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HOW HERITABLE TRAITS OF PARENTAL CARE INFLUENCE BROOD SEX RATIO IN THE CAROLINA WREN (THRYOTHORUS LUDOVICIANUS)

By

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Abstract

Early rearing conditions and sibling rivalry can have sex-specific effects on offspring, favoring the unequal production of sons and daughters according to environmental conditions. Particularly in sexually size-dimorphic species in which males are larger and, thus, more energetically expensive to produce than females, the maternal ability to secure food for offspring and withstand the cost of reproduction should shape the production of sons vs. daughters; generally, high-quality mothers are expected to over-produce sons beyond expectation of Mendelian segregation of sex chromosomes. Such a situation arises in the Carolina wren (*Thryothorus ludovicianus*), a species in which sexual size dimorphism among offspring arises prior to independence from parental care. However, females of this species retain their breeding territories year-round, so high-quality daughters that survive across years and maintain quality breeding territories might actually have greater reproductive value than sons, thus favoring the production of daughters by high-quality mothers. If this hypothesis is true, high-quality mothers might over-produce daughters because those daughters will inherit genes coding for heightened parental care, thereby enhancing the fitness of a given female's grandoffspring. To test these hypotheses, I investigated the heritability of traits associated with fitness and parental care in a wild population of Carolina wrens and related these traits to offspring sex ratios. Indeed, I found that body condition, fecundity, and behavioral measures of parental investment were significantly heritable and, thus, genetically transmitted from parents to offspring. As predicted, these same measures of parental quality also shaped offspring sex ratios, whereby mothers investing heavily into reproduction (as evidenced, for example, by laying larger clutches of eggs) produced more daughters than expected by chance. At the same time, females paired with high-quality fathers also produced relatively more sons, consistent with the female's perception of

male parental care in shaping the cost of reproduction and offspring sex. Collectively, these results suggest that multiple selective forces interact to shape offspring sex in complex ways, meaning the production of sons and daughters is seldom truly random.

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Introduction

In dioecious species, the two sexes are associated with varied life histories upon which selection is expected to act differently. Female gametes require more energy and time to produce than male gametes, and females are limited more strongly in the number of gametes they can produce; females are, consequently, often choosy when selecting mates and have a high likelihood of obtaining a one, with males being required to compete with other males to gain access to females with which to mate (Trivers 1972). Male gametes are inexpensive and readily expended to produce as many offspring as possible; thus, high-quality males often have the opportunity to reproduce with multiple females, greatly increasing their reproductive potential, whereas males of lower quality often go unmated (Bateman 1948; Trivers and Willard 1973; Clutton-Brock et al. 1984). These differences in variation in reproductive success between the sexes suggests that the value of the sexes is not always equal. Parents are, therefore, selected to differ the allocation of resources to their offspring based on the unequal value of each sex (Sheldon 2007).

Sex allocation is the investment of resources directed toward male vs. female reproduction in sexual species (Charnov 1982; West 2009) and has been observed in a multitude of studies in both invertebrates and vertebrates. The Trivers-Willard hypothesis (Trivers and Willard 1973) described a general theory of conditional sex allocation in which high-quality females have more resources for reproduction and in turn, have the ability to produce high-quality offspring; these higher-quality offspring become higher-quality adults, and sons have the potential to provide a higher return on investment for their mother. Thus, sons require more maternal care to become a high-quality adult, produce many quality offspring, and attain high lifetime reproductive success. In many animal species, especially those with polygynous mating systems, males have high variance in lifetime reproductive success, as male-male competition to

mate with females leaves a greater number of males going unmated. Males of these species must be of sufficient size and quality to compete with other males and obtain mates. In polygynous mating systems, it is often assumed that high-quality females will invest more in sons than daughters to ensure the son is a high-quality adult capable of producing many offspring and increasing the mother's inclusive fitness (Clutton-Brock et al. 1984; Kruger 2005).

In the years following its introduction, the Trivers-Willard Hypothesis has been tested numerous times. Many studies have added to and corroborated the predictions laid out by Trivers and Willard (1973) while contributing to the study of sex allocation, but various other studies have reported results contravening predictions of the Trivers-Willard Hypothesis. In certain instances, a female of high quality might actually invest in daughters instead of sons (Leimar 1996; Hewison and Gaillard 1999; Hewison and Galliard 1999; Kruger 2005). Indeed, a number of factors might favor high-quality mothers that invest in daughters over sons, namely when (i) daughters inherit rank or territory from their mother, (ii) individuals compete over limiting resources, such as nesting sites; (iii) females are more prone to dispersal than males, or (iv) when male reproductive success is less variable under monogamy and biparental care (Hewison and Gaillard 1996; Cockburn et al. 2002; Kruger 2005). In an overview of sex allocation theories, Frank (1990) presented an adaptive model to explain variation in brood sex ratios when the condition of the mother remained consistent across multiple breeding seasons, and showed that the expected brood sex ratio changes over multiple breeding seasons (or at different times during a single season) depending on how a son or daughter will increase the lifetime reproductive success or value of their parents and what resources are available.

