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Experimental food supplementation reveals habitat-dependent male reproductive investment in a migratory bird

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Environmental factors can shape reproductive investment strategies and influence the variance in male mating success. Environmental effects on extrapair paternity have traditionally been ascribed to aspects of the social environment, such as breeding density and synchrony. However, social factors are often confounded with habitat quality and are challenging to disentangle. We used both natural variation in habitat quality and a food supplementation experiment to separate the effects of food availability—one key aspect of habitat quality—on extrapair paternity (EPP) and reproductive success in the black-throated blue warbler, *Setophaga caerulescens*. High natural food availability was associated with higher within-pair paternity (WPP) and fledging two broods late in the breeding season, but lower EPP. Food-supplemented males had higher WPP leading to higher reproductive success relative to controls, and when in low-quality habitat, food-supplemented males were more likely to fledge two broods but less likely to gain EPP. Our results demonstrate that food availability affects trade-offs in reproductive activities. When food constraints are reduced, males invest in WPP at the expense of EPP. These findings imply that environmental change could alter how individuals allocate their resources and affect the selective environment that drives variation in male mating success.

1. Introduction

Genetic parentage analyses of socially monogamous species have revealed that extrapair paternity (EPP) is often an important, ecologically mediated component of male fitness [1–5]. Most studies have examined how variation in EPP is related to socio-ecological factors, such as local breeding synchrony and density, that affect opportunities for individuals to encounter and evaluate potential extrapair mates [6–8]. Some studies have found empirical support for the influence of these factors on the frequency of EPP [9,10], but the results are inconsistent among species and populations [2,7,11,12]. Local breeding synchrony and density are often correlated with aspects of habitat quality, such as food availability and vegetation density, which structure both the temporal and spatial interactions among potential extrapair mates [12–15]. Thus, the inconsistent patterns in extrapair mating could be the result of studies not designed to explicitly separate the effects of food and habitat, which also influence variation in EPP. These findings demonstrate that EPP is affected by multiple ecological factors [12,14]. Nevertheless, we still know little about how such factors interact to constrain EPP, and how constraints might differ between the sexes. For example, food availability can affect female investment in extrapair mating [16], but we lack empirical tests of hypotheses that predict how constraints imposed by differences in habitat quality might influence male investment in extrapair mating [12,14]. Investigating the nature of these constraints will advance our understanding of how environmental variability shapes female and male reproductive investment strategies.

The constrained female hypothesis [16] has guided much research into environmental effects on EPP. This hypothesis predicts that females on low-quality territories (i.e. with low food availability) should be less likely to cuckold their mate because they are unable to pay the energetic costs if males reduce parental care when cuckolded and/or females are energetically limited in their ability to circumvent male guarding attempts. Few studies have found evidence for facultative adjustments in male care in response to cues of paternity [12,16]. Moreover, empirical tests of this hypothesis have provided mixed support [17], more commonly finding that females on low-quality territories are more, not less, likely to produce extrapair young, resulting in lower within-pair paternity (WPP) for their social mates [15,18–20]. This pattern might result if females on low-quality territories necessarily forage further from their nest sites, increasing the probability of encountering extrapair males [15,16,18], or if females use territory quality to assess male quality [20].

Environmental constraints on male mating decisions have received less empirical study, despite the importance of EPP to male fitness in many socially monogamous species [2,20,21]. Three hypotheses have been proposed to explain how habitat quality or food availability affects the costs and benefits to males of pursuing EPP. If food availability is reduced (e.g. through unfavourable climatic conditions or habitat degradation), then males may shift allocation of limited resources from mating effort (i.e. mate guarding, pursuit of extrapair copulations) to self-maintenance, and thereby reduce the incidence of EPP, which we refer to as the ‘environmental constraint hypothesis’ [21,22]. This hypothesis predicts both higher WPP owing to increased mate guarding, and higher EPP owing to increased pursuit of extrapair copulations as food availability increases. A second, relatively unexplored hypothesis is that food availability might affect the extent to which males allocate their effort across different mating behaviours owing to conflicting energetic demands on mate guarding against cuckoldry (which enhances WPP) versus pursuit of extrapair copulations (which enhances EPP) [13], which we refer to as the ‘constrained male hypothesis’. Specifically, males in low-quality habitat may be more energetically constrained to pursue extrapair copulations while guarding their social mates, and so would be expected to pursue whichever of these two components has the greatest fitness benefit. This hypothesis predicts that food availability would result in a trade-off between WPP and EPP. A third possibility is that food limitation may increase the value of male parental care to the survival of nestlings and provide males with less time and energy to pursue extrapair copulations, which we refer to as the ‘paternal trade-offs hypothesis’ [13,23]. This hypothesis predicts that an increase in food availability would lead to higher EPP at the expense of paternal care, but it does not make predictions for WPP. Furthermore, if favourable resource conditions permit reneating after a successful first nest, males face a complex trade-off between mate guarding to protect paternity in their second broods, providing parental care to fledglings from their first broods and pursuing extrapair copulations [13]. The relative investment in each of these competing reproductive behaviours should be proportional to the expected gain in their reproductive success [13,20].

