

Environmental mismatch results in emergence of cooperative behavior in a passerine bird

Ahva L. Potticary¹  · Renée A. Duckworth¹

Received: 27 November 2017 / Accepted: 28 February 2018
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Abstract A major problem in the evolution of maternal effects is explaining the origin and persistence of maternally induced phenotypes that lower offspring fitness. Recent work focuses on the relative importance of maternal and offspring selective environments and the mismatch between them. However, an alternative approach is to directly study the origin and performance of offspring phenotypes resulting from mismatch. Here, we capitalize on a detailed understanding of the ecological contexts that provide both the cue and the functional context for expression of maternally induced offspring phenotypes to investigate the consequences of environmental mismatch. In western bluebirds, adaptive integration of offspring dispersal and aggression is induced by maternal competition over nest cavities. When nest cavities are locally abundant, mothers produce nonaggressive offspring that remain in their natal population, and when nest cavities are scarce, mothers produce aggressive dispersers. However, a few offspring neither disperse nor breed locally, instead helping at their parent's nest, and as a result these offspring have unusually low fitness. Here, we investigate whether females produce helpers to increase their own fitness, or whether helpers result from a mismatch between the cues mothers experience during offspring production and the breeding environment that helpers later encounter. We found that producing helpers does not enhance maternal fitness. Instead, we show that helpers, which were the least aggressive of all returning sons in the population, were most common when population density increased from the time sons were produced to the time of their reproductive maturity, suggesting that the helper phenotype emerges when cues of resource competition during offspring development do not match the actual level of competition that offspring experience. Thus, environmental mismatch might explain the puzzling persistence of maternally induced phenotypes that decrease offspring fitness.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10682-018-9933-8>) contains supplementary material, which is available to authorized users.

✉ Ahva L. Potticary
apotticary@email.arizona.edu

¹ Department of Ecology and Evolutionary Biology, University of Arizona, 1041 E. Lowell St, Tucson, AZ 85721, USA

Keywords Predictive adaptive response · Maternally induced phenotype · Competition · Aggression

Introduction

Maternal influence on an offspring's phenotype is one of the most ubiquitous and important sources of organismal variation. From plants to vertebrates, females affect offspring traits by transferring nutrients, hormones and antibodies to the growing embryo (Badyaev 2005; Marshall and Uller 2007; Rossiter 1998). Yet, it is often difficult to distinguish between a passive maternal effect that results from the overlap between generations versus an active maternal strategy that evolved to induce variation in offspring phenotypes in response to changes in environmental conditions (Badyaev 2005). Such a distinction is particularly difficult in cases where maternal influence on traits results in low offspring fitness. In such cases, it is often assumed that mechanisms to buffer offspring from maternal influence have either not had time to evolve, or that there are constraints that prevent the evolution of such buffering (Duckworth 2009). However, the influence of maternal effects on offspring fitness by itself is not enough to conclude that these effects are maladaptive, because selection on mothers can lead to adaptive maternal strategies that benefit the mother while reducing individual offspring fitness (Zeh and Zeh 2000; Crespi and Semeniuk 2004; Uller 2008). Moreover, unexpected mismatches between the cues that induce an adaptive maternal effect and the environment offspring later experience can lead to seemingly maladaptive expression of maternally induced traits.

The evolution of maternal effects that adaptively alter offspring phenotype requires females to have cues during offspring development that reliably predict future environmental conditions (Uller 2008; Marshall and Uller 2007; Burgess and Marshall 2014). Thus, for an adaptive maternal effect to evolve, environmental mismatch should be rare, because a high occurrence would suggest that environmental cues are not predictive of future conditions. However, every natural system experiences environmental stochasticity that can undermine the concordance between cues that induce an adaptive maternal effect and the environment later experienced by offspring. Understanding how such stochastic events might influence the evolution of both maternal and offspring strategies is thus important for understanding the evolution of adaptive maternal influences on offspring phenotype. Moreover, the dynamics of environmental mismatch are important to understand because the idea that mismatch between maternal and offspring environments explains maladaptive offspring phenotypes has received much attention in studies of human disease risk (e.g., Hales and Barker 1992; Gluckman et al. 2005; Godfrey et al. 2007). Finally, the dynamics of environmental mismatch have important implications for how species may respond to global climate change, in which mismatches between environmental cues and previously adaptive phenotypes are expected to become more common.

However, distinguishing environmental mismatch from a maternal effect that increases maternal fitness at the expense of offspring fitness is difficult because it requires a system with a well-characterized maternal effect, where the cue that induces the maternal effect is known so that mismatches can be identified. It also requires comparing the phenotype and fitness of offspring produced in conditions that both “match” or “mismatch” the environment experienced later in life (Sheriff and Love 2013).

