



Original Article

Offspring sex ratio varies with clutch size for female house wrens induced to lay supernumerary eggs

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Theory predicts that a mother's ability to produce high-quality offspring should influence whether she produces sons or daughters. We tested this hypothesis in house wrens (*Troglodytes aedon*) using a within-clutch design in which we induced females to produce more eggs (8–10 eggs) than they normally would (6 or 7 eggs) to determine whether maternal effort and the allocation of resources to supernumerary eggs (those laid beyond the usual number) influence the offspring sex ratio. At the clutch level, we predicted that high-quality females, as defined by their ability to produce supernumerary eggs in response to egg removal, would overproduce sons relative to females treated the same way but producing fewer eggs. At the level of the egg, we predicted that supernumerary eggs would more likely contain daughters than sons. As predicted, females producing extralarge clutches overproduced sons and those producing smaller clutches produced relatively more daughters. Last-laid eggs were also more likely to contain daughters than earlier-laid eggs although there was no difference in the mass of eggs containing males and females. These results suggest that mothers adjust the sex of their offspring strategically to maximize fitness.

Key words: egg removal, maternal effect, parental investment, sex allocation, Trivers–Willard, *Troglodytes aedon*.

INTRODUCTION

Variation in individual quality plays a profound role in shaping parental investment (van Noordwijk and de Jong 1986; Clutton-Brock 1991; McCleery et al. 2008; Weladji et al. 2008; Hamel et al. 2009a,b). The adaptive basis of parental strategies is best revealed by forcing individuals to deviate from their evolutionarily shaped reproductive tactics; to that end, experimental manipulation of egg production has emerged as a powerful tool in studies of reproductive strategies and parental care (Heaney and Monaghan 1995; Monaghan et al. 1995, 1998; Williams 2001; Wagner and Williams 2007). For example, Nager et al. (1999, 2000) removed eggs from nests of lesser black-backed gulls (*Larus fuscus*) during egg production, causing females to produce replacement eggs. The supernumerary eggs (those produced beyond the normal clutch size) weighed less and contained disproportionately lower lipid content than earlier-laid eggs, and the hatchlings from these supernumerary eggs were less likely to survive than young hatchlings from earlier-laid eggs (Nager et al. 1999, 2000). A subset of these females were provided supplemental food during egg laying, and

these females produced more eggs and larger eggs, which improved offspring survival relative to nonsupplemented females (Nager et al. 1999), demonstrating how resource acquisition can influence parental investment and generate positive associations among life-history traits (e.g. clutch size and egg size).

In addition to mediating life-history traits such as fecundity and survival, maternal quality is predicted to influence a mother's relative investment in sons and daughters (Trivers and Willard 1973; Charnov 1982; Frank 1990; West 2009). Trivers and Willard (1973) originally conceived the idea that maternal quality should influence the sex ratio that a mother produces, and their hypothesis has subsequently been broadened to explain why females should invest in 1 sex over the other across a variety of conditions that influence the quality of offspring at the time of independence from parental care (reviewed in Cockburn et al. 2002; West 2009). Generally, increased allocation of resources is predicted to benefit sons' future reproductive success to a greater extent than daughters' (Figure 1A in Krist 2006); thus, Trivers–Willard theory predicts that mothers with above-average ability to invest in offspring should overproduce sons relative to mothers with lower investment ability (see also Carranza and Polo 2012; Pryke and Rollins 2012; Bowers et al. 2013a). Similarly, Myers (1978) hypothesized that the sex ratio should be female biased particularly when resources are in

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short supply in species in which males are more sensitive to stressful conditions than females and emphasized that females should maximize the number of offspring that survive to reproduce rather than the expected reproductive success of individual offspring (i.e., the Trivers–Willard model). Thus, if either sex is more sensitive to stressful conditions, mothers can maximize the number of offspring that survive to independence by overproducing the less-sensitive sex. A critical insight that has begun to emerge from subsequent work is that measures of maternal condition traditionally used by evolutionary ecologists (e.g., body mass or size) often explain less variation in offspring sex ratios than variables that more closely reflect a female's ability to rear high-quality offspring (Sheldon and West 2004; Pryke and Rollins 2012). Although morphological or physiological variables could certainly be indicative of maternal quality, behavioral variables that better reflect overall reproductive effort or investment ability, such as a female's ability to produce supernumerary eggs in response to egg removal, have the potential to offer new insights (see also Sheldon and West 2004; Robert et al. 2010; Bowers et al. 2013a).

