) and the effect is even more pronounced in second broods (July–August), a seasonal effect that is likely caused by lower food availability late in the breeding season (Morton 1984; Styrsky et al. 1999). Thus, egg size may have greater effects on the development of nestlings when resource availability is low because of seasonal changes or spatial variation in food availability (Smith and Bruun 1998). Indeed, on low-quality territories or in times of low food availability, egg-size effects are likely to be major factors affecting growth throughout nestling development (Styrsky et al. 1999; Krist and Munclinger 2015).

In addition to the effect of egg size, food availability within a territory is a major factor affecting postnatal development (Martin 1987; Gebhardt-Heinrich and Richer 1998; Nagy and Holmes 2005), because it shapes parents' ability to provision and the reproductive costs incurred in obtaining that food (Gustafsson and Sutherland 1988; Bryant and Tatner 1991; Maigret and Murphy 1997). Parental effort in food provisioning is probably dependent on the costs that adults incur as a consequence of this effort, which may include energy expenditures (Bryant and Tatner 1991), reduced survival while foraging (Maigret and Murphy 1997), and reduced future reproductive ability (Gustafsson and Sutherland 1988). These costs may be greatly increased in low-quality habitats (e.g. Nagy and Holmes 2005).

We hypothesized that territory quality influences female reproductive allocation independently of parental quality. Specifically, we hypothesized that its effects on reproductive allocation are evident: 1) prenatally through differential investment in eggs and 2) postnatally through differential parental care of nestlings. To test these hypotheses, we assessed the effects of differences in territory quality on nestlings independent of parental quality by altering nest-site attractiveness, which decoupled covariation between territory quality and individual quality. Then, to distinguish between prenatal and postnatal effects of territory quality, we cross-fostered clutches from high- and low-quality territories with those from intermediate-quality territories. We predicted that 1) any differences in nestlings from low- and high-quality territories cross-fostered to intermediate-quality territories would be attributable to differential maternal allocation to eggs (prenatal effect) and 2) any differences in nestlings from intermediate-quality territories cross-fostered to low- and high-quality territories would be caused by differences in parental care (postnatal effect).

METHODS

Study species and study site

The house wren is a small (10–12 g), insectivorous passerine that breeds in north-central Illinois from May (or occasionally the end of April) through August. The arrival of adults from their wintering grounds begins in April; the first brood of the season is produced at the end of April or early May, and the second in late June or early July (Drilling and Thompson 1991). Clutch size varies from 4 to 8 eggs, with one egg laid per day until the clutch is complete. Modal clutch size is 7 eggs for the first brood and 6 eggs for the second. Females incubate the eggs for approximately 12 days after the final egg is laid and brood the nestlings during the first half of the nestling period. Both females and males provision nestlings with food. Fledging occurs 15–17 days after hatching (Johnson 2014). We captured adults either within the nestbox or with mist nets placed near the nestbox entrance. We banded all adults with a numbered, aluminum US Geological Survey band and added three additional color bands (total 2 bands/leg) to males to facilitate

their identification without recapture. We weighed both adults and nestlings on an Acculab Pocket Pro PP-401 balance (± 0.1 g), determined tarsus length with dial calipers (± 0.1 mm), and measured wing length using a stopped ruler (± 0.5 mm).

We carried out our study during the first brood of the 2016 breeding season at the Mackinaw Study Area in McLean County, IL (40.665°N, 88.89°W), a tract of closed-canopy, secondary deciduous forest and restored oak (*Quercus* spp.) savanna bordering the Mackinaw River. House wrens are secondary cavity-nesters, and prefer artificial nestboxes to natural cavities as nest sites (Drilling and Thompson 1988).

We carried out this experiment on the restored oak savanna area in the northwest corner of the study area (see Figure 1 in DeMory et al. 2010), where since 2004 there have been 115 nestboxes arranged 30 m apart on north-south transects that are separated by 60 m (5.4 boxes/ha). Each nestbox is mounted on a 1.5-m pole with a 43.8-cm diameter aluminum disk below the box to reduce nest predation. The standard nestbox on the study area has a 3.2-cm diameter entrance hole on the side with a sliding metal trapdoor behind a block of wood (see Lambrechts et al. 2010). The wall of the box and the trapdoor together create a 4.0-cm “tunnel” for the entrance.

In house wrens, older, larger males are capable of out-competing younger, smaller males for a territory, creating a situation in which larger, older males tend to occupy the best territories (Eckerle and Thompson 2006; DeMory et al. 2010). This intrasexual competition among males for territories, paired with the fact that female house wrens make mate choices based, at least partly, on the territory-holding capabilities of males (Eckerle and Thompson 2006; Grana et al. 2012), could lead to positive-assortative mating with respect to individual quality, as suggested by positive age-assortative mating in our study population (Bowers et al. 2017b). Indeed, in our study population, settlement patterns for house wrens based on territory quality, as determined by the number of successful young fledging over a previous timespan, deviate from the pattern