Western bluebirds (*Sialia mexicana*) provide a unique opportunity to distinguish between these possibilities because this species has a well-documented, egg-based adaptive

maternal effect that influences offspring aggression and dispersal (Fig. 1; Duckworth et al. 2015). Moreover, the maternal effect is known to be induced by competition over nest cavities—the main limiting breeding resource in this species (for further species natural history, see Guinan et al. 2000). Females breeding on territories with few nest cavities experience heightened competition and produce aggressive sons that disperse and are able to compete for and acquire territories on their own, whereas females on territories with extra nest cavities experience less competition, produce less aggressive sons that remain in their natal population and acquire territories by budding off their parent's territory (Duckworth 2008; Aguillon and Duckworth 2015). Previous work has shown that this maternal effect is adaptive, as nonaggressive males generally have high fitness when they can breed adjacent to family members, whereas aggressive, dispersive males perform better in lower density populations (Duckworth 2006b, 2008). Females influence offspring phenotype by altering where males are produced in the lay order of the eggs in a clutch. Specifically, clutches where sons are produced in early positions have higher levels of androgens compared to clutches where sons are produced later (Fig. 1), producing an organizational effect that establishes lifetime expression of aggression and dispersal propensity (Duckworth et al. 2015). Thus, the maternal effect can be directly linked to environmental conditions during embryonic development, and the degree of match or mismatch between the maternal and offspring environments can be assessed by tracking changes in the competitive environment across years.

Moreover, in this system, there is reason to suspect the maternal effect on aggression and dispersal also influences a rarely expressed male offspring strategy of helping at the nest. Western bluebirds are facultative cooperative breeders, with a small proportion of breeding pairs having male helpers at the nest (3–7%; Dickinson et al. 1996; Duckworth and Badyaev 2007). However, prior research has shown that helpers have lower fitness compared to sons that breed independently in their first year (Dickinson and Akre

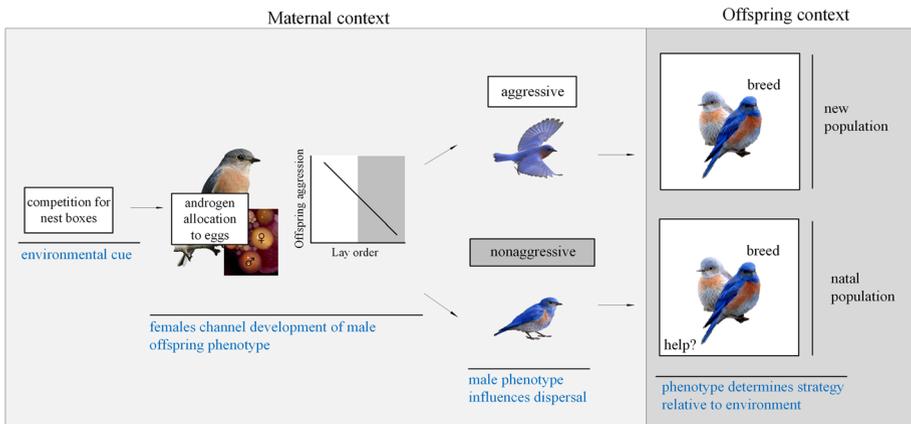


Fig. 1 Mothers that experience high levels of competition for their nest boxes allocate more androgens to their clutch and produce sons in earlier positions in the lay order compared to females that experience low competition. Offspring lay order is correlated with aggression in adulthood such that sons produced early have higher aggression as adults compared to sons produced late in the lay order. This maternally induced aggressive phenotype determines the dispersal decision of sons with nonaggressive males remaining philopatric and generally breeding on territories adjacent to parents, whereas aggressive males disperse and usually breed in a new population (see text for details). The relationship between this known maternal effect and helping behavior is unknown, and is the focus of this study

1998; Dickinson et al. 1996). Generally, expression of cooperative breeding behavior is thought to result from resource limitation and dispersal costs experienced by offspring (Emlen 1982; Koenig and Dickinson 2004). For this reason, it is unclear why the helper strategy persists in this system, given that the adaptive maternal effect on dispersal and aggression reduces these costs by producing males that are matched to the environment where they will perform best. There are two possibilities. First, because females generally receive the highest benefit from helpers relative to other group members (Koenig and Dickinson 2004; Russell and Lummaa 2009), it is possible that producing helpers increases female fitness by reducing the costs of reproduction (Russell and Lummaa 2009). If so, then maternal production of helpers should increase female fitness, even if it leads to a low fitness phenotype for some male offspring. Alternatively, production of helpers may not be adaptive for females, but may instead emerge occasionally as the result of rare, stochastic events. Such events could undermine predictability of the cues that induce the maternal effect, but may be rare enough that they do not substantially alter selection on the maternal effect overall. In this scenario, helpers would be non-aggressive sons that stay and are “mismatched” to their environment because females have a cue of low competition and produce nonaggressive sons, but competition unexpectedly increases by the time these sons are ready to breed on their own, making helping their only option.