To examine these non-mutually exclusive hypotheses for how food availability may affect both male and female mating decisions, we used a combination of correlational and experimental approaches in a free-living population of the

insectivorous, migratory black-throated blue warbler, *Setophaga caerulescens*. Habitat quality for this species increases from low to high elevations at our study site. At higher elevations, food availability is greater and the forest shrub layer used by the black-throated blue warbler for nesting is denser, which also corresponds to higher breeding densities relative to lower elevations [24]. We used both natural variation in food availability estimated for each territory and a food supplementation experiment in low-quality and high-quality habitat (low and high elevations, respectively) to investigate the effects of food availability on three components of male reproductive success: WPP, EPP and fledging two broods. We previously showed that food-supplemented males appeared to increase mate-guarding effort over extrapair mate attraction while their social mates were fertile [25], but we did not determine if mate guarding was associated with higher WPP, or if supplemental food allowed males to subsequently invest greater effort into extrapair mate attraction, which would lead to higher EPP overall. Hence, we predicted that increases in food availability (either naturally or owing to food supplementation) would increase WPP and EPP. These results would be consistent with the environmental constraints and paternal trade-offs hypotheses, but would not support the constrained male or constrained female hypotheses. Studies of this population have also shown that that food supplementation can increase the likelihood of reneating after a successful first nest [26], hence double brooding is predicted to increase with food availability. Overall, we predicted that food supplementation would more strongly affect the three components of male reproductive success in the predicted directions in low-quality habitat than in high-quality habitat, and that adjustments in male reproductive investment would reflect the relative contributions of WPP, EPP and fledging two broods to overall male fitness in each habitat.

2. Material and methods

(a) Population monitoring

The black-throated blue warbler is a sexually dichromatic songbird that breeds in northern hardwood forests in eastern North America and migrates to the Greater Antilles for the non-breeding season [27]. We intensively monitored a marked population of black-throated blue warblers breeding in the 3160 ha Hubbard Brook Experimental Forest, Woodstock, New Hampshire, USA (43°56'N, 71°45'W). We collected data from May–August, 2009–2012 on three study plots established at low (250–350 m; 85 ha), mid (450–600 m; 65 ha) and high (750–850 m; 35 ha) elevations [24]. Males defend 1–4 ha territories, with the smallest territories in areas with the densest shrub layer [27]. All males hold territories and we have no evidence of floaters [28]. Pairs are socially monogamous with low levels of polygyny (5–10%) [29] and moderate levels of EPP (34%; 1995–1998) [30]. Females build open-cup nests in the understory vegetation, primarily in hobblebush (*Viburnum alnifolium*) [27]. Females lay one egg per day (mean and modal clutch size = 4, range = 2–5 eggs) [27]. Throughout the nest-building and egg-laying stages, males guard their fertile mates [31]. Males do not participate in incubation and rarely feed their social mate at the nest during the 12-day incubation stage, but they do assist females in provisioning nestlings [27]. Females will attempt second broods when breeding conditions are favourable [32].

In each breeding season, we captured, colour-banded and obtained blood samples from adults, and monitored nesting attempts by social parents (those defending territories,

incubating clutches and provisioning broods). At capture, we classified individuals as yearlings or older breeders using plumage characteristics [27]. We banded and collected blood samples from nestlings on the sixth day of the 9-day nestling stage. We mapped the boundaries of male territories throughout the breeding season relative to the 50 × 50 m grid that delimited each study plot. We found nests by following females carrying nest material and adults carrying food and by searching vegetation. We monitored nests every other day throughout all nest stages, and daily near hatch and fledge dates.

(b) Habitat quality

The study area is an intact northern hardwood forest dominated in the canopy by sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*) and yellow birch (*Betula alleghaniensis*), with red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*) increasing in abundance on the ridges [33]. The dominant vegetation in the understory is hobblebush, striped maple (*Acer pensylvanicum*) and saplings of canopy species. The abundance of Lepidoptera larvae, the primary food source and important predictor of territory quality for black-throated blue warblers [27], is positively correlated with elevation at Hubbard Brook [24,34]. Natural variation in food availability is similar between the mid and high elevations, relative to the low elevations [24,34]. Therefore, we grouped data by habitat quality according to elevation (low quality = low elevation plot, high quality = mid and high elevation plots).