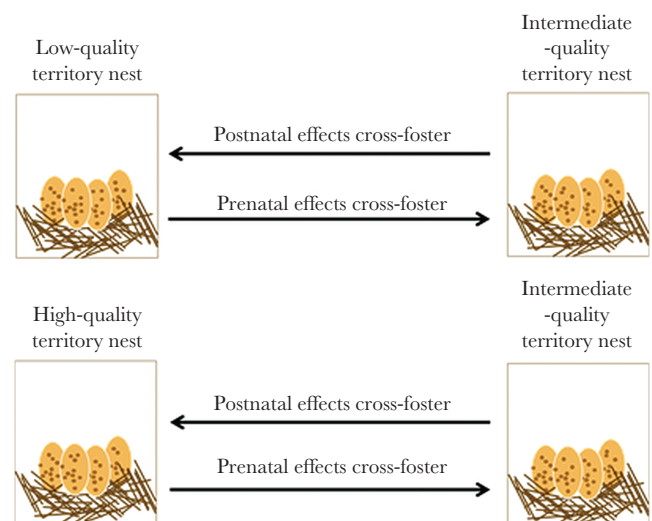


Figure 1

Schematic representation of treatment groups. Prenatal effects would be manifested through effects on nestlings originating from nests in low- or high-quality territories but cross-fostered to nests in intermediate-quality territories. Postnatal effects would be manifested through effects on nestlings originating from nests in intermediate-quality territories, but reared in high- or low-quality territories.

expected by chance, with high-quality territories being over-occupied and low-quality territories under-occupied (see Figure 1 in Bowers et al. 2017a). This indicates that historic fledging success is a strong predictor of true territory quality.

Prior to the breeding season, we estimated the quality of all available territories (i.e. the immediate area around each nestbox) by calculating the number of offspring successfully fledged from each nestbox over a recent 6-year period (2009–2014); we excluded data from 2015 because of an experiment that altered nestbox attractiveness. We assigned nestboxes to one of three territory categories for the purpose of applying treatments: low quality (≤ 15 fledglings over 6 years), intermediate quality (16–25 fledglings over 6 years), and high quality (≥ 26 fledglings over 6 years).

Nestbox entrance-size manipulation

As house wrens make settlement decisions based on the quality of available habitat (Eckerle and Thompson 2006; DeMory et al. 2010; Grana et al. 2012), we were presented with the issue that positive-assortative mating according to phenotypic quality in house wrens is linked to the quality of territory on which they settle. To sever this link, we altered settlement through manipulation of the diameter and depth of the nestbox entrance hole. Dorset et al. (2017) showed that house wrens avoid settling in nestboxes with larger, shallower entrance holes (hereafter large-entrance boxes) when given a choice between them and the standard small-entrance boxes (hereafter small-entrance boxes). To take advantage of this and the fact that house wrens prefer high-quality territories over low-quality territories (Bowers et al. 2017a), we assigned large entrances (5.0 cm diameter, 2.0 cm depth) to all of the nestboxes on high-quality territories, thereby making them relatively less attractive. We randomly assigned nestboxes on intermediate-quality territories either large or small entrances. Then we assigned small entrances to all nestboxes on low-quality territories, making them relatively more attractive. We maintained these conditions through the settlement and egg-laying periods until full incubation began the day the last egg of the clutch was laid, after which we returned the entrances of all boxes to the standard small entrances. As site fidelity to a particular territory/nestbox is low (Bowers et al. 2017a), we anticipated that this manipulation would be sufficient to decouple effects of parental and territory quality.

Field procedures: cross-fostering, provisioning, and body condition

We randomly paired nests on intermediate-quality territories for cross-fostering with either a nest on a low-quality territory or a nest on a high-quality territory (Figure 1). Thus, we reciprocally cross-fostered clutches between nests. This design allowed for the determination of the relative contribution of egg size and composition (prenatal effects) and parental care of nestlings (postnatal effects) to offspring growth and development across a range of territories that varied both in their suitability for rearing altricial nestlings and across which parental quality had been randomized. We swapped clutches within 3 days of the onset of full incubation to avoid any effects that differences in incubation behavior might have on development. During cross-fostering, we placed dummy eggs in nests while clutches were transferred. Dummy eggs are readily accepted and incubated by females and their use eliminates the risk that females will abandon their nest during the transfer. While cross-fostering eggs, we measured their breadth and length (± 0.01 mm) with a Mitutoyo Quick Mini Thickness Gauge to estimate egg volume.

We estimated egg volume with the equation $V = LB^2C$, where L is egg length, B is egg breadth, and C is a constant specific to house wren eggs equal to 0.000491 (Soukup S, unpublished data). This measure of egg size is strongly correlated with egg mass (Strysky et al. 2002; Bowers et al. 2015a).

Beginning 11–12 days after full incubation began, we checked nests on a daily basis for hatching to determine brood-day 0 (the day on which hatching begins within a nest). On brood-day 3, we placed dummy cameras 1 m from the nestbox to allow parents to become accustomed to their presence. The following day, we swapped the dummy camera for a Kodak Zx1 video recorder, which we used to record parental provisioning of nestlings for at least 1 h during the morning. Recordings of this duration result in observations that are representative of parental behavior when assessed over much longer observation periods and multiple days (Murphy et al. 2015). Brood-day 4 was used for video recording as this stage in nestling development is the inflection point of the nestling growth curve, and the provisioning rate on this day, particularly by the male, is positively correlated with nestling recruitment into future breeding populations (Bowers et al. 2014a).