Here, we capitalize on a 14-year dataset in which we have full information on annual variation in resource availability (measured as nest box availability), population density, aggressive phenotype, cooperative behavior and lifetime fitness of a population of western bluebirds to test these alternative hypotheses. We compare changes in competitive environment across years to assess the extent of environmental mismatch from the time of offspring production to the time of offspring reproductive maturity. Specifically, we use changes in resource availability and population density across years as measures of the competitive environment, as both of these have been shown to be cues for inducing the maternal effect (Duckworth et al. 2015). Moreover, aggression is also an important contributor to competitive environment as aggressive bluebirds acquire territories with more nest cavities (Duckworth 2006a), and thus high population aggression may alter resource availability behaviorally even in the absence of high population density. We combine these measures of competitive environment with lifetime fitness measures for both mothers and sons to test alternative predictions of the mismatch versus maternal strategy hypotheses. Specifically, if males help as a result of mismatch, the fitness benefits of both being and producing a helper should be negligible, and helpers should be most prevalent in years when the environment becomes more competitive from the time of offspring production to the time of offspring reproductive maturity. Alternatively, if production of helpers is a maternal strategy to increase female fitness, then the prevalence of helpers should not be related to changes in competitive environment across years, helpers should most frequently help their mother, and females that produce helpers should have higher fitness than females that do not.

Both the mismatch and maternal strategy hypotheses assume that helping behavior of sons is influenced by the known egg-based maternal effect on aggression and dispersal. This is a reasonable assumption, given that the maternal effect increases the probability that sons will stay in their natal population and thus have the opportunity help family members. We explicitly test this assumption by investigating whether there is a correlation between helping behavior and aggression and whether helpers are more often from eggs laid late in the laying order.

Materials and methods

General methods and field site

Western bluebirds are an insectivorous passerine birds species that live approximately 2–3 years (Keyser et al. 2004; unpublished data). Data were collected from a population of western bluebirds in western Montana (*see* Duckworth 2009, for a detailed description of field site) during the 2002–2015 breeding seasons (mid-April to mid-August). All breeding adults in the population were captured to mark them with a unique color band combination for individual recognition, to collect a blood sample for paternity analyses, and to take standard morphological measurements. Nest boxes were visited at least once a week to monitor nest progress, mark eggs, and to band, bleed, and measure nestlings. Nestlings were sexed using plumage differences that appear at 15 days of age, at which time male nestlings were banded with unique combination of color bands for later recognition. Female offspring are more dispersive and rarely return to the site, thus females were only banded with an aluminum band and a single color band that varied depending on year of banding.

Philopatric males were defined as males who were banded as nestlings on the study site and returned to breed at the site as adults. A breeding pair was defined as having a helper if more than one male was observed consistently with them, provisioning the nest and/or defending the nest box. Western bluebirds only have male helpers and the maximum number of helpers observed at any nest was one. Juvenile helpers (males helping within the same breeding season they were born) were excluded from analyses because they have not yet made the decision to either disperse or forego breeding and therefore could not be definitively categorized as a cooperative breeder.

Relationship between maternal effect and helping behavior

To address the assumption that helping behavior is influenced by the maternal effect, we determined offspring lay order by marking eggs as they were laid and linking lay to hatch order. When exact lay order was not known, we used size hierarchies of nestlings, as previous work has shown it is a good proxy for both lay and hatch order (Duckworth 2009; Duckworth et al. 2015). Given that we only had lay order for a subset of helpers in the focal population, to increase sample size we included lay order data for helpers from other populations that have been shown previously to have the same maternal effect ($n = 10$ from focal population, $n = 3$ from nearby experimental populations; Duckworth et al. 2015).

We measured aggression of all breeding western bluebirds at the site using standardized and experimentally verified behavioral assays that simulate a territorial intrusion by a heterospecific competitor for nest boxes, the tree swallow (*Tachycineta bicolor*; *see* Duckworth 2006b for full details on aggression trial protocol). Western bluebird aggressive response toward a heterospecific competitor is highly correlated with response toward a conspecific competitor (Duckworth 2006b), is highly repeatable both within and across breeding stages as well as across a male's life, and is related to resource holding potential (Duckworth 2006a, b; Duckworth and Sockman 2012). Tree swallows were used because they are the most frequent nest site competitor of bluebirds (Duckworth 2006b). Briefly, to conduct aggression trials, we placed a live tree swallow in a wire cage at a focal male's nest box and recorded responses concurrently by an observer and a camera. During the

2 min trials, observers noted the number of times an individual flew by, attacked, and hovered and aggression scores were assigned according to the following scale: (1) no aggressive behaviors, (2) hovering or flying by 1–5 times and 0 attacks, (3) hovering or flying by more than 5 times and 0 attacks, (4) 1–5 attacks, (5) 6–9 attacks, and (6) 10 or more attacks. Counts of these behaviors by the real time observer were independently verified by a separate observer from the video. The measurement error due to variation between these two observers was assessed with a subsample of 10 individuals that had been measured in the field in real time and by an observer in the lab from video using one-way ANOVA. The effect of inter-observer measurement error was $<2\%$ of the individual identity effect (mean squares 0.11 vs. 8.1), and was therefore negligible. To control for the possibility that helpers behave differently when helping to raise the offspring of relatives and to compare helper and non-helper aggression scores in the same context, we only used helper aggression scores from aggression assays conducted at a helper's first nesting attempt where he was the primary breeding male.