In a theoretical analysis, Leimar (1996) showed that mothers should produce the sex that most greatly benefits from high-quality maternal care. Rather than investing in sons and

increasing their lifetime reproductive *success*, mothers may, instead, invest in daughters to increase their lifetime reproductive *value* (Leimar 1996; West 2009), which considers the quality of offspring an individual's own offspring will then go on to produce (i.e., production of grandchildren). For example, investment in daughters may be favored in light of maternal transmission of condition, rank, or territory (Silk 1983), whereas the son of a high-quality mother, although physiologically capable of producing more offspring than his sister, may mate indiscriminately and potentially pair with lower-quality females, thereby reducing the quality of a female's grandoffspring and negating any increased reproductive success enjoyed by her son. Alternatively, daughters that inherit the condition or quality of their mothers, and that, being the choosy sex, go on to select a high-quality male would be expected to produce high-quality offspring, thus increasing the reproductive value of their grandmother.

This set of circumstances occurs in a subset of avian species, including the Carolina wren (*Thryothorus ludovicianus*), in which breeding pairs are both socially and genetically monogamous and form lifetime pair bonds, sometimes within about two months of fledging (Morton and Shalter 1977). Moreover, interannual return rates of adults are high (ca. 85% in my study population; Mueller et al. 2019a), with females in this non-migratory species retaining their territories year-round (Haggerty and Morton 2020). Given that a high-quality female can transfer her superior condition to her daughters, I posit that her fitness may be augmented by producing daughters over sons.

Females in a variety of species have been observed to manipulate the sex of their offspring (Cockburn et al. 2002; West 2009; Bowers et al. 2011, 2013, 2014, 2015b). In birds, females are the heterogametic sex and determine the sex of their offspring by contributing either a Z or W sex chromosome during meiosis, thereby allowing sex-ratio adjustments to occur (i)

before or during meiotic segregation (i.e., pre-ovulation control) through the selection of either a Z or W chromosome, or (ii) after oviposition through sex-specific mortality or embryo retention, possibly shaped by maternal hormones (Love et al. 2005; Pike and Petri 2006). Environmental changes affect female hormones (e.g., corticosterone and progesterone) while breeding, and these have been linked to offspring sex determination (Pike and Petri 2006). For example, Pike and Petri (2006) showed that, when mating with less-attractive males, female peahen plasma corticosterone concentration increased and this was associated with female-biased offspring sex ratios. When mating with an attractive male, females exhibited elevated testosterone levels and produced male-biased sex ratios. Thus, hormonal changes provide a potential mechanism through which females might adjust the sex of their offspring.

High-quality mothers provide high levels of parental care to enhance the probability that their offspring survive to reproduce. The level of care given to offspring by parents heavily influences the condition of the offspring at fledgling, and the state of the offspring at fledging often predicts their recruitment into the local breeding population and condition in adulthood (e.g., Clutton-Brock et al. 1987, Tinbergen and Boerlijst 1990, Both et al. 1999; Bowers et al. 2014a,2015; AAC and EKB, unpublished data). Parental care is the total amount of time and energy allocated to care of offspring and is typically measured by the amount of food parents deliver to their young (as quantified, for example, by the number of feeding events; e.g., Dor and Lotem 2009). Although parental care is essential to the survival and reproductive success of offspring, levels of parental care vary widely among individuals of the same species.

Like other quantitative traits, such as life-history and physiological traits, variation in behavioral phenotypes, including parental care, is expected to be shaped by allelic/genetic variation, environmental effects, and interactions between genotype and environment (Kruuk et

al. 2008; Manuck and McCaffery 2014). Parental care is often considered to be mostly controlled by the environment, with less known about the level of genetic influence in many species. However, variation in behavior can seldom be attributed entirely to environmental effects (Freeman-Gallant and Rothstein 1999). In the studies that have examined the partial influence of genetic control of behavior, significant narrow-sense heritability has been reported (Freeman-Gallant and Rothstein 1999; MacColl and Hatchwell 2003; Dochterman 2019). Heritability measures the fraction of the variance of a trait within a population due to genetic factors and helps determine how much of the variation is due to environmental effects (Falconer and MacKay 1996; Dor and Lotem 2010; Dochterman 2019). In a meta-analysis conducted by Dochterman (2019) average heritability of animal behavior across taxa was found to be (0.235); which is close to that of life-history and physiological traits.

In several empirical studies, heritability of parental behavior was detected, but was dependent on sex. For example, Freeman-Gallant and Rothstein (1999) quantified parental effort over several generations of savannah sparrows, finding that variation existed among individuals, but, within a family, the level of parental effort provided by males was consistent over generations (see also Schwagmeyer and Mock 2003) and, thus, heritable. Offspring that had received high-quality parental care as nestlings exhibited high parental effort (frequent provisioning trips) as adults. This consistency in male care was strongly influenced by genetic factors, with the behavioral phenotype of parents predicting the feeding rate of an individual male offspring. However, parental care was not heritable in females.

I posit that high-quality females produce daughters with high reproductive value. Since the level of maternal care ultimately influences offspring survival, quality, and reproductive value (Royle et al. 2012), and the quality of maternal care is highly variable in this species, it

may be under partial genetic control. Thus, I assessed whether maternal care is based solely on environmental effects or partially under genetic control by partitioning variance within and among parent-offspring groups across several generations of female Carolina wrens. I quantified parental care by totaling provisioning trips and number of nestlings that survive to fledging, and related these measures of parental investment to offspring sex ratios. If my hypothesis is true, that matrilineal transmission of quality favors the production of daughters by high-quality mothers, then I predict that heritable traits associated with parental investment (e.g., clutch size) will also predict the offspring sex ratio such that females investing more into reproduction tend to overproduce daughters relative to the null expectation.