On brood-day 11, after banding nestlings with a numbered, aluminum band, we weighed them and measured tarsus length and wing length in the same manner as adults. Mass and tarsus length typically approach growth asymptotes by brood-day 11 (Lago et al. 2000) and provide measures of nestling quality and likelihood of recruitment into the breeding population (Bowers et al. 2014b). Starting on brood-day 13, we checked nests daily for fledging to determine the number of young fledging successfully from each nest.

Video analysis

We analyzed video recordings to assess the provisioning rate of adults on brood-day 4. House wrens are “single-load provisioners,” bringing only 1 prey item at a time to the nest (Greenewalt and Jones 1955; Barnett et al. 2011). We used videos to determine the number of trips to the nestbox with prey items and the size of prey provisioned. We then categorized prey size as small (< 10 mm in length), medium (10–20 mm in length), and large (> 20 mm) based on the average 12-mm bill length of an adult house wren (Barnett et al. 2011).

Permits

We obtained all required research permits necessary for this work: Illinois State University IACUC permit 865938, US Fish and Wildlife Service and State of Illinois collecting permits (MB692148-0 and NH15.0004a, respectively), and US Geological Survey banding permit 09211.

Statistical analysis

We used SAS (ver. 9.4) for all statistical analyses. All analyses were two-tailed ($\alpha = 0.05$) and met assumptions of normality and homogeneous variances. Unless otherwise noted, all means and parameter estimates are reported ± 1 SE.

To determine if settlement patterns in our experiment were random with regard to territory quality, we sorted nestboxes into 10 bins using zero fledglings produced over the 6-year sample period with independent bins at increments of five, ranging from no fledglings produced over the 6-year sample period to 45 fledglings produced over the period. We sorted settled nestboxes (defined as those in which at least 1 egg was laid in the 2016 season) into the bins based on our devised territory-quality proxy. We then tested for a

difference between distributions of available and settled nestboxes using a chi-square test (PROC FREQ in SAS) comparing the relative frequencies of nestboxes available across territory qualities with the relative frequencies of nestboxes settled in 2016. We additionally performed an ANCOVA (PROC MIXED in SAS) on female and male size-adjusted mass, with tarsus length as the size-adjusting covariate, to identify if parental body condition varied across territory qualities, as in Bowers et al. (2014b). Mass and tarsus measurements were made on all birds caught in 2016; if, however, males had been caught in previous years and identified visually by their color bands in 2016, we used the measures taken the last year that the male had been captured. Furthermore, we used Pearson correlations (PROC CORR in SAS) to determine if age was correlated with the quality of the territory on which males and females settled.

To determine if there was a territory-quality effect on fledging success in the 2016 season, we performed binomial regression (PROC GLIMMIX in SAS) on the number of young ultimately hatching and fledging across territory qualities. For this analysis, we assessed fledging success by analyzing the number of fledglings produced from a nest as the dependent variable with the number of eggs cross fostered to that nest as the binomial denominator (i.e. events/trials syntax) and included our proxy of territory quality as the independent variable.

To test for an effect of territory quality on egg volume, we performed a mixed-model Anova (PROC MIXED in SAS), with nest identity as a random effect to avoid pseudoreplication. We included egg-1 day (the day the first egg in a given nest was laid) and clutch size as covariates. We additionally tested for an effect of nestbox entrance size on egg volume using the same statistical procedures. We then tested for an effect of egg volume on nestling size for both groups of offspring: those produced as eggs on low- and high-quality territories and reared on intermediate-quality territories, and those produced as eggs on intermediate-quality territories and reared on low- or high-quality territories. For the former group, we initially included an interaction between the quality of the territory on which eggs were produced (low vs. high) and egg size in their effect on nestling body mass, tarsus length, and wing length; for the latter group, we included an interaction between the quality of the territory on which nestlings were reared (low vs. high). However, neither of these interactions, nor the main effects of territory quality, were significant, and we removed them from the final models in favor of a simpler test of main effects, which included only egg size as the independent variable (we included nest of rearing as a random effect).

To test for an effect of egg volume on nestling body condition, we performed regression analyses (PROC MIXED in SAS) of egg size on pre-fledging mass, tarsus length, wing length, and a single principle component derived from these traits for each individual (obtained from PROC FACTOR in SAS). We performed each set of regression analyses for both our prenatal effect cross-fostered groups, young produced as eggs on low- and high-quality territories and reared on intermediate-quality territories, and our postnatal effect cross-fostered groups, young produced as eggs on intermediate-quality territories and reared on low- and high-quality territories.