Direct and indirect fitness measures

Annual and lifetime fitness measures for 449 individuals (235 females, 214 philopatric sons) were calculated as the number of genetic offspring that survived at least 2 weeks post-fledge, which is when most offspring become independent. We determined the relatedness of focal individuals to offspring fledged from their social nest by genotyping nestlings and adults at four or five polymorphic microsatellite loci (either Cuu 02, Cuu 04, Ssi 8–19 and Ssi 9–32 or Smex 1, 6, 8, 10 and 14; *see* Duckworth 2006b; Ferree et al. 2008 for details). Parentage was assessed for each nest, every year of the study, by manually comparing genotypes of offspring and the attending adults. All females matched their offspring's genotype, and the attending male was excluded as the father if one or more loci did not match. Extrapair offspring were assigned to a sire if their genotypes matched completely and there was no other male in the population with a matching genotype. In cases where there were two males that matched the genotype of an extrapair nestling, we genotyped with additional markers (Smex 2, 4, 5, 7, 9, 11, and 13; Ferree et al. 2008) to assign paternity. Out of 1544 offspring, 14.96% were extrapair and over 83% of these extrapair offspring were assigned to a sire. Divorce among pair mates is uncommon across years and rarely happens within season (Guinan et al. 2000).

Helper lifetime fitness and yearly reproductive success were calculated as the sum of indirect and direct fitness. Helpers typically only help in their first year and usually breed independently in subsequent years. Thus, helper direct fitness was defined as the number of genetic offspring fledged from nests where they bred independently or produced extra-pair offspring. Importantly, helpers do not sire offspring in nests they help at (*see* "Results" below). Indirect fitness was calculated based on the number of offspring fledged from nests males helped at. For this measure, we accounted for the relationship of the helper to the breeders at the nest using a multi-generational pedigree for the population that was constructed based on genetic relationships among individuals (Duckworth and Kruuk 2009). For example, if helpers assisting their biological parents were feeding full siblings, indirect fitness was calculated as 0.5 per nestling in the nest (Dickinson 2004). However, since divorce, adult mortality and extra-pair paternity are frequent in this system, helper-nestling relatedness was calculated on a per-nestling basis using the pedigree data to account for differential relatedness of the helper to each offspring they helped to raise (per Dickinson 2004).

Measuring population level competitive environment to assess mismatch

The study site is an island of bluebird habitat surrounded by dense forest to the west and a housing development on the south, east and north, allowing us to reliably quantify all breeding adults and nest boxes at the site each year. Annual population density was determined as the number of individuals residing and breeding in the population per hectare. To quantify the area of suitable bluebird habitat (defined as open meadow with no more than 50% tree cover and at least one nest box), maps with GPS locations of nest boxes were made using Google Earth and polygons were drawn to encompass areas of contiguous bluebird habitat. For nest boxes on the edge of suitable habitat, we extended the polygons 300 m from the nest box as this encompasses the maximum bluebird territory size (Duckworth 2013). The areas of polygons were measured in hectares and the numbers of actively nesting western bluebird pairs per polygon were counted. Densities were local measurements in that they only included contiguous bluebird habitat and there were multiple distinct polygons in the population. Overall population density was calculated as the mean density of all polygons for each year.

We determined resource availability, measured as nest box availability, using the same polygons that were used for density. Nest box availability at the population-level was calculated as the number of unoccupied nest boxes relative to the number of individuals in the population. Finally, we calculated population level aggression by averaging scores of all breeding individuals in the population for each year of the study. To assess the extent of environmental match or mismatch, we determined the change across years in resource availability, population density and aggression.

Statistical analyses

All statistical analyses were performed using SAS (v. 9.4). Results are \pm standard error (SE) unless otherwise indicated. Because fitness data were not normally distributed, we used two-sample two-sided Wilcoxon Rank Sum to compare lifetime fitness of males who were helpers versus philopatric males who bred independently in their first year and to compare lifetime fitness of females who produced versus did not produce helpers. To determine whether presence of a helper directly impacted female fitness within a particular breeding season, we analyzed reproductive success in two ways. First, to account for the fact that some females bred in multiple years, we used a linear mixed model with female identifier as a random effect. We examined residual plots to verify assumption of homogeneity of variance. Second, to account for the fact that the same female may be assisted by helpers in some years but not in others, average reproductive success in years when females did versus did not have helpers was analyzed using a paired *t* test. We also tested for the possibility that female relatedness to the helper male impacted the effect of helper presence on female fitness by using a Wilcoxon Rank Sum test to compare reproductive success of females being helped by sons versus females being helped by males that were not their sons.