(c) Food availability

We estimated an index of food availability for each territory based on knowledge of the diets of adult and nestling black-throated blue warblers and their common foraging substrates. Black-throated blue warblers are insectivorous during the breeding season, feeding extensively on adult and larval Lepidoptera taken mostly from the surfaces of leaves in the understory and sub-canopy [35,36], and deliver mostly Lepidoptera larvae to their nestlings [37]. The index of food availability was a function of caterpillar biomass per leaf and the estimated number of understory leaves per territory (see the electronic supplementary material for details). The index was based on visual caterpillar surveys in the shrub layer and understory leaf sampling [28,38]. We counted and measured caterpillars (mm) on striped maple and hobblebush leaves in the understory along plot-wide transect surveys conducted during four biweekly survey periods (1 June–31 July). Caterpillar measures were converted to wet biomass (mg) using length–mass regressions [39]. We estimated leaf abundances of each plant species on each territory with the Geospatial Modelling Environment [40] from interpolated surfaces of leaf density derived from extensive understory leaf sampling (0–3 m height) on each study plot and territory boundaries digitized in ArcGIS 10 [41]. Territory size represented the area males defended over the entire breeding season. We totalled transect estimates of caterpillar biomass (mg), averaged per-transect estimates and divided by 1000 leaves to obtain the mean caterpillar biomass per leaf for each plant species in each survey period. Then, we multiplied the two per-leaf quantities by leaf abundances within territories and summed each value. Hereafter, we refer to this index as ‘food availability’.

(d) Food supplementation experiment

After males were paired, we randomly assigned six to eight territories on each plot to the feeding treatment. We monitored 15–20 control territories per plot, which were separated from food-supplemented territories by one or more territories to reduce the probability of control males finding and using feeding trays. We began supplemental feeding on first nest attempts 2–3

days after the onset of incubation and delivered food daily throughout all nest stages and at each nest. We established feeding trays 1 m from nests and initially delivered 5 g (37 kJ) of waxmoth larvae (Lepidoptera: *Galleria mellonella*). We moved feeding trays 5 m from nests once pairs were documented feeding and increased the amount of food delivered to 7 g (52 kJ). We provided 5 g of mealworms (Coleoptera: *Tenebrio monitor*) that we had gut-loaded with cricket meal (Zilla Gut Load Cricket & Insect Food) to increase protein and calcium content, and 2 g of waxmoth larvae. We delivered 14 g (104 kJ) of food during the nestling stage (10 g of mealworms and 4 g of waxmoth larvae) because adults regularly fed from feeding trays themselves and fed larvae to their young. Additional details on the design of the feeding tray and feeding experiment are described elsewhere [25,26]. We fed 11 pairs in 2009, 21 pairs in 2010, 18 pairs in 2011 and 18 pairs in 2012, and we found no bias in the distribution of male age classes between food-supplemented and control treatments (Fisher’s exact test: $p = 0.57$).

(e) Genetic parentage analyses

We genotyped 900 nestlings from 271 broods and nearly all adults (more than 95%) in the study area at six highly polymorphic microsatellite loci and assigned paternity to offspring with known social mothers using CERVUS v. 3.0 [42]. We evaluated CERVUS assignments using likelihood scores and decision rules previously developed for this species [43] (see the electronic supplementary material for details). We excluded 15 broods from our analyses (47 nestlings) because we were unable to obtain blood samples from their social fathers. The combined probability of paternal exclusion for all loci was more than 99.9%.

From the paternity data, for each breeding male, we calculated three measures of reproductive success for each breeding season: within-pair young (total number of young sired in the nests of a male’s social mate), extrapair young (total number of young sired in the nests of other males) and total reproductive success (total number of young sired in the population). We determined the number of successful broods attempted during each season by each breeding male’s social mate. Although we find most nests within our study area, it is possible that some males sired young in nests located outside of these boundaries. Thus, extrapair young and total reproductive success may be underestimates, while within-pair young and the number of successful broods for focal males are accurate.

(f) Statistical analyses

We examined the relationship between food availability and WPP, EPP and fledging two broods. We constructed three generalized linear mixed models (GLMM) with a binomial error distribution and logit link function using ‘lme4’ in R v. 3.1.1 [44]. The binary response variable was WPP (equal to one if a male sired all young in his own nest and zero if he was cuckolded), EPP (whether a male sired extrapair young at a focal nest or not) or double brooding (whether a male fledged two broods or not). Each model included food availability, habitat quality (low and high) and their interaction as fixed effects standardized to have sample mean = 0 and sample variance = 1, year and male identity as random effects, and male age (yearling or older breeder) as a nuisance variable. In the paternity models, we used food availability from the survey period coinciding with the female’s fertile stage at the focal nest and included date of clutch completion to account for potential seasonal effects on extrapair mating. In the EPP model, for each focal nest with paternity data, we defined a candidate male as an individual present in the same year and with a territory on the same plot. This resulted in a dataset equal to the sum of candidate males across plots and years multiplied by the number of focal nests (5871 observations of unique focal nest/candidate male-year pairings). We included nest identity (random) in the

EPP model to account for repeated observations of the focal nest. We also included the Euclidean distance between nests (female locations) and the centroids of candidate males' territories (see the electronic supplementary material for details) and pairwise interactions to account for potential effects of breeding density on EPP. The model predicting double brooding was restricted to males that fledged young from their first nest, because those pairs had the opportunity to attempt a second brood. We included the date of fledge for first broods because birds that breed earlier are more likely to renest after a successful first nest [45]. We modelled the interaction between date of fledge and food availability to examine whether the effect of food on fledging two broods depends upon when first broods fledged. In this model, we used food availability averaged across the mid-June and early-July survey periods, corresponding to the initiation of second broods [27,32].