We tested the effect of territory quality on provisioning using ANCOVA (PROC GLM in SAS). We performed analyses of the effect of territory quality on provisioning for both a potential prenatal effect and postnatal effect. We designed the prenatal analysis to examine differences in provisioning to nestlings originating on low- and high-quality territories that were cross-fostered to intermediate-quality territories and, thus, were provisioned under similar

conditions. We further designed the postnatal analysis to examine differences in provisioning to nestlings that had originated on intermediate-quality territories and that were cross-fostered as eggs to, and ultimately provisioned on, territories of low- and high-quality. In both prenatal and postnatal analyses, we examined the rate of provisioning, and the number of small, medium, and large prey items brought to the nest. We also compared provisioning rates to offspring in the postnatal analysis conditions to test for a potential prenatal effect of entrance size by testing for an effect of entrance size on provisioning rates. For all comparisons, we included brood-day 0 and clutch size as covariates.

We tested for an effect of territory quality on brood-day 11 nestling condition using mixed-model Anova (PROC MIXED in SAS). To assess the effect of territory quality on pre-fledging condition, we performed analyses of both prenatal and postnatal effects of territory quality with respect to nestling mass, tarsus length, and wing length. In the prenatal analysis, we examined differences in nestling size for nestlings originating on low- and high-quality territories that were cross-fostered to intermediate-quality territories and thus experienced similar conditions. In the postnatal analysis, we examined differences in nestling size for those originating in intermediate-quality territories that were cross-fostered to, and ultimately provisioned on, territories of low- and high-quality. For all comparisons, we included brood-day 0 and clutch size as covariates.

RESULTS

Nestbox settlement and territory quality

After nestbox entrance size was manipulated, the relative frequency of available nestboxes and the observed settlement pattern across levels of territory quality were not significantly different (chi-square test: $\chi^2_9 = 7.85$, $P = 0.450$; Figure 2). Thus, this manipulation removed the strong preferences for high-quality territories, unlike the normal situation (Bowers et al. 2017a). Under these manipulated conditions, female and male size-adjusted body condition was also not significantly different across territory qualities (Females: High-quality $N = 11$, 11.919 ± 0.195 g; Intermediate-quality $N = 30$, 12.077 ± 0.118 g; Low-quality $N = 18$, 12.038 ± 0.152 g; Males: High-quality $N = 11$, 10.931 ± 0.150 g; Intermediate-quality $N = 29$,

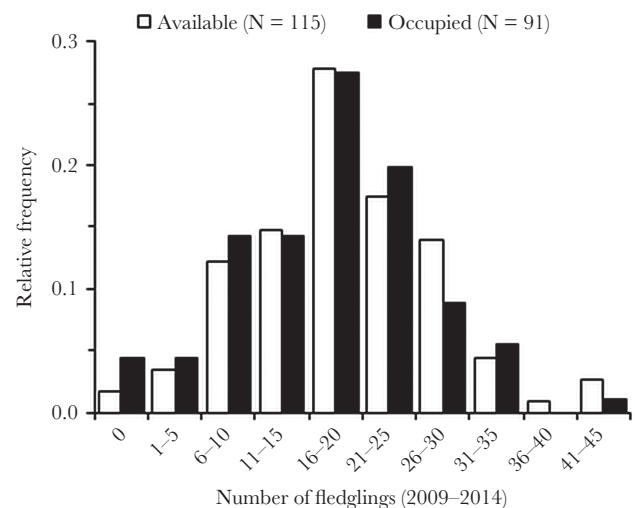


Figure 2

Settlement patterns in nestboxes with the entrance size manipulated. Expected and observed patterns were not statistically different.

11.066 \pm 0.092 g; Low-quality $N = 18$, 11.113 \pm 0.117 g; Table 1), further indicating that the experimental manipulation succeeded in decoupling environmental and parental quality. Additionally, age was not correlated with territory quality for adult males (Pearson correlation: $r_{18} = -0.161$, $P = 0.499$) or adult females (Pearson correlation: $r_{22} = 0.088$, $P = 0.682$). There remained, however, a positive relationship between the probability of nestlings fledging from territories during the experiment and the number of fledglings on those territories in 2009–2014 (Binomial regression: $F_{1,84} = 47.18$, $P \leq 0.001$). In other words, there was an effect of territory quality on fledging success, but parents of varying quality had settled on these territories at rates indistinguishable from random.

Egg size

Egg volumes did not differ significantly across the 3 territory-quality levels (Low-quality: $N = 171$ eggs, 1.302 \pm 0.020 mL; Intermediate-quality: $N = 251$ eggs, 1.337 \pm 0.016 mL; High-quality: $N = 80$ eggs, 1.343 \pm 0.028 mL; Table 2A). Egg volumes were also found to not be significantly different across entrance manipulations within intermediate-quality territories (Large-hole: $N = 73$ eggs, 1.355 \pm 0.032 mL; Small-hole: $N = 178$ eggs, 1.334 \pm 0.020 mL; Table 2B). Nonetheless, the effects of egg size on nestling pre-fledging body mass and size differed for offspring produced and reared

Table 1

Effects of territory quality on adult body condition using an ANCOVA on female (A) and male (B) body mass with tarsus length as a covariate