In a recent study, we used an egg-removal treatment that increased the number of eggs laid by female house wrens (*Troglodytes aedon*) and found that supernumerary eggs declined in mass relative to earlier-laid eggs (Bowers et al. 2012a). Females laying extra eggs were less likely than unmanipulated females to attempt another brood later in the same season, and manipulated females that attempted another brood took longer to do so and laid fewer eggs than unmanipulated females (Bowers et al. 2012a). The ability to produce extra eggs beyond what a female would normally produce is strongly resource dependent: females with access to greater nutritional resources are able to produce more eggs in response to an egg-removal treatment than females on poorer quality diets (Nager et al. 1999; Williams and Miller 2003; Mänd et al. 2007). Therefore, in this study, we used the egg-removal treatment to reveal an aspect of maternal quality, as high-quality mothers are more capable of producing extralarge clutches than low-quality mothers. We then used this measure to predict the sex ratio among their eggs.

Adult male house wrens frequently obtain multiple mates and engage in extrapair copulations (Soukup and Thompson 1997; Johnson 1998; Albrecht and Johnson 2002; Forsman, Vogel, et al. 2008; Johnson et al. 2009), thus increasing variance in the reproductive success of males relative to females. Moreover, the quality of the posthatching environment persists into adulthood and carries sex-specific consequences, as sons that receive increased allocation as neonates and are in good condition prior to independence enjoy increased reproductive success relative to daughters reared in similar conditions (E. K. Bowers, unpublished data). Thus, females with above-average ability to invest in offspring are predicted to overproduce sons relative to those with a lower capacity to invest. As such, mothers able to produce more eggs (i.e., 9 or 10 eggs) in response to the manipulation were predicted to produce a male bias relative to mothers that were subjected to the same manipulation but producing fewer eggs (i.e., 6 or 7 eggs).

Aside from adjusting clutch sex ratios, mothers have also been shown to modify the sex of individuals within clutches in relation to prehatching investment (Rutkowska and Cichoń 2002; Cichoń et al. 2003; Rubolini et al. 2009; Martyka et al. 2010; Saino et al. 2010). Female house wrens often produce sons and daughters in unequal frequency along the egg-laying sequence, and the position of sons and daughters in the posthatching size hierarchy has sex-specific effects on offspring quality, as sons suffer to a greater extent than daughters from hatching late and having to compete

with older siblings (Bowers et al. 2011; see also McDonald et al. 2005; Bogdanova and Nager 2008). Thus, we compared individual eggs within clutches to test whether the reduced allocation of resources to supernumerary eggs influenced the sex of individual offspring. Within clutches, we predicted that the proportion of daughters would increase among supernumerary eggs (eggs 8–10), which would hatch offspring that would be younger and smaller than offspring hatching from earlier-laid eggs (eggs 5–7; Carranza 2004).

METHODS

Study site and species

We studied a box-nesting population of house wrens in 2010 at the East Bay study area in north-central Illinois, United States (40°39'12"N, 88°55'W) in secondary deciduous forest. Nestboxes ($N = 120$) were mounted above aluminum disks (diameter = 48.3 cm) on 1.5-m metal poles to discourage nest predators and spaced 30 m apart along transects oriented in the north and south direction separated by 60 m (density = 5.4 nestboxes/ha). Lambrechts et al. (2010) provide details on nest-box construction materials and dimensions. House wrens are small (10–12 g), migratory songbirds with a breeding range spanning the midsection of North America (Johnson 1998). Males typically arrive on the study area in late April, and select and defend a nest-box within which they begin nest construction by creating a platform of sticks. Females arrive slightly later than males, select a mate, and complete nest construction prior to laying eggs; females lay 1 egg/day until their clutch is completed, laying a mean of 6.7–7.0 eggs for clutches produced in the first half of summer (Table 1 in Dobbs et al. 2006). Only females incubate eggs and brood hatchlings, and the time at which the female initiates incubation relative to clutch completion determines the degree of hatching asynchrony of the eggs within a clutch, which has a profound influence on subsequent offspring development and survival (Bowers et al. 2011, 2013b). Approximately half of the females that complete a successful nesting attempt early enough in the breeding season attempt a second brood on the study area (Bowers et al. 2012a,b). Female house wrens readily produce additional eggs if eggs are removed from the nest during the laying stage (see Procedures and experimental design and further details in Bowers et al. 2012a).