To compare the aggression of philopatric males who were helpers versus philopatric males who bred independently, we used *t*-tests with pooled variances (Folded *F*: $F=2.13$, $p=0.12$). We used a one-tailed binomial test to test whether helpers were more likely produced later in the clutch. A one-tailed test was used because previous work on this system showed that less aggressive males are produced later in the clutch

(Duckworth et al. 2015) and we are specifically testing whether this same maternal effect also influences propensity of males to become helpers. Thus, we have a priori information that warrants asking a directional question: whether helpers males are also produced later in the clutch.

We used three within-season (population density, resource availability, and population aggression), and three between-season measures (changes in population density, resource availability, and aggression) to compare the degree of match or mismatch in the competitive environment between the maternal and offspring contexts. We included within-season measures because competitive environment within a breeding season is known to influence the decision to help (Emlen 1982). As these variables were highly correlated with one another (*see* Duckworth and Aguillon 2015), we used a principal components analysis to reduce them to a single variable. All principal components (PC's) with an eigenvalue greater than one were retained for further analysis. PC1 accounted for 46.0% and PC 2 accounted for 22.6% of the variance. We used Pearson correlation analysis to determine whether the principle components were related to the percentage of helpers in the population.

Results

Is helping behavior influenced by maternal effect on aggression?

Helpers were less aggressive (mean \pm standard error (SE) = 2.90 ± 0.28 aggression score) than other philopatric males (mean \pm SE = 4.04 ± 0.08 aggression score) of their cohort across all years of the study (*t* test; $t_{350} = 2.73$, $p = 0.01$; Fig. 2). Helpers were produced in late positions of the clutch for the 10 of 13 clutches where helper birth order was known (one-tailed binomial test; $p = 0.03$).

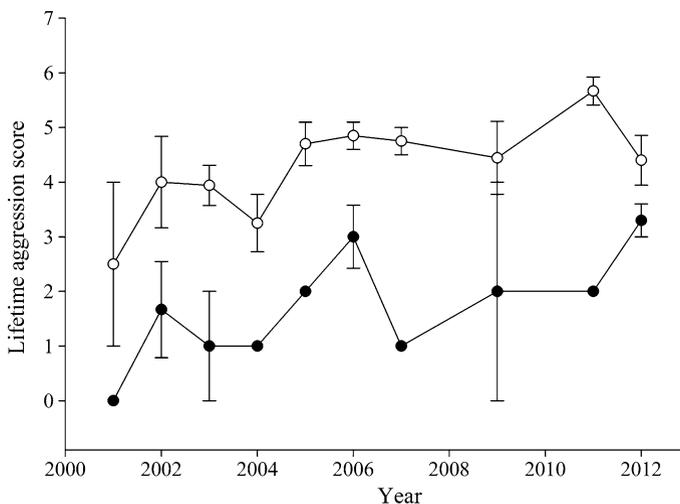
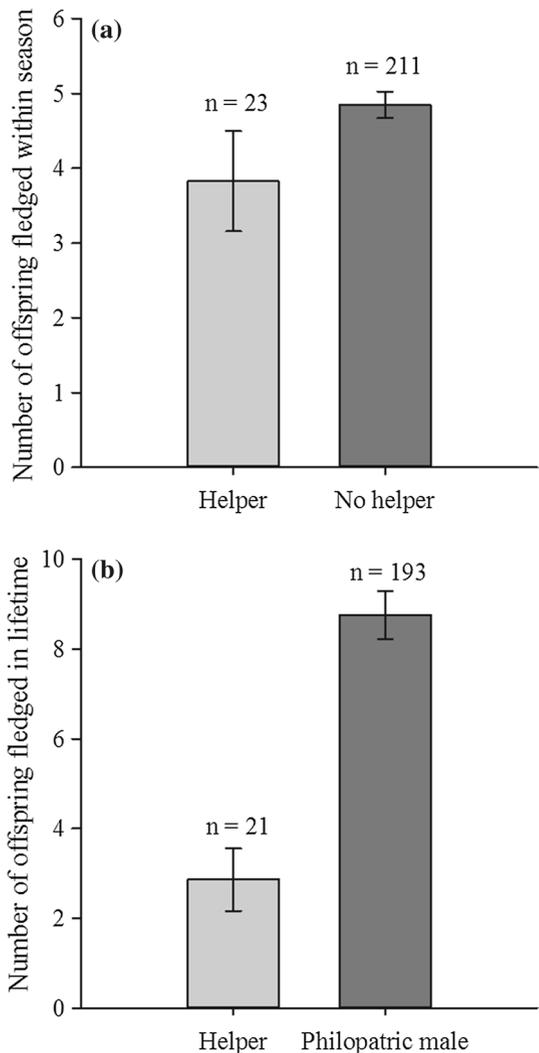