	Estimate \pm SE	<i>F</i>	df	<i>P</i>
A. Female mass				
Territory quality		0.24	2, 55	0.788
High-quality ^a	-0.119 \pm 0.247			
Intermediate-quality ^a	0.039 \pm 0.193			
Tarsus	0.214 \pm 0.141	2.30	1, 55	0.135
Intercept	8.011 \pm 2.656			
B. Male mass				
Territory quality		0.47	2, 54	0.626
High-quality ^a	-0.182 \pm 0.191			
Intermediate-quality ^a	-0.047 \pm 0.150			
Tarsus	0.422 \pm 0.145	8.51	1, 54	0.005
Intercept	3.088 \pm 2.758			

^aRelative to low-quality territories

Table 2

Effects of territory quality (A) and entrance size (B) on volume of eggs laid using mixed-model Anova with egg-1 day and clutch size as covariates and nest identity as a random effect

	Estimate \pm SE	<i>F</i>	df	<i>P</i>
A. Territory quality				
Treatment		1.13	2, 69.3	0.330
High-quality ^a	0.041 \pm 0.035			
Intermediate-quality ^a	0.035 \pm 0.025			
Egg-1 day	0.001 \pm 0.001	1.06	1, 69.5	0.307
Clutch size	0.007 \pm 0.016	0.19	1, 70.6	0.665
Intercept	1.112 \pm 0.188			
B. Entrance size				
Treatment		0.33	1, 33.1	0.568
Large entrance ^b	0.215 \pm 0.037			
Egg-1 day	0.001 \pm 0.001	0.15	1, 33.1	0.698
Clutch size	0.004 \pm 0.021	0.03	1, 33.8	0.862
Intercept	1.228 \pm 0.261			

^aRelative to low-quality territories. ^bRelative to small-entrance boxes.

on different kinds of territories. When nestlings originating as eggs on low- and high-quality territories were reared on intermediate-quality territories, egg size did not have any effect on their pre-fledging body mass (Table 3A, Figure 3A), tarsus length (Table 3A, Figure 3C), or wing length (Table 3A, Figure 3E); however, when nestlings were produced as eggs on intermediate-quality territories and reared on low- and high-quality territories, egg size did have a significantly positive effect on pre-fledging body mass (Table 3B, Figure 3B), a marginally non-significant effect on tarsus length (Table 3B, Figure 3D), but no effect on wing length (Table 3B, Figure 3F). Analyzing overall nestling size as a principal component that loads strongly and positively on nestling mass (Pearson correlation: $r_{66} = 0.807$, $P < 0.001$), tarsus length (Pearson correlation: $r_{66} = 0.842$, $P < 0.001$), and wing length (Pearson correlation: $r_{66} = 0.814$, $P < 0.001$) produces qualitatively similar results for the 2 groups of offspring (Table 3).

Provisioning of food to nestlings—prenatal effects

Foster parents on intermediate-quality territories reared offspring that had originated on either a low-quality or a high-quality territory. These parents provisioned food to nestlings hatching from eggs produced on low-quality territories at a significantly higher rate than nestlings from eggs produced on high-quality territories (Low-quality origin: $N = 13$ nests, 14.961 \pm 1.306 trips per hour; High-quality origin: $N = 8$ nests, 8.065 \pm 1.698 trips per hour; Table 4, Figure 4A). Nestlings from eggs produced on low-quality territories were provisioned with more small prey items than were nestlings from high-quality territories, but there was no difference in the number of medium-sized and large prey items provisioned (Table 4). Prenatal effects of territory quality on nestling mass, tarsus length, and wing length were not significant (Table 5).

Provisioning of food to nestlings—postnatal effects

Foster parents on low- and high-quality territories reared offspring that had all originated on territories of intermediate quality. The rates of food provisioning to these nestlings were not significantly different between low- and high-quality territories (Table 6, Figure 4B). There was also no difference in the distributions of prey size across

Table 3

Regression models depicting the effect of egg size on pre-fledging mass, tarsus length, wing length, and a single principle component derived from these traits for each individual

	Estimate \pm SE	<i>F</i>	df	<i>P</i>
A. Prenatal effects				
Mass	1.354 \pm 2.242	0.36	1, 8.95	0.561
Tarsus	2.078 \pm 1.146	3.28	1, 9.42	0.102
Wing length	-0.142 \pm 8.621	0.00	1, 11.5	0.987
Principal component	1.333 \pm 1.805	0.55	1, 9.76	0.478
B. Postnatal effects				
Mass	4.632 \pm 1.539	9.05	1, 10.5	0.013
Tarsus	3.088 \pm 1.441	4.59	1, 11.4	0.055
Wing length	5.079 \pm 10.021	0.26	1, 10.1	0.623
Principal component	4.649 \pm 2.084	4.98	1, 10.1	0.049

Estimates \pm SE represent the slope of the effect of egg size on these traits. The prenatal effect (A) represents young produced as eggs on low- and high-quality territories and reared on intermediate-quality territories, whereas the postnatal effect (B) represents young produced as eggs on intermediate-quality territories and reared on low- and high-quality territories.