Methods

Study Species and Site

The Carolina wren is a small (18-22 g) cavity-nesting songbird that is a year-round resident of southeastern North America, breeding from March to early September. They are sexually monochromatic, but males are larger in size (mass: 13%, tarsus length: 4%, wing chord and tail lengths: 6%), on average, than females (Twedt 2004; Haggerty and Morton 2020). This species is also reportedly both socially and genetically monogamous, forming lifetime pair bonds (Haggerty and Morton 2020).

Fieldwork was conducted from 2017-2021 at the Edward J. Meeman Biological Station in west Tennessee, USA (35.363°N, 90.017°W), where a network of nestboxes is distributed over ca. 150 ha of mature, secondary deciduous forest. From 2017 to 2018, there were 220 nestboxes distributed in a 50-m by 100-m grid. Nestboxes were added prior to the 2019 field season, bringing the total to 600 boxes distributed in a 50-m by 50-m grid. Prior to the 2020 field

season, 25 more nestboxes were added to create a network of 625 total boxes, each placed atop an aluminum predator baffle (diameter = 51 cm) to discourage ground-dwelling predators. These boxes are readily accepted by nesting Carolina wrens (see Mueller et al. 2019b for further details, including nestbox dimensions and construction materials).

Field and Lab Procedures

Throughout the breeding season, each nestbox is checked at least once every five days for the formation of new nests, and more frequently thereafter to monitor clutch completion, incubation and hatching of eggs, and the progress and status of nests and to capture and band adults and nestlings prior to fledging. We capture adults at the nest during the second half of the incubation period with a mesh bag over the nest opening or by using playback of conspecific song and a mist net placed directly outside the nestbox. Occasionally, difficult-to-capture birds are identified via binocular sightings or provisioning recordings. Upon capture, adults are banded with a uniquely numbered U.S. Geological Survey (USGS) aluminum leg band and three additional colored leg bands (two bands per leg), with the four total bands arranged in unique combinations to allow for visual identification and observation without capture (males are often more difficult to recapture than females). Body mass (±0.1 g) is measured using a digital scale, and tarsus length (±0.1 mm) using dial calipers. Tail length and flattened wing chord (±0.5 mm) are measured with a stopped rule. Once eggs hatch, we subsequently monitor nests until fledging.

Four days after the hatching began in a nest (hereafter 4 d 'posthatching'), I recorded provisioning trips made by parents to the nestbox using a digital camera (Kodak Zx1 or Zx5) placed approximately 1 m from the box on a 1.5-m metal pole, standing level with the nestbox. I placed cameras at an angle facing the nestbox opening to view parental food deliveries,

recording activity for 1.5-2.5 hr (Bowers et al. 2019; Jenkins et al. 2021). On day 9 posthatching, prior to fledging, I banded nestlings with a USGS aluminum leg band and obtained measures of body mass and tarsus length, as described for adults above. I also collected a small blood sample (~50 μL) from the brachial vein with a heparinized microhematocrit capillary tube, storing samples on ice until returning to the laboratory for processing and storage. Nests were checked daily beginning on day 11 posthatching to check for fledging and attempted to capture all adults breeding in subsequent years to assess the recruitment of offspring into the population as breeding adults. Prior to the 2021 breeding season, a prolonged winter storm characterized by ca. two weeks of ground coverage by snow and ice appeared to kill nearly all individuals in the population (known to occur in this species; Haggerty and Morton 2020), with the only return from a prior year being a recruited female who was produced in 2019. Thus, no offspring from 2020 were present in 2021, so this year was excluded from analyses of interannual returns.

In the laboratory, I centrifuged blood samples on the day of collection to separate plasma from red blood cells, which I stored in Queen's lysis buffer (Seutin et al. 1991) at 4°C for later extraction of DNA using a high-salt extraction protocol. Carolina wren nestlings cannot be sexed by external morphology; thus, to determine nestling sex, I used a polymerase chain reaction (PCR) to amplify sex-specific regions of the Z and W sex chromosomes using primers described by Kahn et al. (1998). I then separated PCR products, along with those from known-sex adults, using gel electrophoresis.

After the field season ended, I scored videos of parental provisioning 4 d posthatching, the age at which nestling growth is most rapid (Mueller et al. 2019a), observing a total of 1 hr beginning with the first arrival by a parent to provision. Not all parental behaviors were recorded for every nest; thus, here I focus on the number of provisioning visits for the male and female,

which, when measured over the course of an hour, provides a relevant measure of parental investment that reflects consistent individual differences in parental behavior and has consequences for nestling growth (Schwagmeyer and Mock 1997; Bowers et al. 2014b; Lendvai et al. 2015; Murphy et al. 2015; but see also Schwagmeyer and Mock 2008).

Data and Analyses

Not all offspring could be sexed successfully (89% of 1144 young sexed), but offspring mortality prior to sexing would have to be strongly sex-biased to create departures from the primary sex ratio (Fiala 1980; Krackow and Neuhäuser 2008; West 2009). As advised by Krackow and Neuhäuser (2008), I retained broods with incomplete sex-ratio data as their exclusion would otherwise result in a non-random sample. Thus, over the course of the 2017-2020 breeding seasons, I obtained sex-ratio data for 283 broods, which is often regarded as a sufficient sample for minimizing the probability of type II error in these kinds of studies (West 2009).