We examined the effect of food supplementation on the probability of males siring within-pair young, siring extrapair young and fledging two broods using GLMMs with a binomial error distribution and logit link function, and we examined differences in total reproductive success between food-supplemented and control males using a GLMM with a Poisson error distribution. Here, we defined WPP as a binary variable indicating whether a male sired at least one young in his social female's nest or sired none (complete cuckoldry or failed nest). For assessing the probability of WPP in food-supplemented males, we only considered nestlings from broods in which feeding was established prior to clutch initiation. We included in the dataset all males that had a social mate that attempted at least one nest (successful or failed) and/or that were assigned to at least one fledgling from the paternity analysis. All models included treatment, habitat quality and male age as fixed effects, and male identity as a random effect. We modelled the interaction between treatment and habitat to test whether the effects of food supplementation on each measure of reproductive success differed between habitats.

We investigated the relative contributions of WPP, EPP and fledging two broods to total reproductive success using a Poisson GLMM. We specified binary variables for WPP (whether a male sired all young as in the observational model), EPP or double brooding and their pairwise interactions as fixed effects, and included year and male identity as random effects. We combined data from control and food-supplemented males because results were similar when we ran separate analyses by treatment (electronic supplementary material, figure S1). We also examined the fixed effect of EPP on total reproductive success for each of the four habitat-treatment categories using separate Poisson GLMMs. We included male age (fixed) and identity (random) as nuisance variables.

3. Results

(a) Extrapair parentage

Out of the 900 genotyped nestlings, we assigned paternity to 821 (91.2%). The social father sired 505 (56.1%) and 316 (35.1%) were assigned to an extrapair sire. The remaining 79 offspring were not assigned to any sire, but were considered to be extrapair young because they mismatched their social father. The paternity analyses revealed that 395 (43.4%) offspring were extrapair young and 152 nests (55.6%) contained at least one nestling sired by an extrapair male. EPP rates were similar across the four years (electronic supplementary material, table S1).

(b) Effect of food availability on reproductive success

Among controls (i.e. territories without supplemental food), male differences in WPP, EPP and double brooding were related to food availability. Males on territories with high food availability during their social mate's fertile stage had

higher WPP (table 1) and this effect was greatest in low-quality habitat (food availability \times habitat; table 1). The probability of a male siring extrapair young in a nest decreased as food availability increased (table 1) and decreased as distance from a female's nest increased (food availability \times distance; table 1). The probability of fledging two broods significantly declined with the date first broods fledged; the later the first brood, the less likely that a second brood would be fledged during that year (table 1). However, males on territories with higher mid-season food availability were significantly more likely to have social mates that produced two broods late in the breeding season relative to males on territories with less food (food availability \times date of fledge; table 1).

(c) Effect of food supplementation on reproductive success

Food-supplemented males had significantly higher total reproductive success than did control males (table 2), but some of the effects of food supplementation on fitness components differed between habitats (table 2 and figure 1). In both habitats, food supplementation significantly increased WPP. Food supplementation in low-quality habitat significantly increased the likelihood of fledging two broods, but significantly reduced EPP (treatment \times habitat; table 2). The total effect of food supplementation was to significantly increase total reproductive success for males in both habitats (table 2), which ranged from 0 to 14 genetic young (mean \pm s.e. = 2.5 ± 0.1). The food supplementation experiment appears to have had similar effects on components of male reproductive success, as did natural variation in food availability.

(d) Fitness returns from male reproductive success

Relative success by males in behaviours that influenced WPP, EPP and successful reneating after first nests contributed to differences in fitness returns (figure 2a; electronic supplementary material, figure S1). Total reproductive success was greater for males that were not cuckolded (partial or complete) (GLMM: $z = 7.73$, $p < 0.001$) or that sired extrapair young (GLMM: $z = 8.42$, $p < 0.001$). Males that were not cuckolded and sired extrapair young had higher expected total reproductive success than in either strategy alone, but less than the sum of the two strategies (WPP \times EPP: GLMM: $z = -4.29$, $p < 0.001$). Fledging two broods increased total reproductive success (double brooding: GLMM: $z = 6.44$, $p < 0.001$) and the interaction between WPP and double brooding was not significant (GLMM: $z = -1.70$, $p = 0.09$). Males that fledged two broods and sired extrapair young had higher expected total reproductive success than in either strategy alone, but less than the sum of the two strategies (EPP \times double brooding: GLMM: $z = -3.34$, $p < 0.001$). We found no significant interaction between WPP, EPP and double brooding (GLMM: $z = 1.84$, $p = 0.07$). No control or food-supplemented males in low-quality habitat that sired within-pair young in two broods also sired extrapair young, which contrasts with some males in high-quality habitat (electronic supplementary material, table S2 [DB + WPP + EPP]). Males that sired extrapair young had significantly higher total reproductive success than males that did not gain EPP across habitats and treatments, although the sample size for 'low quality-fed' was low (electronic supplementary material, table S3; figure 2b).