House wrens are suitable for studying sex allocation because mothers routinely allocate the sexes of their offspring according to sex-allocation theory across a range of social and ecological conditions, despite the fact that male and female offspring are sexually size monomorphic (Bowers et al. 2011, 2012b). Although Trivers–Willard theory has traditionally been thought to be more applicable to sexually size-dimorphic species than to species with sexual size monomorphism (Sheldon and West 2004; West 2009), there is accumulating evidence that a unit change in parental investment, or variation in the rearing environment, can induce sex-specific effects on offspring that are sexually size-monomorphic (Rosivall et al. 2010; Bowers et al. 2011; Pryke et al. 2011). Thus, sexually size-monomorphic species are useful for testing sex-allocation theory because sex-ratio adjustment should be attributable to differences in the effect that variation in parental effort has on the reproductive potential of male and female offspring rather than to differences in the physiological or energetic costs of producing either sex (see also McDonald et al. 2005; Bowers et al. 2013a).

Procedures and experimental design

Beginning in May 2010 and continuing over the next 4 weeks (i.e., the first brood of the breeding season), we visited nest-boxes at least twice weekly to check for female settlement. On finding evidence of female settlement (presence of a lined nest), we visited nests daily thereafter to number eggs with nontoxic markers and to weigh them the morning each was laid to the nearest 0.001 g with an electronic balance (Acculab Pocket Pro 2060D). We removed eggs 2–5 in the laying sequence on the morning each was laid, leaving 1 egg in the nest throughout this time to avoid female abandonment. We stored eggs 2–5 in the laboratory at constant, air-conditioned room temperature (ca. 21 °C) and returned them to nests on the morning that females laid their sixth egg. Most females continued to produce eggs for several days until the tactile stimulation of eggs on their brood patch led to a cessation of egg production and initiation of full incubation (Lea and Klandorf 2002; Vleck 2002). Egg production did not end instantaneously, so females produced supernumerary eggs (Bowers et al. 2012a). These subsequently laid eggs were numbered and weighed on the morning each was laid. Once females finished laying eggs and commenced full incubation, we trapped them inside their nest-box using a sliding trap door or using mist nets outside the nest-box. We delayed capturing females until approximately halfway through incubation because they abandon the nest if captured earlier (C.F. Thompson, unpublished data), so we were unable to obtain data on females prior to implementing the egg-removal treatment. Although we standardized the timing of female capture, our data on female body mass does not represent female mass immediately prior to oviposition; thus, we did not attempt to establish a correlation between maternal body mass and the sex ratio here (see Sheldon and West 2004).

We removed eggs 5–10 (if present) from nests once females had completed their clutch and commenced full incubation. On the same day, we transferred these eggs to the laboratory for incubation in a Grumbach 8014 compact S84 incubator for 7–8 days (conditions described in Robinson et al. 2008). After incubation, we extracted embryos, rinsed them thoroughly with sterile water, and stored them in Queen's lysis buffer (Seutin et al. 1991) for later DNA extraction and PCR-based sexing using the primers described by Kahn et al. (1998; see Bowers et al. 2011 for further detail). Because we sought to test whether offspring sex varied among eggs 5–10, only these eggs were transferred to the incubator and subsequently sexed. Thus, our sex-ratio data are for eggs 5–10 and not for the entire clutch.

Data and analyses

The eggs analyzed here were produced by females in a previous study (Bowers et al. 2012a), in which we demonstrated that the egg-removal treatment significantly increased clutch sizes relative to what females ordinarily would produce. Here we analyze the sex of offspring produced by these females but do not analyze clutch size or the effect of our treatment on egg mass per se, as these data are reported elsewhere (Bowers et al. 2012a). We included data only for clutches for which the female ceased egg laying and commenced full incubation ($N = 31$), and each clutch was produced by a different female. We used SAS statistical software (SAS 9.3, SAS Institute, Cary, NC) for our analyses, and all tests are two tailed. We first analyzed among-nest variation in sex ratios of the collected eggs (i.e., eggs 5–10 if all were present or had been produced) using logistic regression (PROC GENMOD in SAS) with the number of male offspring among the collected eggs as the dependent variable and the number of offspring sexed as the binomial denominator (i.e.,

Table 1

Distribution of eggs that were not sexed in relation to egg number and clutch size (see text for details)