A subset of offspring were cross-fostered between nests, resulting in (i) unmanipulated broods ($N = 123$) in which parents reared their own young, (ii) fully cross-fostered broods ($N = 88$) in which clutches of eggs were swapped between nests prior to hatching, and (iii) partially cross-fostered broods ($N = 72$) in which a subset of nestlings were exchanged between nests shortly after hatching. However, as there was no effect of the cross-fostering on any of the traits in this study (all $P > 0.1$), this variable was removed from final analyses.

All analyses were conducted using Statistical Analysis Software (ver. 9.4), all tests are two-tailed ($\alpha = 0.05$), and data were converted to z-scores prior to analysis such that parameter estimates serve as reliable measures of effect size (Schielzeth 2010). I estimated narrow-sense heritability of (i) body condition (residuals from a log(mass) × log(tarsus) linear regression) or

size-adjusted body mass (Barnett et al. 2015), (ii) clutch size (of female offspring specifically in addition to the clutch sizes in nests of male recruits), (iii) parental provisioning rate (trips to the nest per hr), (iv) annual reproductive success (fledglings produced), and (v) offspring sex ratio. To estimate these heritabilities, I used parent-offspring regression to compare quantitative traits (e.g., parental provisioning, body condition, reproductive success) in offspring with midparent averages (Falconer and Mackay 1996), along with offspring sex as a fixed effect, in addition to two-way interactions between these effects (with removal of non-significant interactions). I then analyzed offspring sex ratios using a generalized linear mixed model with 'events/trials' syntax (i.e., number of sons/number of offspring sexed) assuming a binomial response distribution. If my hypothesis that heritability of parental care favors the production of high-quality daughters, then I predict that high-quality females (i.e., those providing a heightened level of care, or those of increased body condition) should overproduce daughters beyond the null expectation.

Results

Effects of Parental Care on Offspring Mass and Recruitment

While controlling for brood size, hatching date, and year, offspring prefledging mass was positively and significantly influenced by male, but not female, provisioning rate (Table 1). Heavier nestlings were also more likely to be recruited into the breeding population the following year (Table 1; Fig. 1).

Heritability of Parental Condition, Care, and Reproductive Success

I detected significant heritability of body condition, clutch size, provisioning rate, and annual reproductive success, as reflected by the positive covariances between parents and offspring

(Table 2, Fig. 2). When analyzing clutch size matrilineally, I found that daughters tended to produce a similar number of eggs in their clutches as their mothers. This positive covariance was also present and significant when including sons in this analysis (i.e., clutch sizes produced in the nests of male recruits by unrelated females), but this effect was weaker and the correlation nearly half of that detected for daughters alone.

In addition to the covariance between parent and offspring traits, I also detected persistent effects of rearing conditions on recruited adults. Specifically, being reared among relatively more brothers had a stronger, negative effect on male body condition in adulthood than it did on daughters (Fig. 3A,B), as reflected by a statistical interaction between sex and natal brood sex ratio in their effect on adult body condition (Table 2). The natal brood sex ratio also had an influence on the clutch sizes produced by female recruits, where being reared among relatively more brothers predicted a reduction in clutch size as an adult (Table 2, Fig. 3C). Prefledging mass also positively predicted the clutch size of female recruits (Table 2, Fig. 3D).

Brood Sex Ratios

At the population level, offspring sex ratios varied slightly, but significantly, with measures of parental quality (i.e., clutch size, maternal age, and paternal provisioning rate; Table 3) and environmental conditions (clutch-initiation date; Table 3). Females laying relatively larger clutches produced relatively more daughters (Table 3; Fig. 4A), and overproduced daughters as breeding seasons progressed (Table 3; Fig. 4B). Maternal age and paternal provisioning also predicted offspring sex; increasing maternal age and paternal provisioning rate was each associated with an increase in the relative number of sons within broods (Table 3; Fig. 4C,D).

An effect of male provisioning on offspring sex ratio (determined weeks before males actually provision nestlings), may reflect the female 'anticipation' of the level of male parental care, or, since sons tend to be larger than daughters, might be an artifact of males responding to male-biased broods (or signals of begging/hunger). To exclude either possibility, I tested for an interaction between male provisioning rate and offspring cross-fostering treatment in their effect on offspring sex. There was no interaction between these effects ($F_{2, 186} = 0.11$, $P = 0.9003$), indicating that the relationship between male provisioning and offspring sex ratios was similar for both unmanipulated and cross-fostered broods.

Discussion

I found that offspring receiving high-quality parental care were heavier, and these heavier young were more likely to be subsequently recruited as adults into the local breeding population. Recruitment of offspring into the breeding population is a useful measure of fitness (e.g., McCleery et al. 2004; Williams 2012), and, in non-migratory species like Carolina wrens, the first winter for a juvenile often presents a significant bottleneck for survival, with ca. 20% of neonates surviving to reproductive age (Gill and Haggerty 2012). Survival during the first year of life, thus, is a reliable indicator of fitness and the quality of parental care, which is clearly essential to shaping offspring fitness with effects lasting throughout their adult lives.