Table 1. Fixed effects from GLMMs examining the effects of natural variation in food availability on WPP (whether a male sired all of the young in his own nest or was cuckolded), EPP (whether a male sired extra-pair of the young at a focal nest or not) and double brooding (whether a male fledged two broods or not) in black-throated blue warblers. Significant terms are in italic.

model term	WPP			EPP			double brooding		
	$\beta \pm \text{s.e.}$	<i>z</i>	<i>p</i>	$\beta \pm \text{s.e.}$	<i>z</i>	<i>p</i>	$\beta \pm \text{s.e.}$	<i>z</i>	<i>P</i>
	<i>n = 228 nests</i>			<i>n = 5871 focal nest/candidate male-year pairings</i>			<i>n = 157 males</i>		
food availability	0.58 ± 0.25	2.34	0.020	-0.72 ± 0.28	-2.58	0.010	-0.51 ± 0.80	-0.64	0.52
habitat (low quality)	0.15 ± 0.21	0.73	0.46	0.11 ± 0.11	1.03	0.31	-1.37 ± 0.99	-1.38	0.17
food availability × habitat	0.94 ± 0.48	1.96	0.050	0.02 ± 0.11	0.14	0.89	-3.01 ± 1.89	-1.59	0.11
male age (yearling)	-0.01 ± 0.14	-0.04	0.97	0.07 ± 0.18	0.40	0.69	-0.76 ± 0.32	-2.38	0.018
date of clutch completion	-0.06 ± 0.14	-0.43	0.67	-0.02 ± 0.11	-0.22	0.83			
date of fledge – first brood							-2.48 ± 0.71	-3.52	<0.001
food availability × date of fledge							0.63 ± 0.30	2.07	0.038
distance				-1.31 ± 0.17	-7.62	<0.001			
food availability × distance				-0.59 ± 0.22	-2.73	0.006			
distance × male age				0.64 ± 0.15	4.23	>			

Table 2. Fixed effects from GLMMs examining the effects of food supplementation and habitat quality on the probability of males siring any within-pair young (WPP), siring extrapair young (EPP), fledging two broods (double brooding) and total reproductive success in black-throated blue warblers. Significant terms are in *italic*.

model term	WPP			EPP			double brooding			total reproductive success		
	$\beta \pm \text{s.e.}$	<i>z</i>	<i>p</i>	$\beta \pm \text{s.e.}$	<i>z</i>	<i>p</i>	$\beta \pm \text{s.e.}$	<i>z</i>	<i>p</i>	$\beta \pm \text{s.e.}$	<i>z</i>	<i>p</i>
treatment (fed)	1.32 ± 0.41	3.19	0.007	0.21 ± 0.33	0.62	0.54	-0.40 ± 0.48	-0.85	0.40	0.32 ± 0.13	2.41	0.016
habitat (low quality)	-0.16 ± 0.33	-0.49	0.62	-0.18 ± 0.31	-0.58	0.56	-1.10 ± 0.77	-1.42	0.16	-0.25 ± 0.15	-1.69	0.09
treatment × habitat	0.20 ± 0.79	0.26	0.80	-1.69 ± 0.87	-1.94	0.053	3.59 ± 1.06	3.41	<0.007	0.03 ± 0.29	0.11	0.92
male age (yearling)	-0.12 ± 0.25	-0.48	0.63	-0.71 ± 0.23	-3.12	0.002	-1.16 ± 0.38	-3.09	0.002	-0.38 ± 0.10	-3.81	<0.001

4. Discussion

(a) Habitat-dependent reproductive success

We demonstrate that food availability—one key aspect of habitat quality—had strong effects on mating patterns and variability in total reproductive success among male black-throated blue warblers. Environmental effects on extrapair mating have traditionally been ascribed to aspects of the social environment often correlated with habitat quality [12–15]. For example, black-throated blue warblers occur at higher breeding densities in higher quality habitat [46], and habitat quality tends to increase from low to high elevations at Hubbard Brook [24]. We designed our experiment to separate the effects of food availability on patterns in extrapair mating across the distribution of habitat quality. Food availability affected three components of male reproductive success: WPP, EPP and fledging two broods. We found that high natural food availability was associated with higher WPP and fledging two broods late in the breeding season, but lower EPP. Food supplementation increased total reproductive success for males in habitats that differed in food availability, but specific patterns of reproductive investment depended on habitat quality (figure 1 and table 2). Food-supplemented males in low-quality habitat were more likely to sire within-pair young and to fledge two broods, leading to higher total reproductive success, but were less likely to sire extrapair young than control males. Food-supplemented males in high-quality habitat were also more likely to sire within-pair young than controls. In sum, the results of this study demonstrate that food availability can affect individual variation in WPP, EPP and fledging two broods by influencing either male reproductive trade-offs and/or female reproductive decisions. Our findings are consistent with the predictions of the constrained male hypothesis (trade-off between WPP and EPP), but do not support the environmental constraints hypothesis (higher WPP and EPP), paternal trade-offs hypothesis (higher EPP) or constrained female hypothesis (lower WPP). Below we discuss potential behavioural mechanisms and the adaptive significance of changes in extrapair mating and reneating after a successful first nest in response to habitat quality.