Fig. 2 Helpers (closed circles) were less aggressive than independently breeding philopatric males (open circles) in all years of the study. Each point represents a year of this study

Fitness consequences for mothers and helpers

For helpers whose genetic relationship to the individuals they helped was known (all but two individuals), helpers helped their mothers and an unrelated male 25.0% of the time, fathers and an unrelated female 33.33% of the time, a sibling 8.33% of the time and both biological parents 33.33% of the time. There was no difference in reproductive success between females with helpers (mean \pm SE = 3.83 ± 0.67 offspring, $n = 23$) versus females without helpers (mean \pm SE = 4.85 ± 0.18 offspring, $n = 211$; Fig. 3a). In fact, among females within a season there was a nonsignificant trend for females with helpers to have lower reproductive success (mixed effect model; $F = 3.27$, $p = 0.07$). There was no difference in reproductive success for the same females that had a helper for some breeding attempts (mean \pm SE = 3.59 ± 0.66) but not others (mean \pm SE = 4.81 ± 0.19 ;

Fig. 3 Fitness consequences of producing and being a helper. **a** There was no difference in the number of genetic offspring that survived to independence for females with and without helpers. **b** Independently breeding philopatric males had higher lifetime reproductive success (measured as number of genetic offspring that survived to independence including indirect, extra-pair and direct fitness) compared to males that were helpers



paired t test; t value = 0.06, $p = 0.95$, $n = 15$). Females helped by sons did not have higher reproductive success (mean \pm SE = 3.94 ± 0.64 offspring, $n = 6$) than females that were helped by males who were not their sons (mean \pm SE = 3.47 ± 1.09 offspring, $n = 9$; Wilcoxon two-sample two-sided test; $Z = 0.75$, $p = 0.46$). Lastly, females that produced helpers did not have higher lifetime fitness (mean \pm SE = 8.62 ± 1.87 offspring, $n = 13$) than females who did not (mean \pm SE = 8.31 ± 0.52 offspring, $n = 122$; Wilcoxon two-sample two-sided test; $Z = -0.42$, $p = 0.67$).

Males that were helpers fledged fewer offspring in their lifetime (mean \pm SE = 2.86 ± 0.69 offspring, $n = 21$) than other philopatric males of their cohort (mean \pm SE = 8.75 ± 0.54 offspring, $n = 193$), resulting in lower lifetime fitness even though all within-pair, extra-pair and indirect fitness were taken into account (Wilcoxon Rank Sums; $Z = -3.12$, $p < 0.01$; Fig. 3b). Helpers did not sire offspring at any nests at which they helped in this study.

Effects of competitive environment on the percentage of helpers

There was a strong positive relationship between the percent of helpers in the population and PC1 ($r = 0.62$, $p = 0.04$; Fig. 4), indicating that there were more helpers in years when the population was less aggressive and in years when there was a strong increase in population density from the previous year (Table 1). PC2, which mainly explained variance in resource availability (Table 1) was not related to the percent helpers each year ($r = -0.27$, $p = 0.42$).

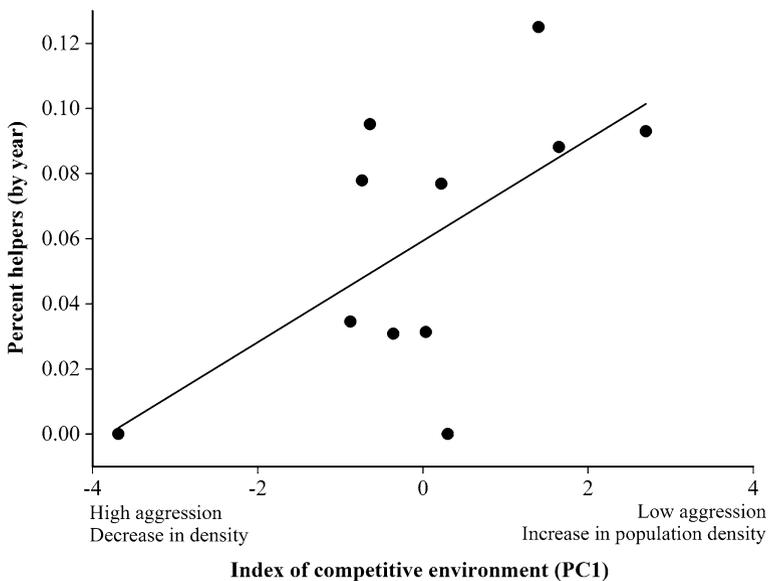


Fig. 4 Helpers were more prevalent in years in which population aggression was low and there was a strong increase in population density from the previous year (see Table 1 for full description of PC loadings). Each point represents a year of this study