Not unexpectedly, I detected heritability of several traits that reflect parental care in a general sense. These traits included body condition, clutch size, provisioning rates, and overall annual fecundity. That provisioning rates are consistent over generations matches findings of previous studies in other species (e.g., Freeman-Gallant 1999), suggesting that parental care is a heritable trait and that its variation is not determined solely by environmental pressures.

Offspring reared by parents that exert high levels of parental care (i.e., high provisioning rates) will benefit and likely reach independence at above-average mass and condition, reflecting heightened energy stores that promote survival (e.g., Schamber et al. 2009). Indeed, pre-fledging mass is an important component of offspring fitness, as those that recruited into the breeding population were heavier than average just prior to fledging. Heavy daughters, from high-quality mothers, that were recruited into the breeding population also laid larger clutch sizes, as their mothers did. I also found that high quality mothers laying large clutches over-produced daughters. That these high-quality mothers over-produced daughters is presumably because high-quality daughters enhance their reproductive value to a greater extent than high-quality sons. At the same time, by producing a female-biased brood in a larger-than-average-sized clutch may mitigate costs associated with producing sons (Frank 1990), especially since sons are often more susceptible to sibling competition early in life (Bowers et al. 2011, 2015). The covariance between parent and offspring clutch sizes was weaker when including the clutch sizes produced in recruited sons' nests (i.e., clutches produced by unrelated females who paired with a recruited son). Thus, when a male mates or pairs indiscriminately with a lower-quality female, the number of eggs in the clutches he rears may be smaller, contain fewer daughters, and consequently limit the fitness gains of this mother relative to what a daughter would likely provide.

On the other hand, some patterns I observed are consistent with the cost-of-reproduction hypothesis (Cockburn et al. 2002; Merkling et al. 2015), or the notion that higher-quality females tend to produce relatively more sons, as they are better able to cope with the cost of producing larger male offspring. For example, Carolina wren females that live to produce multiple broods over many years are presumably of high quality, and I found that older Carolina wren females have male-biased broods, consistent with other studies that found females of high-quality

produce male-biased broods (Whittingham and Dunn 2000; West 2009). Similarly, I also found that males can influence offspring sex ratios through heritable behaviors, such as provisioning rates. In broods where males provisioned at high rates, females produced relatively more sons, and this most likely was the result of females' anticipation of the level of parental care a male would provide, for example by observing cues from males that are predictive of paternal care (either prior to mating or as a result of previous experience with a given male). Such a process is made possible as females in a variety of species have reportedly been able to pick up on the extent of genetic compatibility with their mates and then adjust their brood sex ratio to maximize fitness (Brekke et al. 2010; Pryke and Griffith 2009a,b; Pryke et al. 2011; Rioux-Paquette et al. 2011; Sardell and DuVal 2014).

In conclusion, females in my study population of Carolina wrens seem to be subject to a unique combination of constraints that shape the optimal sex-allocation strategy, consistent with previous studies that provided evidence of the adaptive ability to shift offspring sex ratios in relation to environmental conditions or the ability of parents to invest in offspring (Whittingham and Dunn 2001; Bowers et al. 2013). Low-quality parents, unable to deliver high levels of parental care, may adjust their brood sex ratio to favor the less expensive sex, whereas the opposite occurs if parents are of higher quality. However, there are many factors that influence optimal brood sex ratios, and exactly how parents should adjust sex ratios may not remain static over their lifetime. Consistent with the adaptive model provided by Frank (1990), expected brood sex ratios may change across breeding seasons or at different times within a season, even if maternal quality remains unchanged, depending on how a son or daughter will impact a mother's reproductive value. Thus, high-quality mothers may produce male-biased broods at one point during the season and female-biased broods at other times. When various heritable traits

and quality parental care, which may be dependent on resources currently available, determines the fitness of offspring, the optimal brood sex ratio may change over time for each individual or pair.

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Table 1. Effects on nestling mass and recruitment.

	Estimate ± SE	*F*	df	*P*
Nestling mass				
Male provisioning trips per hr	0.2125 ± 0.1024	4.31	1, 195	0.0392
Female provisioning trips per hr	–0.0291 ± 0.0964	0.09	1, 193	0.7630
Hatching date	–0.0723 ± 0.1062	0.46	1, 176	0.4969
Brood size	–0.1593 ± 0.0970	2.70	1, 190	0.1022
Year		5.49	3, 194	0.0012
2017[a]	1.5441 ± 0.3830			
2018[a]	0.2640 ± 0.4465			
2019[a]	0.3165 ± 0.2208			
Intercept	–0.5745 ± 0.2791			
Recruitment				
Nestling mass	0.4662 ± 0.1931	5.83	1, 195	0.0167
Clutch size	0.2042 ± 0.2202	0.86	1, 185.8	0.3549
Hatching date	–0.0951 ± 0.2080	0.21	1, 195	0.6482
Year		0.68	2, 195	0.5074
2017[b]	0.0250 ± 0.7496			
2018[b]	0.4558 ± 0.4029			
Intercept	-1.7459 ± 0.2946			

[a]relative to 2020; [b]relative to 2019

Table 2. Effects on phenotype and productivity of adult offspring.