Clutch size	Egg number					
	5	6	7	8	9	10
6	2	2	—	—	—	—
7	0	2	1	—	—	—
8	2	2	3	1	—	—
9	1	0	1	1	1	—
10	0	3	2	3	2	0

events/trials syntax) using binomial error variance and a logit link function. This analysis included the total number of eggs a female produced (i.e., clutch size) as a fixed effect. We were unable to sex 29 of 129 eggs collected from nests because the egg was either infertile or embryonic development in the incubator stopped at such an early stage that we were unable to obtain useable DNA for amplification. There was no association between clutch size, female body mass, and relative egg mass or laying order on the probability of sexing an egg successfully (all $P > 0.3$; using absolute values of egg mass and laying order yields the same conclusions; see also Table 1). Although the percentage of unsexed offspring (22%) was higher than desired, it is important to note that this does not preclude a reliable analysis of sex-ratio data and should create only noise, not a bias, in our results (see Krackow and Neuhauser 2008). Indeed, the sample of unsexed offspring would have to be extremely biased toward either sons or daughters to create a difference between the true primary sex ratio and the sex ratio we measured (West 2009).

We then analyzed variation in the sex of individual offspring among eggs 5–10 ($N = 100$ eggs) using a generalized linear mixed model (GLMM; PROC GLIMMIX) with maternal identity as a random effect and a binary distribution and logit link function (Krackow and Tkadlec 2001). We tested whether relative egg mass (the difference between the fresh weight of each egg and the clutch mean; Krist and Remeš 2004), relative laying order (egg number divided by clutch size), and the interaction of the 2 influenced the sex of individual offspring. We used values relative to the rest of the clutch to facilitate comparisons of clutches that differed in size, and we also used absolute values of fresh egg mass and laying order in a separate model to compare the 2 approaches. We used 2 separate models that differed by their use of relative versus absolute values of egg mass and laying order to avoid multicollinearity, but analyzing offspring sex using absolute and relative values in a single model yields the same qualitative results (not shown). We did not use a model-simplification procedure (i.e., remove the nonsignificant interaction between relative laying order and relative egg mass) because we had predicted a priori an interaction between these variables in their effect on offspring sex.

RESULTS

Offspring sex ratio

As reported previously, our egg-removal manipulation significantly increased the number of eggs produced by females relative to that which they would normally produce (means \pm SE = 8.2 ± 0.3 eggs for females in this study vs. 6.6 ± 0.1 eggs for unmanipulated females; Bowers et al. 2012a). Females also varied widely in their response to our manipulation, as females subjected to the egg-removal treatment displayed much more variation in clutch size

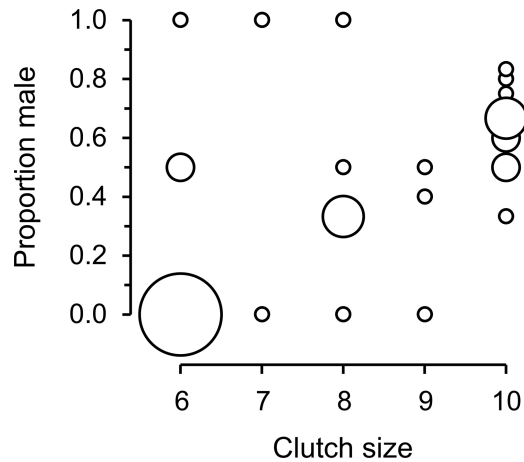


Figure 1

Sex ratio (proportion of male offspring) of collected eggs 5–10 in relation to clutch size. Bubble sizes are proportional to the number of overlapping data points: the smallest bubbles represent a single clutch, the next 2 larger sizes represent 2 and 3 clutches, and the largest bubble represents 6 clutches.

(coefficient of variation = 0.205) than unmanipulated females (coefficient of variation = 0.127). The sex ratio of offspring produced from eggs 5–10 was positively correlated with clutch size (logistic regression parameter estimate \pm SE = 0.387 ± 0.152 , $\chi^2 = 6.51$, $P = 0.011$; Figure 1). The females that produced the largest clutch sizes in response to our egg-removal treatment overproduced sons, and the females that produced fewer eggs in response to the egg-removal treatment overproduced daughters (Figure 1).

Individual offspring

As we previously documented (Figure 4 in Bowers et al. 2012a), the mass of eggs increased with the order in which they were laid until females produced the sixth egg, after which the mass of subsequent, supernumerary eggs declined. The sex of individual eggs was correlated with relative laying order (parameter estimate \pm SE = -2.77 ± 1.33 , $F_{1,96} = 4.35$, $P = 0.040$), such that the proportion of sons was higher in earlier-laid than in last-laid eggs (Figure 2A), but there was no effect of relative egg mass (parameter estimate \pm SE = 19.3 ± 16.5 , $F_{1,96} = 1.36$, $P = 0.246$), and no interaction between relative egg mass and laying order in their effects on offspring sex (parameter estimate \pm SE = -25.5 ± 16.5 , $F_{1,96} = 1.71$, $P = 0.195$).