Table 1 Results from principal components analysis for population level variables, including eigenvalue and percentage of variance each PC explains

Variables	PC1	PC2	PC3	PC4	PC5	PC6
Population aggression	– 0.51	0.17	0.21	0.45	– 0.39	– 0.55
Population density	0.42	0.42	– 0.15	0.5	0.54	– 0.28
Population resource availability	– 1.10	0.77	0.4	– 0.1	– 0.08	0.47
Change in aggression across seasons	– 0.49	– 0.25	– 0.07	0.53	0.35	0.54
Change in density across seasons	0.51	– 0.12	– 0.01	0.5	– 0.61	0.32
Change in resource availability across seasons	0.20	– 0.35	0.88	0.07	0.24	– 0.08
Eigenvalue	2.76	1.36	0.922	0.75	0.18	0.03
% of variance explained	46.00	22.60	15.37	12.57	0.03	0.004
Cumulative % variance	46.00	68.60	84	96.5	99.52	100

Bold numbers indicate the most important variables (>0.4) for each PC

Discussion

Maternal effects are ubiquitous in nature and often strongly influence offspring trait variation, yet the degree to which they reflect active maternal strategies to match offspring to subsequent conditions is unclear (Marshall and Uller 2007). Moreover, the evolutionary persistence of maternal effects is particularly puzzling when they result in a fitness cost for offspring.

Here, we found that a maternal effect on dispersal and aggression influences the propensity of male offspring to be helpers: cooperatively breeding male offspring were less aggressive than independently breeding philopatric males in every year of this study (Fig. 2) and were more often produced late in the laying order than is expected by chance. We also show that producing helpers did not increase female fitness—neither females that produced helpers nor females that were assisted by helpers had higher reproductive success or lifetime fitness (Fig. 3a). Moreover, helpers themselves had lower lifetime fitness relative to other philopatric males of their cohort (Fig. 3b), consistent with findings in other populations (Dickinson and Akre 1998). Lastly, we found that changes in population density between seasons predicted the percentage of helpers in any given year. Specifically, there were more helpers in the population in years following an increase in population density (Fig. 5a).

Taken together, these results do not support the hypothesis that production of helpers is a maternal strategy to increase her personal fitness, and instead support the mismatch hypothesis. Our results suggest that an adaptive maternal effect may be undermined in years when there is an increase in population density, resulting in a more competitive environment, such that nonaggressive, philopatric males are “mismatched” to their breeding environment. Such an unexpected increase in density between seasons can limit the ability of sons to breed adjacent to their parents, resulting in sons helping instead. This idea is further supported by the fact that females had a tendency to have lower fitness in years where they had helpers at the nest and helpers themselves have lower lifetime fitness (see also Dickinson and Akre 1998; Fig. 3), which indicates that females pay a price when producing sons that do not “match” the ecological context. Mismatches between the cue that induces the maternal effect and the competitive environment that offspring experience, if common, should prevent the evolution of an adaptive maternal effect on dispersal and

aggression; however, given that helpers are rare, it seems that the maternal effect produces a match between offspring phenotype and environment the vast majority of the time.

Interestingly, we found that changes in population aggression across years were not associated with the number of helpers in the population; however, within a breeding season, the more aggressive the population was, the fewer helpers there were (Fig. 5b). This result was unexpected because aggressive individuals are known to defend more nest boxes (Duckworth 2006a) and therefore higher population aggression should result in resource availability being limited behaviorally (e.g. Pruett-Jones and Lewis 1990; Komdeur 1992). A potential explanation for this finding is that more aggressive parents are less tolerant of offspring breeding nearby, as suggested by previous research in this system (Aguillon and Duckworth 2015). Thus, the correlation between population level aggression and number of helpers may reflect variation in sociability of the population across years.

There are several possible sources of stochasticity that may undermine the predictability of cues of population density. Rapid shifts in density between seasons may reflect years of higher than average recruitment or an influx of immigrants (Duckworth and Aguillon 2015). Importantly, while the maternal effect is predicated on a females' assessment of local competition for nest boxes (Duckworth et al. 2015), it is ultimately an interaction between local (e.g. interactions with family; Aguillon and Duckworth 2015) and population-level variables (e.g. population density; this study), that determine the breeding opportunities available to a male searching for a territory the next year. If many females have a cue of high local resource availability, this may result in a population-wide overproduction of philopatric sons, leading to high recruitment and a denser population in the subsequent year. Alternatively, higher than usual immigration levels in some years may similarly decouple reliability of the maternal effect in predicting the subsequent environment. It is currently not known what factors influence variation in immigration rates in this population, but there is large variation across years in the percent of first-time breeders that are immigrants (Duckworth and Aguillon 2015).