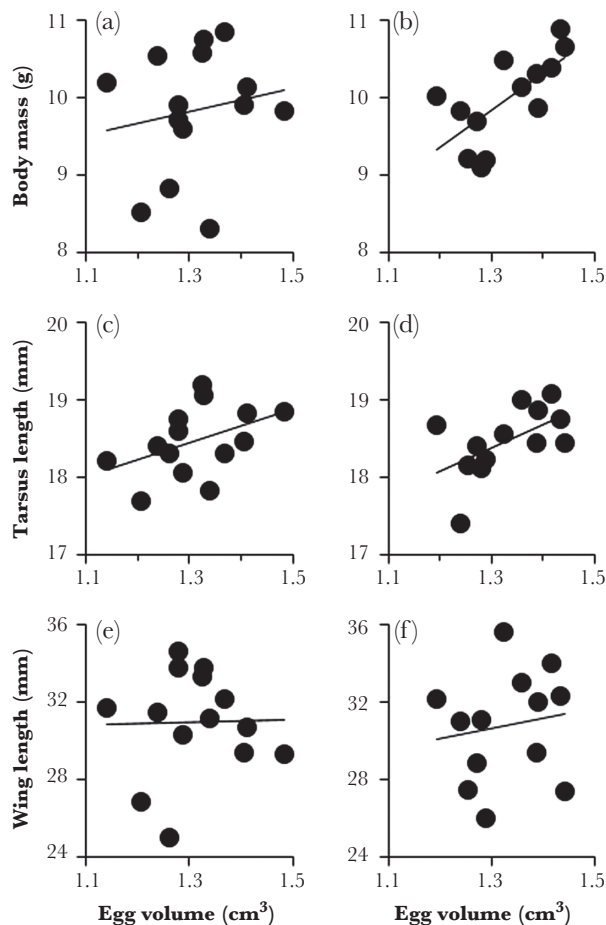


Figure 3
Effects of egg size on nestling body mass, tarsus length, and wing length (brood means). Nestlings in (A, C, and E) were produced as eggs on low- and high-quality territories and reared on intermediate-quality territories, whereas nestlings in (B, D, and F) were produced as eggs on intermediate-quality territories and reared on low- or high-quality territories.

treatments (Table 6). Postnatal effects of territory quality on nestling mass, tarsus length, and wing length were not significant (Table 7). Within these same nestboxes, we did not detect a difference in provisioning rates linked to entrance size of origin nest (Large-hole: $N = 4$ nests, 11.504 ± 3.068 food items per hour; Small-hole: $N = 17$ nests, 12.528 ± 1.406 food items per hour; Table 8).

DISCUSSION

Covariation between provisioning effort, egg quality, and territory quality may confound any attempt to determine the effects of territory quality, per se, on prenatal investment in eggs and postnatal parental care of nestlings (Gebhardt-Heinrich and Richner 1998). Cross-fostering eggs or nestlings between nests on territories differing in quality decouples the effects of maternal quality from territory quality, making it possible to determine the role that territory quality plays in reproductive allocation to eggs and offspring (Magrath 1992; Krist 2009). Indeed, typical settlement patterns were disrupted by our modification of the size of nestbox entrances across the range of territory qualities. Under the usual conditions on the study area (small diameter nestbox entrances), settlement of nestboxes with regard to their availability across the range of

Table 4
Effects of prenatal territory quality on provisioning rates using ANCOVA with brood-day 0 and the number of young present on brood-day 4 as covariates

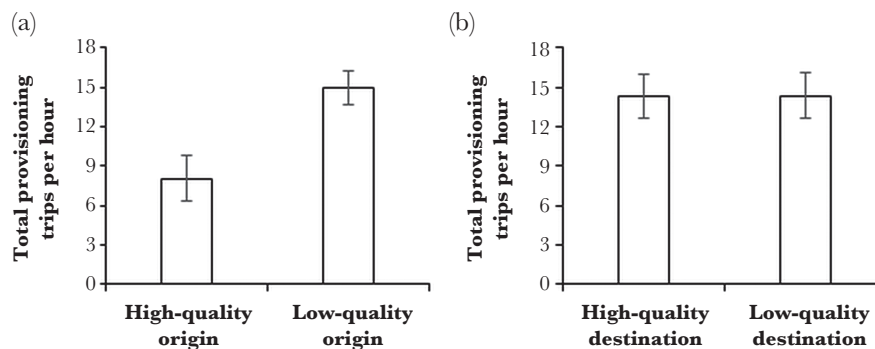
	Estimate \pm SE	<i>F</i>	df	<i>P</i>
A. Small-sized food items				
Prenatal territory quality		8.59	1, 17	0.009
High-quality ^a	-5.477 ± 1.869			
Brood-day zero (BD0)	0.010 ± 0.075	0.02	1, 17	0.896
Number of young on BD4	1.405 ± 0.597	5.55	1, 17	0.031
Intercept	3.133 ± 11.717			
B. Medium-sized food items				
Prenatal territory quality		2.93	1, 17	0.105
High-quality ^a	-1.601 ± 0.936			
Brood-day zero (BD0)	0.037 ± 0.038	0.96	1, 17	0.342
Number of young on BD4	0.674 ± 0.299	5.09	1, 17	0.038
Intercept	-5.683 ± 5.866			
C. Large-sized food items				
Prenatal territory quality		0.21	1, 17	0.651
High-quality ^a	0.183 ± 0.397			
Brood-day zero (BD0)	0.003 ± 0.016	0.03	1, 17	0.874
Number of young on BD4	0.138 ± 0.127	1.20	1, 17	0.290
Intercept	-0.443 ± 2.487			
D. Total provisioning				
Prenatal territory quality		9.62	1, 17	0.007
High-quality ^a	-6.895 ± 2.223			
Brood-day zero (BD0)	0.049 ± 0.090	0.30	1, 17	0.588
Number of young on BD4	2.217 ± 0.710	9.76	1, 17	0.006
Intercept	-2.993 ± 13.941			