(b) Potential behavioural mechanisms

The ‘constrained male hypothesis’ proposes that food availability mediates the allocation of male effort to different mating behaviours owing to conflicting demands of mate guarding against cuckoldry versus obtaining additional matings [13]. At Hubbard Brook, black-throated blue warbler males effectively prevent cuckoldry by guarding their social mates closely during egg laying [31]. Males that also sire extrapair young can substantially increase their reproductive success above population mean levels (figure 2; see also [30]). We previously showed that food-supplemented males in low-quality habitat appeared to shift to more mate guarding or territorial defence (another form of mate guarding) at the expense of extrapair mating effort during their social mate’s fertile stage [25]. The WPP and EPP rates presented here support these previous results. Males on food-abundant territories favoured investment in behaviours that increased their paternity assurance and increased WPP over pursuing extrapair copulations. These EPP patterns are unlikely to be affected by inadequate sampling because we sampled more

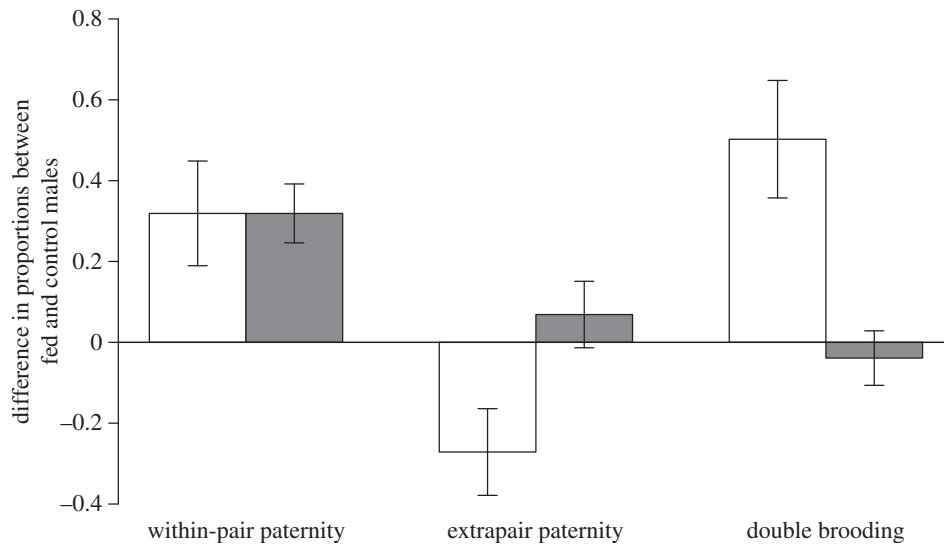


Figure 1. The differences in the proportions of food-supplemented versus control male black-throated blue warblers that sired any young on their territory (WPP), sired extrapair young (EPP) and fledged two broods (double brooded) by habitat quality. Bars show the differences \pm s.e. in the proportions of food-supplemented 'fed' males relative to control males (n = males; low quality: fed = 16, control = 58; high quality: fed = 45, control = 226). Significance assessed with binomial GLMMs after accounting for male identity and age (table 2). Unfilled bars denote low quality and filled bars denote high quality.

than 95% of the study population each year and we have no evidence of floaters [28]. Furthermore, our previous results showed that food-supplemented males had above-average body mass during their social mate's fertile stage relative to controls [25]. Mate guarding is energetically costly [47], and maintaining more energetic reserves probably improved males' ability to effectively guard their social mates, possibly while foraging together. These findings support the hypothesis that food availability mediates habitat-dependent shifts in allocation to mate guarding from seeking extrapair copulations and suggests that mate guarding depends on a male's energetic state.

The 'paternal trade-offs hypothesis' predicts that males on territories with abundant resources can afford to pursue extrapair copulations over competing parental behaviours because they are less energetically limited and suffer fewer reproductive costs from reduced parental effort (e.g. nestling mortality) [13,48]. When food is abundant, less effort is required by males to feed their offspring if females compensate for reduced male participation in feeding [49,50]. We previously showed that food-supplemented females in low-quality habitat increased their nestling-feeding rates, amount of food delivered and time spent at the nest relative to control females [25]. Males did not adjust their parental effort in response to food supplementation [25], although males in high-quality habitat were more efficient at provisioning (e.g. fewer trips to the nest, larger food loads per trip [25]). Moreover, food-supplemented males did not invest greater effort into song rate, assumed to be associated with extrapair mate attraction, while feeding their offspring [25]. The parentage results reported here support these results, as food-supplemented males in low-quality habitat were less, rather than more, likely to sire extrapair young than control males. We found no evidence that the value of male parental care decreased with increasing habitat quality and led to more time and energy to pursue extrapair copulations. Consistent with these findings, most studies have failed to find direct evidence supporting a trade-off between mating effort and parental effort during the nestling-feeding period [48,51], although a few have examined the factors

that might mediate a trade-off between mating and parental effort.