	Estimate ± SE	*F*	df	*P*
Condition of adult offspring				
Midparent condition	0.4067 ± 0.0912	19.90	1, 79	< 0.0001
Prefledging mass	0.1829 ± 0.1213	2.27	1, 79	0.1355
Natal brood size	0.1389 ± 0.1055	1.73	1, 79	0.1918
Sex		1.50	1, 79	0.225
Female[a]	–0.2938 ± 0.2402			
Natal brood sex ratio[b]	–0.7856 ± 0.1651	21.55	1, 79	< 0.0001
Offspring sex × Brood sex ratio	0.6509 ± 0.2009	10.50	1, 79	0.0017
Intercept	0.4604 ± 0.1865			
Clutch size of adult daughters				
Midparent clutch size	0.5057 ± 0.1897	7.10	1, 53	0.0102
Prefledging mass	0.5219 ± 0.2286	5.21	1, 53	0.0265
Natal brood sex ratio[b]	–0.3039 ± 0.1414	4.62	1, 53	0.0361
Intercept	–0.0014 ± 0.1760			
Clutch size of adult offspring (daughters and sons pooled)				
Midparent clutch size	0.2963 ± 0.1287	5.30	1, 82	0.0239
Prefledging mass	0.4039 ± 0.1355	8.89	1, 82	0.0038
Natal brood sex ratio[b]	–0.2880 ± 0.1032	7.79	1, 82	0.0065
Intercept	–0.0516 ± 0.1095			
Provisioning trips per hr by adult offspring				
Midparent provisioning trips per hr	0.6154 ± 0.2813	4.78	1, 24	0.0387
Clutch-initiation date	0.2244 ± 0.2344	0.92	1, 24	0.3479
Clutch size	–0.0427 ± 0.2845	0.02	1, 24	0.8819
Intercept	0.2239 ± 0.2222			
Fledglings produced by adult offspring per yr				
Midparent fledglings per yr	0.3565 ± 0.0898	15.77	1, 84	0.0002
Intercept	–0.3046 ± 0.0867			

[a]relative to males; [b]proportion sons

Table 3. Effects on offspring sex ratio (proportion male offspring) within broods.

	Estimate ± SE	*F*	df	*P*
Clutch size	–0.1798 ± 0.0787	5.22	1, 182.7	0.0234
Clutch-initiation date	–0.2005 ± 0.0907	4.89	1, 188.3	0.0282
Maternal age	0.1522 ± 0.0713	4.56	1, 143.4	0.0345
Maternal provisioning[a]	0.0002 ± 0.0731	0.00	1, 175.7	0.9975
Paternal provisioning[a]	0.1680 ± 0.0726	5.36	1, 186.9	0.0217
Year		1.35	3, 188.4	0.2590
2017[b]	0.2669 ± 0.3118			
2018[b]	0.2150 ± 0.3618			
2019[b]	0.3423 ± 0.1708			
Intercept	–0.0713 ± 0.1150			

[a]trips per hr; [b]relative to 2020

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Figure 1

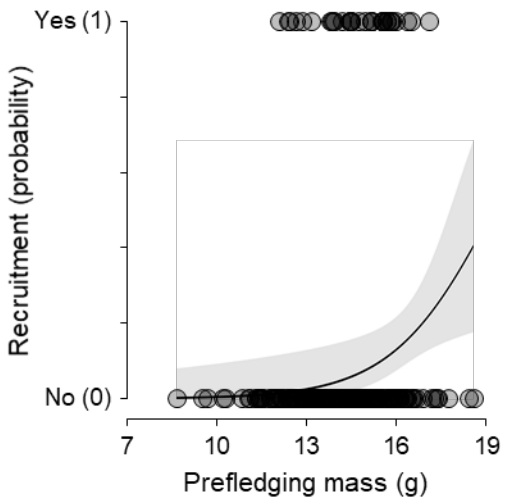

Figure 1. Probability of recruitment in relation to offspring mass prior to fledging. Regression line depicts the fitted prediction ± 95% CI from a generalized linear mixed model while accounting for the other factors (see Table 1); light points indicate individual observations, darker points overlapping observations.