^aRelative to low-quality territories.

territory quality is nonrandom, with low-quality territories under-occupied and high-quality territories over-occupied (Bowers et al. 2017a). In our study, however, when poor-quality territories were made more attractive by giving them nestboxes with small entrances and high-quality territories made less attractive with large-entrance nestboxes, bias in settlement was removed with respect to territory quality. Furthermore, female and male body condition and age did not differ across territory qualities, suggesting that biases based on adult quality and age/experience were also eliminated.

The effect of territory quality was retained throughout our manipulation of settlement and cross-fostering. Despite the effect of territory quality on nestling fledging success, independent of parental quality, egg volume did not differ among eggs produced on low-, intermediate-, and high-quality territories. Furthermore, egg volume was found not to differ across entrance size manipulations, indicating that our entrance size manipulation did not confound analysis of egg size. We expected some of the among-clutch variation in egg size that we typically see to be linked to the environment in which they were produced because of 1) the energetic input required by eggs in income breeders (Nager et al. 1999; Williams and Miller 2003; Mänd et al. 2007), and 2) the positive relationship between egg size and hatchling and nestling size (Styrsky et al. 1999; 2002). However, the experimental manipulation clearly distributed parents of different quality across the entire range of territory qualities, so that the lack of differences in average egg volume across territory qualities may simply reflect female quality alone, rather than a combination of parental and territory quality. Furthermore, in earlier experiments that manipulated female condition by activating the immune system or by feeding females corticosterone-injected mealworms (*Tenebrio molitor*), egg size did not change, but the amount of yolk and corticosterone in the yolk did (Bowers et al. 2015b; Bowers et al. 2016, respectively).

Most surprising was the higher rate of provisioning of nestlings from low-quality territories than nestlings from high-quality

**Figure 4**

(A) Provisioning to offspring of high-quality and low-quality origin reared on intermediate-quality territories (Low-quality origin: $N = 13$ nests; High-quality origin: $N = 8$ nests). (B) Provisioning to offspring of intermediate-quality origin reared in high-quality and low-quality territories (Low-quality destination: $N = 10$ nests; High-quality destination: $N = 11$ nests).

Table 5

Effects of prenatal territory quality on nestling body condition using mixed-model Anova with brood-day 0 and number of young present on brood-day 11 as covariates and nest identity as a random effect

	Estimate \pm SE	<i>F</i>	df	<i>P</i>
A. Mass				
Territory quality		0.00	1, 7.64	0.982
High-quality ^a	-0.011 ± 0.487			
Brood-day zero (BD0)	-0.014 ± 0.018	0.57	1, 7.72	0.472
Number of young on BD11	0.176 ± 0.193	0.83	1, 9.37	0.386
Intercept	11.182 ± 2.963			
B. Tarsus length				
Territory quality		0.42	1, 7.46	0.536
High-quality ^a	0.157 ± 0.242			
Brood-day zero (BD0)	0.006 ± 0.009	0.37	1, 7.53	0.562
Number of young on BD11	0.136 ± 0.102	1.76	1, 11.6	0.211
Intercept	16.866 ± 1.491			
C. Wing length				
Territory quality		0.05	1, 9.42	0.832
High-quality ^a	-0.346 ± 1.582			
Brood-day zero (BD0)	-0.110 ± 0.059	3.52	1, 9.52	0.092
Number of young on BD11	0.733 ± 0.625	1.37	1, 11.3	0.265
Intercept	45.232 ± 9.620			

^aRelative to low-quality territories.

territories when both were reared on intermediate-quality territories. As these nestlings originated from eggs swapped to their destination nests at the beginning of incubation, they received a minimal contribution of incubation (≤ 3 days) and, of course, no provisioning on their original territories. Thus, this is a prenatal effect originating from their territory of origin. In contrast, provisioning ability in postnatal analyses did not differ between low- and high-quality territories. This suggests that although low- and high-quality territories differ in the likelihood of nestlings persisting to the time of fledging, the ability of parents to provision nestlings on these territories does not differ. We additionally show that our entrance size manipulation did not confound these analyses by influencing egg composition similarly to territory quality. We conclude from this that, postnatally, quality of the habitat from which food items were acquired did not have an effect on ability to provision nestlings.