Males and females on territories with high mid-season food availability were buffered from the adverse effects of attempting second broods late in the breeding season. In species with multiple broods, males often provide substantial parental care to fledglings once their social mate initiates a second clutch [52]. This could reduce the time and energy available for males to pursue extrapair copulations, as well as limit their effectiveness at guarding their social mates against cuckoldry in their second broods [13]. Despite the importance of post-fledging care, few studies have quantified male parental care of fledglings, particularly in songbirds. Moreover, a full evaluation of the effects of habitat quality and food availability on these complex trade-offs would require examining how food influences when males are more likely to sire extrapair young relative to their social mate's nest stage [4,53,54]. The influence of food availability on temporal patterns in extrapair mating would reveal how habitat quality influences trade-offs to shape male reproductive investment strategies.

We found no support for the constrained female hypothesis, which predicts that females on high-quality territories are more likely to solicit extrapair copulations (resulting in lower WPP) because they have less to lose if their social mate withdraws parental care [16]. We found the opposite pattern: food-supplemented males and those with naturally high food availability were less, rather than more, likely to be cuckolded (high WPP). These results are consistent with most studies that have experimentally increased food availability ([15,18–20], but see [17]). One benefit of female faithfulness could be increased parental care by males [55], and we do have correlative evidence that older male black-throated blue warblers reduce parental care when cuckolded [56]. Male parental care was not associated with food supplementation, although food-supplemented females did provision more [25]. A potential explanation for the observed WPP patterns is that females were less likely to cuckold their social mates when supplemental feeding improved both the perceived quality of their social mates and resource availability on their territories. This is the