Figure 2

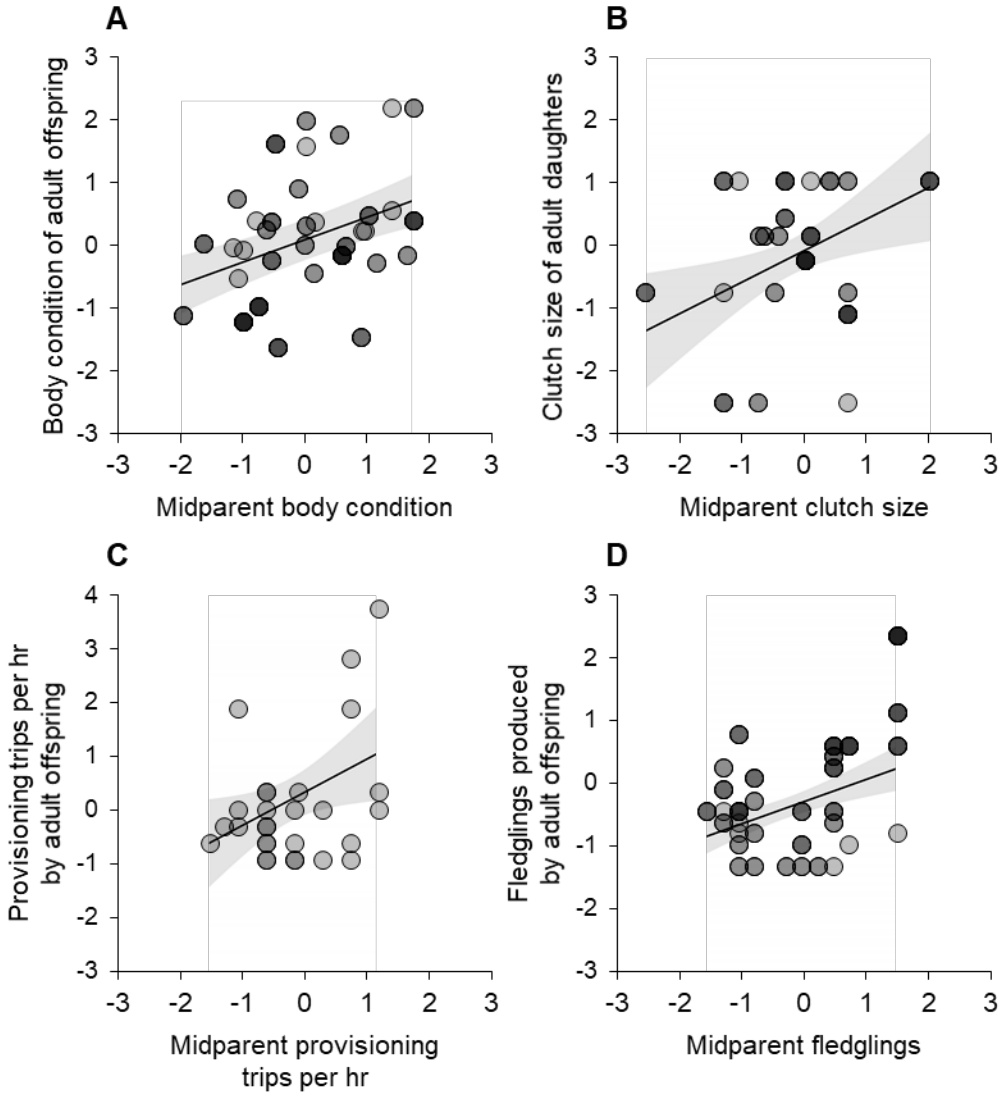

Figure 2. (A) Body condition, (B) clutch size, (C) parental provisioning rate (trips per hr), and (D) total annual fecundity of adult offspring in relation to midparent averages. Regression line depicts the fitted prediction ± 95% CI from a general linear mixed model while accounting for the other factors (see Table 2); light points indicate individual observations, darker points overlapping observations.