It is unclear whether the egg-based maternal effect acts on cooperative behavior directly or indirectly through its effects on aggression. Less aggressive males invest more in offspring care, a common pattern across species (Ketterson et al. 1992; McGlothlin et al. 2007; Ridder et al. 2000), and are more likely to breed near their parents (Duckworth 2006b; Aguillon and Duckworth 2015). Thus, the maternal effect could influence cooperative behavior through its effects on aggression rather than directly targeting the propensity to cooperate itself. Helpers are the least aggressive males in the population each year, but this is relative to overall cohort aggression, as males that become helpers are more aggressive in some years than others (Fig. 2). This suggests that helpers emerge as a result of the inability of the least aggressive males of each cohort to effectively compete for territories, rather than as a unique cooperative phenotype in its own right.

Why do females not have higher reproductive success in years when they have helpers? It is unlikely that females with helpers are "substandard", as these same females have comparable reproductive success to other females in years when they did not have helpers. It is possible that helper presence and lower female reproductive success are independently influenced by increased competition across years. Territories are smaller when population density is high, as more birds are packed into the same area (Arcese and Smith 1988; Duckworth 2008), and having an extra bird on the territory may negatively impact other factors important to reproductive success, such as food availability. It is also possible that parents provide decreased care when helpers are present, as has been shown in other species (e.g., Green et al. 1995; Potticary et al. 2016), which could lead to lower reproductive success if helpers do not provide as high quality of care as the breeding pair.

While the ability of females to influence offspring behavior are well-established for some phenotypes, such as dispersal (e.g. Clobert et al. 2012) or castes in social insects (e.g. Simola et al. 2016), an egg-based maternal effect on cooperative breeding behavior is, to the best of our knowledge, previously unreported. Thus, our results have important implications for the evolution of cooperative behavior because it is generally assumed that the decision to cooperate is a flexible response arising from offspring's assessment of breeding resource availability and dispersal cost (Emlen 1982; Koenig and Dickinson 2004; Cockburn 1998), such that all individuals have an equal likelihood of pursuing a particular strategy. Even when studies acknowledge that maternal effects might be important for cooperative behavior, they generally assume that mothers will produce helpers for their own benefit (Russell and Lummaa 2009). However, this study provides evidence that individuals vary not only in their propensity towards cooperative breeding, but that this behavior may emerge, not as a complex assessment by offspring of environmental conditions, but as a compensatory mechanism to deal with maternal influence on competitive traits. In this sense, phenotypic variation induced by mothers changes the costs and benefits for offspring of pursuing different behavioral strategies, which may indicate why some philopatric individuals help while others float in response to resource limitation (Austad and Rabenold 1986).

Given the rarity of environmental mismatch, how can it lead to evolution of a reproductive strategy like cooperative breeding? Typically, the evolution of complex behaviors are thought to require strong, consistent selection to evolve, which makes traits that are only expressed in rare, stochastic events perplexing (Duckworth et al. 2018). However, it has been argued that cooperative breeding emerges as a result of deletion of a typically required breeding cue (i.e., mating) in a behavioral repertoire (Jamieson 1989; West-Eberhard 2003). This idea seems particularly likely for the origin of cooperative breeding behavior, as all of the behaviors that constitute cooperative breeding in this system (e.g., feeding nestlings, guarding territories, etc.) are the same as those exhibited by breeding males. The only differences are that helpers express these behaviors without mating and towards offspring that are not their own. However, the cues that induce male parental care are still present; for example, the sound of begging offspring are known to elicit feeding behavior even when it is superficially obvious that they are unrelated (e.g. in the case of brood parasitism). Thus, while these helper males have lower lifetime fitness than males who bred independently, it may be that selection to maintain both male parental care and reactivity to the cues that induce male parental care is sufficiently strong to override the costs of a few males expressing these behaviors out of context (e.g., towards their siblings instead of their own offspring).

In conclusion, while maternal effects on offspring phenotype are an inevitable consequence of the overlap of generations, evolution of active maternal strategies depend on predictable environmental cues that allow females to match offspring phenotype to future contexts (Burgess and Marshall 2014). While the maternal effect influencing dispersal and aggression is adaptive in western bluebirds and the cues that induce it are reliable the vast majority of the time, this maternal strategy can reduce offspring fitness when there is discordance in the competitive environment across seasons which undermines the predictability of the environmental cue.

Acknowledgements We thank Alex Badyaev, Erin Morrison, Dawn Higginson, Kelly Hallinger, Anne Storey, Kathryn Chenard, Georgy Semenov, and Chris Seliga for comments that greatly improved the manuscript. We thank Stephanie Aguillon, Nerissa Hall, Megan Jacobson and numerous field and lab assistants

for invaluable help with data collection and processing. Support for this project was provided by NSF DGE-1143953 to ALP and NSF DEB-918095 and DEB-1350107 to RAD).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This study was carried out in accordance with the recommendations and guidelines approved by University Institutional and Animal Care and Use Committees, as well as complied with all state and federal permitting guidelines for using bluebirds in this study.

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