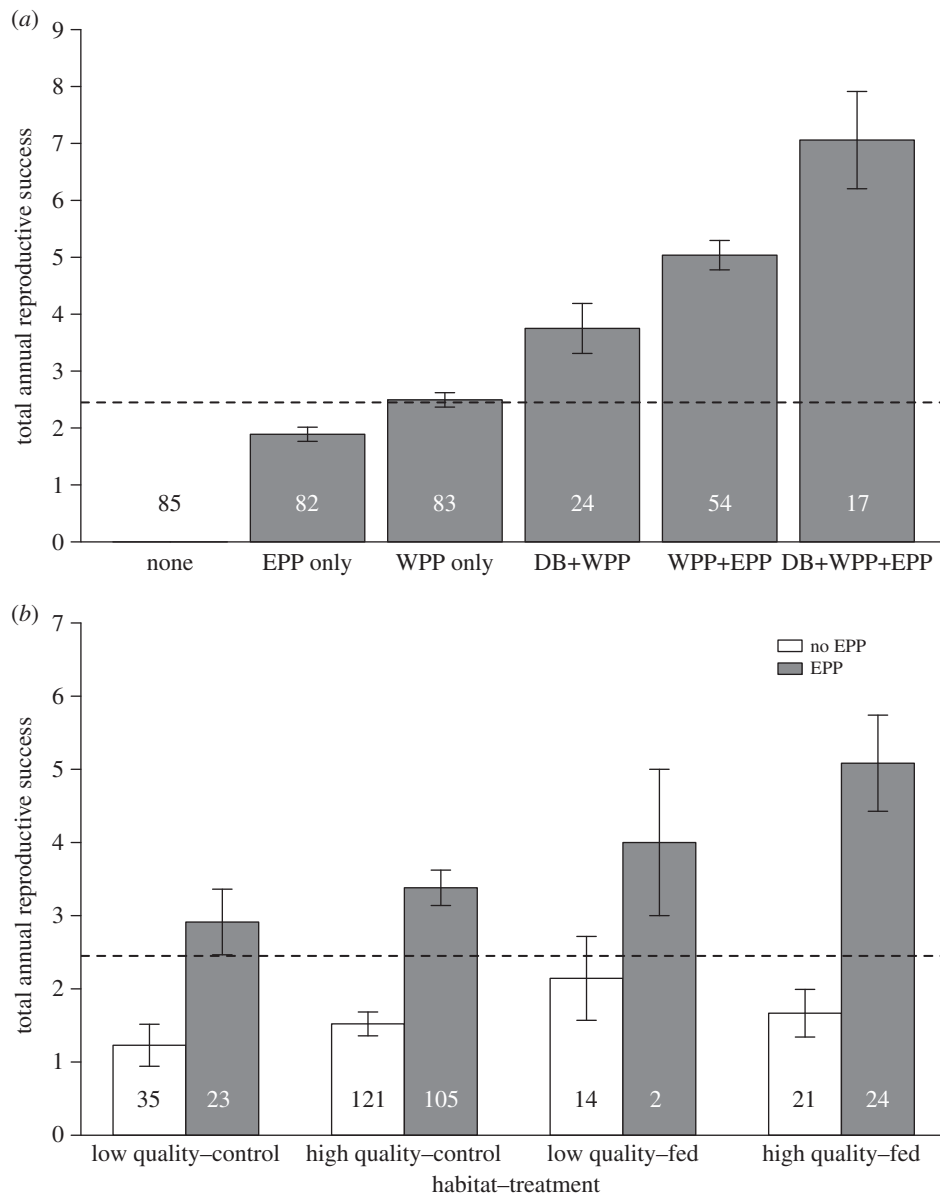


Figure 2. (a) Relative contribution of within-pair paternity (WPP), extrapair paternity (EPP) and fledging two broods (double brooding, DB) on total reproductive success for all males pooled across treatments and habitats (mean \pm s.e.). Categories include males that were: unsuccessful (none), single brooded, lost WPP and gained EPP (EPP only), single brooded and gained WPP (WPP only), double brooded and gained WPP (DB + WPP), single brooded, gained WPP and EPP (WPP + EPP) and double brooded, gained WPP and EPP (DB + WPP + EPP). (b) Comparison of total reproductive success (mean \pm s.e.) for males that gained EPP or not by habitat and treatment. Significance was assessed with Poisson GLMMs after accounting for male identity and age (electronic supplementary material, table S3). The dashed lines indicate the mean total annual reproductive success, 2009–2012. Samples sizes are given at the base of the bars.

mechanism used to explain higher WPP in food-supplemented broods in other passerines [15,20]. Females on low-quality territories are expected to be receptive to neighbouring extrapair males if they gain access to additional food resources to feed nestlings and fledglings [57].

An alternative hypothesis consistent with our results is that food availability influenced the foraging movements of males and females involved in extrapair mating interactions [58], which we call the ‘foraging encounter hypothesis’. If individuals on low-quality territories had to travel further distances to forage, they would have had a greater opportunity to encounter potential extrapair mates than individuals that remained within or closer to their territories to forage [15,18,19]. Thus, a male with a high-quality territory would have higher WPP, as their social female encounters fewer males, and lower EPP, as the male encounters fewer females. Recent advances in automated radiotelemetry have enabled researchers to monitor the activity and extraterritorial forays

of both males and females [59] and could be used in combination with estimates of territory quality to disentangle the foraging encounter and constrained male hypotheses.

(c) Adaptive significance of male reproductive investment

Our results indicate that males nearly always benefit from pursuing extrapair copulations (figure 2b). Many males at Hubbard Brook only achieved reproductive success through EPP (24%) because of high rates of nest predation in the population (up to 42%, [27]) and/or because they were completely cuckolded (4%). Some males that sired at least one extrapair young did sire within-pair young (21%), although 9% were partially cuckolded. These results suggest that males should be under strong selection to seek extrapair copulations to increase their total reproductive success. Nevertheless, males in high-quality habitat appeared to

shift activities towards achieving within-pair success at the expense of extrapair success.

Theory predicts that if environmental constraints, such as habitat quality, affect the costs of male reproductive behaviours, then the relative investment in within- versus extrapair mating should reflect the relative contribution of each to total reproductive success [13]. Male reproductive investment in WPP, at the expense of EPP, under reduced food limitation, may at first seem maladaptive. However, males nesting in high-quality habitat were more likely to gain reproductive success via reneating after a successful first brood (figure 2a; [26,37,45]). In species that attempt more than one brood, WPP can contribute more to total reproductive success than EPP [13,60,61]. Double brooding often has more of an impact on the variance in male reproductive success (i.e. measure of the strength of selection) than does EPP [61]. Indeed, the contribution of EPP to male variance in reproductive success is lower than the contribution of WPP at Hubbard Brook [30], in part because EPP is not biased towards a few successful males [30] but only one-third of pairs fledge two broods [45]. Thus, black-throated blue warbler males achieved higher reproductive success when food constraints were reduced, by investing in behaviours that increased WPP when the probability of fledging two broods was high.

5. Conclusion

We have demonstrated that food availability affects three components of male reproductive success: WPP, EPP and successfully fledging two broods. Our results indicate that male black-throated blue warblers increase reproductive success by allocating more to behaviours that reduce cuckoldry, rather than pursuing extrapair copulations, especially when habitat quality increases the likelihood of fledging two broods. This study highlights the importance of considering environmental factors related to habitat quality in addition to socio-ecological factors when seeking to explain extrapair

mating patterns and male variance in total reproductive success. The extrapair mating patterns we observed in response to food availability suggest that both male and female reproductive investment in extrapair mating is affected by habitat quality. Further investigation of the role of habitat quality in the reproductive behaviours of socially monogamous species will clarify how female preference selects for male traits that affect mating and fledging success. Such research will also elucidate how environmental change may alter how individuals allocate their resources and the selective environment that drives variation in male mating success.

Ethics statement. We followed protocols approved by our Institutional Animal Care and Use Committees to capture, handle, mark and sample black-throated blue warblers (Cornell University, 2009–0133; Smithsonian National Zoological Park, 08–11, 12–12; Wellesley College, 1304). All work was performed under scientific permits from the US Geological Survey Bird Banding Lab (22665) and the New Hampshire Department of Fish and Game (MB207492-1). All procedures performed in this study were in accordance with the ASAB/ABS 'Guidelines for the treatment of animals in behavioural research'. Sampling and processing had no discernable negative impacts on individuals.

Data accessibility. Data are available via the Dryad data repository: doi:10.5061/dryad.t34m9.

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