Figure 3

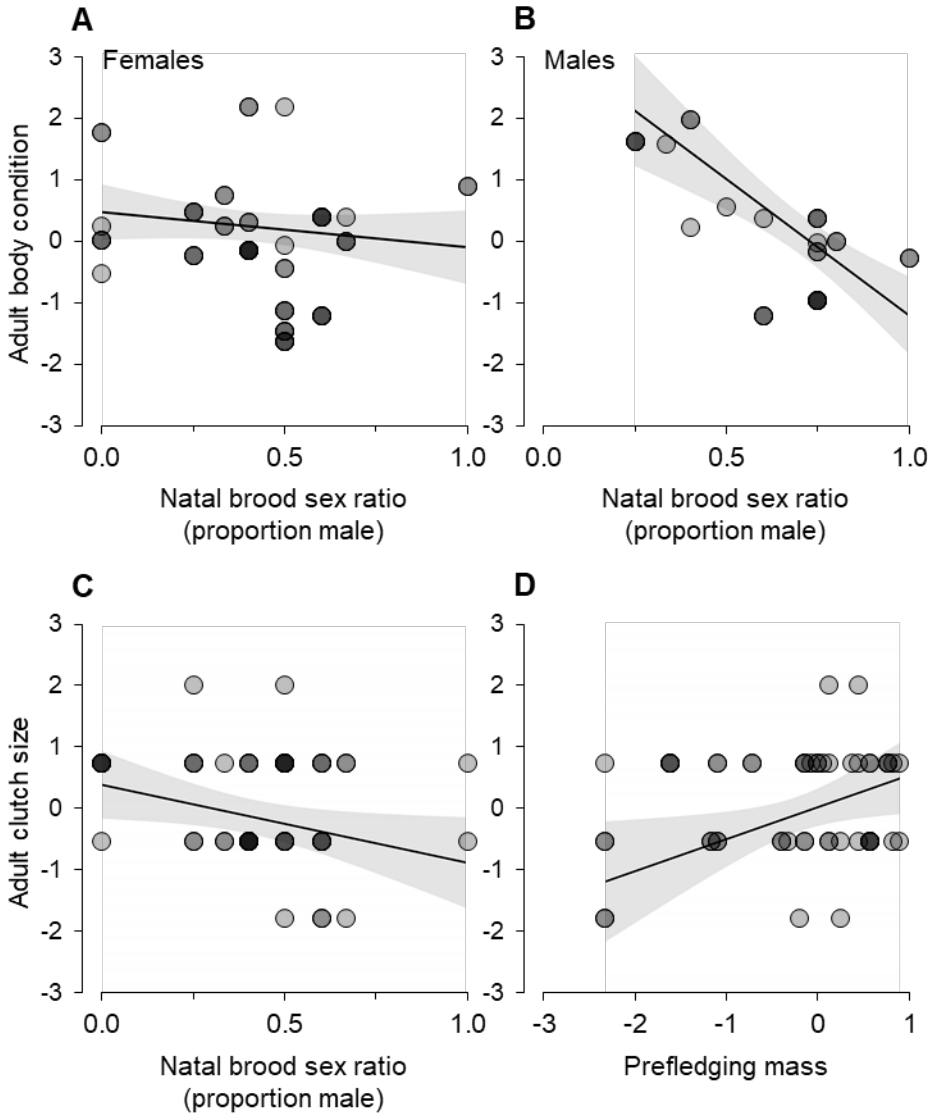

Figure 3. Effects of early rearing conditions on adult offspring condition and clutch size. (A,B) depict the body condition of adult daughters and sons in relation to the brood sex ratio (proportion male) of the brood in which they were reared; clutch sizes produced by adult daughters are plotted in relation to (C) natal brood sex ratio and (D) prefledging body mass. Regression line depicts the fitted prediction ± 95% CI from a general linear mixed model while accounting for the other factors (see Table 2); light points indicate individual observations, darker points overlapping observations.

Figure 4

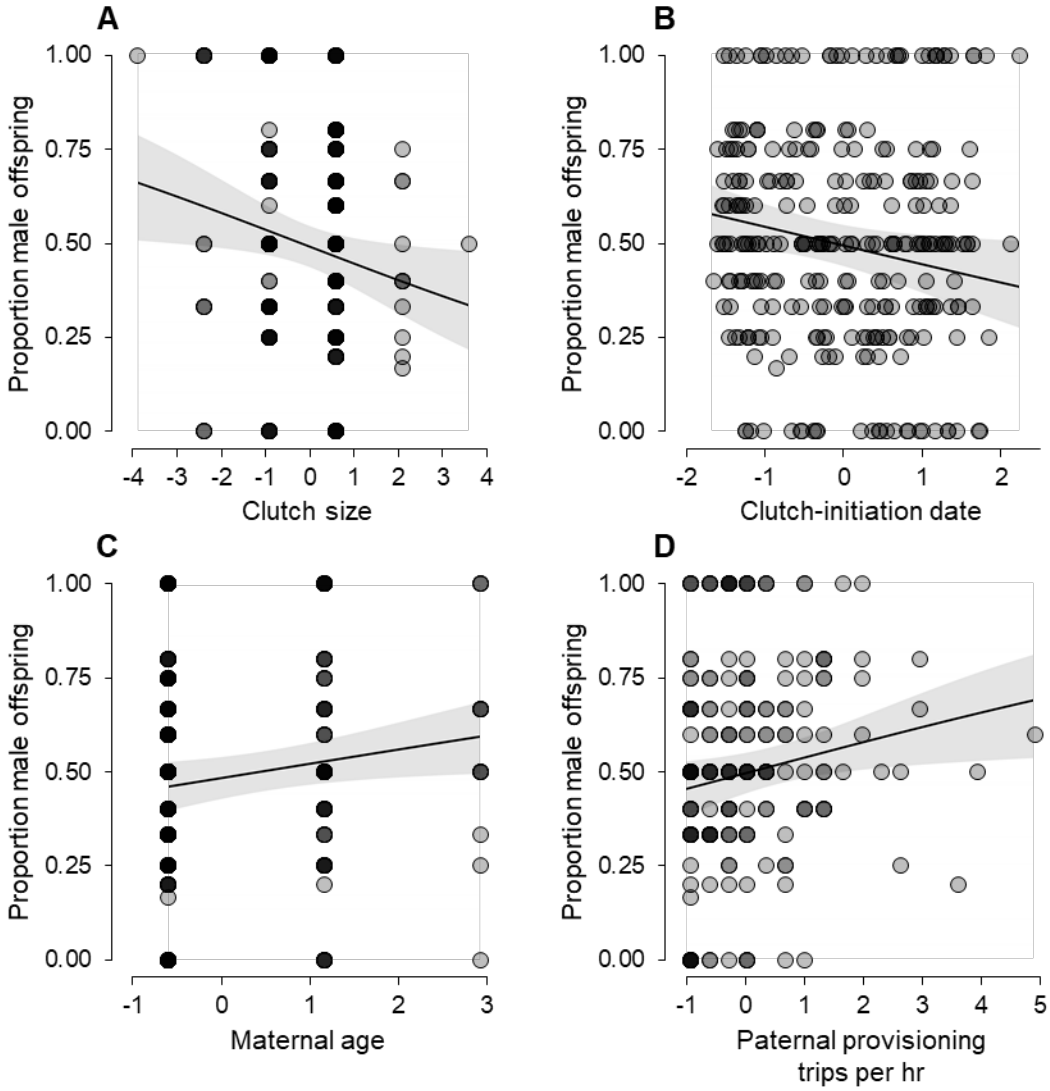

Figure 4. Brood sex ratios (proportion male) in relation to (A) clutch size, (B) clutch-initiation date, (C) maternal age, and (D) paternal provisioning rate (trips per hr) among all broods. Regression line depicts the fitted prediction ± 95% CI from a general linear mixed model while accounting for the other factors (see Table 3); light points indicate individual observations, darker points overlapping observations.