The lack of differences in nestling body condition metrics in postnatal analyses is unsurprising in light of the provisioning results of the postnatal analysis, as provisioning rates and egg sizes for these nestlings were not different. However, we did detect evidence that

Table 6

Effects of postnatal territory quality condition on provisioning rates using ANCOVA with brood-day zero and the number of young present on brood-day four as covariates

	Estimate \pm SE	<i>F</i>	df	<i>P</i>
A. Small sized food items				
Postnatal territory quality		0.74	1, 17	0.402
High-quality ^a	-1.599 ± 1.861			
Brood-day zero (BD0)	-0.004 ± 0.073	0.00	1, 17	0.957
Number of young on BD4	0.583 ± 1.032	0.32	1, 17	0.580
Intercept	7.542 ± 13.259			
B. Medium sized food items				
Postnatal territory quality		0.38	1, 17	0.544
High-quality ^a	-0.041 ± 1.211			
Brood-day zero (BD0)	-0.420 ± 0.047	0.77	1, 17	0.393
Number of young on BD4	-0.420 ± 0.671	0.39	1, 17	0.539
Intercept	12.366 ± 8.623			
C. Large sized food items				
Postnatal territory quality		1.17	1, 17	0.294
High-quality ^a	0.825 ± 0.762			
Brood-day zero (BD0)	-0.005 ± 0.030	0.03	1, 17	0.865
Number of young on BD4	0.256 ± 0.423	0.37	1, 17	0.552
Intercept	0.450 ± 5.430			
D. Total provisioning				
Postnatal territory quality		0.00	1, 17	0.993
High-quality ^a	-0.024 ± 2.494			
Brood-day zero (BD0)	-0.050 ± 0.097	0.27	1, 17	0.611
Number of young on BD4	0.419 ± 1.383	0.09	1, 17	0.766
Intercept	20.358 ± 17.769			

^aRelative to low-quality territories.

the effect of egg size on overall nestling size prior to fledging differed for nestlings reared on different-quality territories. If the increase in food provisioning to nestlings originating on low-quality territories (when reared on intermediate-quality territories) is indeed explained by a maternal effect via the egg, then it appears that these effects can cancel out any potential effect of egg size on nestling development by virtue of their effects on food provisioning. Not surprisingly, then, when nestlings originating as eggs on intermediate-quality territories were reared on either low- or high-quality territories, we see no “compensatory” increase in provisioning, and, thus, a strong effect of egg size on nestling pre-fledging size.

The likeliest explanation for the increased provisioning on intermediate-quality territories of nestlings derived from low-quality territories compared with those from high-quality territories is that a compound such as testosterone (Barnett et al. 2011) or corticosterone

Table 7

Effects of postnatal territory quality on nestling body condition using mixed model Anova with brood-day 0 and number of young present on brood-day 11 as covariates and nest identity as a random effect

	Estimate ± SE	F	df	P
A. Mass				
Territory quality		2.47	1, 9.85	0.254
High-quality ^a	−0.510 ± 0.421			
Brood-day zero (BD0)	0.012 ± 0.014	0.77	1, 9.28	0.402
Number of young on BD11	0.062 ± 0.191	0.11	1, 10.9	0.751
Intercept	8.002 ± 2.480			
B. Tarsus length				
Territory quality		1.28	1, 9.95	0.285
High-quality ^a	0.388 ± 0.343			
Brood-day zero (BD0)	−0.006 ± 0.001	0.25	1, 9.32	0.629
Number of young on BD11	−0.030 ± 0.156	0.04	1, 11.2	0.849
Intercept	19.294 ± 2.022			
C. Wing length				
Territory quality		0.80	1, 9.1	0.394
High-quality ^a	−1.470 ± 1.644			
Brood-day zero (BD0)	−0.089 ± 0.055	2.64	1, 8.55	0.141
Number of young on BD11	1.209 ± 0.746	2.63	1, 10.2	0.136
Intercept	39.997 ± 9.683			

^aRelative to low-quality territories.

Table 8

Effects of prenatal nestbox entrance size on total provisioning rates using ANCOVA with brood-day 0 and the number of young present on brood-day 4 as covariates

	Estimate ± SE	F	df	P
Treatment				
Large entrance ^a	−1.024 ± 3.466	0.09	1, 17	0.771
Brood-day zero (BD0)	−0.005 ± 0.117	0.00	1, 17	0.968
Number of young on BD4	1.667 ± 0.858	3.78	1, 17	0.069
Intercept	5.761 ± 18.181			

^aRelative to small-entrance nestboxes.

(Bowers et al. 2016) influenced begging behavior. Specifically, differential allocation of the glucocorticoid hormone corticosterone to eggs originating from poor-quality territories may explain this result as increased in ovo corticosterone is known to increase begging behavior in nestling birds (Kitaysky et al. 2001; Loiseau et al. 2008; Bowers et al. 2016). Corticosterone transfer to developing eggs by stressed mothers (Saino et al. 2005; Bowers et al. 2015b) is a condition that may be expected on low-quality territories (van de Crommenacker et al. 2011). In an earlier study, house wren nestlings hatching from corticosterone-injected eggs in our study population were lighter than control nestlings at hatching, but, through compensatory growth, were heavier near the time of nest-leaving (Strange et al. 2016), perhaps because of increased begging (Bowers et al. 2016). If nestlings originating from low-quality territories were similarly lighter at hatching, this could explain the seeming paradox of the prenatally linked differences in foster-parent provisioning rates, but the absence of any differences in nestling mass prior to fledging.

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