We also performed these analyses using absolute values of egg mass and egg number instead of values relative to the rest of the clutch. Unlike relative laying order, there was no correlation between absolute egg number and offspring sex (parameter estimate \pm SE = 2.08 ± 2.18 , $F_{1,96} = 0.91$, $P = 0.342$; Figure 2B); there was also no association between fresh egg mass and sex (mean egg mass \pm SE = 1.41 ± 0.1 g for each sex; parameter estimate \pm SE = 10.2 ± 11.2 , $F_{1,96} = 0.91$, $P = 0.365$), and no interaction between egg mass and egg number (parameter estimate \pm SE = -1.54 ± 1.57 , $F_{1,96} = 0.95$, $P = 0.332$).

DISCUSSION

Our egg-removal manipulation increased egg production and reduced allocation into individual eggs (see Bowers et al. 2012a). Given the extent to which egg production is limited by nutrient availability (Graveland et al. 1994; Johnson and Barclay 1996; Tilgar

et al. 2002; Mänd and Tilgar 2003; Zanette et al. 2006), females clearly have a limited capacity to invest in eggs beyond what they normally produce (Williams and Miller 2003; Wagner and Williams 2007). As predicted, mothers producing larger clutches in response to egg removal produced a male bias relative to mothers that produced fewer eggs. Although it is predicted that an increase in parental ability, as reflected by the number of young produced, should correlate with an increase in the proportion of sons within a clutch or litter (Williams 1979; Figure 3 in Frank 1990), our findings conflict with those of other studies that did not detect a correlation between clutch size and sex ratio (Westerdahl et al. 1997; Kölliker et al. 1999; Whittingham and Dunn 2000; Leech et al. 2001; Rosivall et al. 2004) although one might not necessarily expect a correlation between clutch size and the sex ratio in unmanipulated clutches if clutch size is individually optimized. Indeed, variation in the size, number, and sex of offspring can create confusion surrounding predictions of sex-allocation theory, as high-quality mothers might maximize their fitness simply by producing more offspring rather than by manipulating the sex of a smaller number of progeny (Frank 1990; Carranza and Polo 2012). Myers (1978) suggested that if either sex is more sensitive to harsh environmental conditions, mothers should produce an excess of the less-sensitive sex under such conditions to maximize the number of surviving offspring. This differs from the Trivers–Willard model, in which sex ratios are adjusted to maximize the expected reproductive potential of offspring at independence, and Myers' model predicts that the less-sensitive sex should be overproduced when resources are in short supply (see also Merklings et al. 2012). In house wrens and other species, sons are more sensitive than daughters to environmental conditions early in life (Bogdanova and Nager 2008; Sockman et al. 2008; Rosivall et al. 2010; Bowers et al. 2011; E. K. Bowers, unpublished data). Thus, our data on the sex ratio of collected eggs are consistent with Myers' (1978) model, as females producing small clutches overproduced daughters; on the other hand, our finding that females overproduced sons among earlier-laid eggs and daughters among later-laid eggs is also consistent with the prediction that parents should respond to the anticipated reproductive potential of individual offspring. Similarly, in a recent study on collared flycatchers (*Ficedula albicollis*), the proportion of sons that females produced among their own young was positively correlated with the body mass of foster offspring they reared to independence (Bowers et al. 2013a).

We previously determined that sons and daughters occur in relatively equal frequencies across the laying sequence in synchronously hatching broods, but that there is a sex-biased laying order for asynchronously hatching broods (Figure 5 in Bowers et al. 2011; see also Albrecht 2000). We could not determine whether eggs would have hatched synchronously or asynchronously in this study because we removed eggs from nests on the day they were laid, thus disrupting the normal course of incubation the eggs would otherwise have undergone. It is important to note, however, that differences in allocation toward individual offspring still predict a sex bias among eggs of differing size, regardless of hatching asynchrony. It is also worth noting that a correlation between relative laying order and offspring sex was detected within clutches (Figure 2A) despite the fact that sons and daughters were produced in equal frequencies among nests with respect to egg number (Figure 2B), thereby demonstrating the value of within-clutch comparisons (see Krist and Remeš 2004; Rosivall 2008). The discrepancy in results suggests that females allocate sex to eggs in the laying sequence in a manner that is clutch-size dependent and not in relation to absolute egg number although evidence for this from other studies is mixed

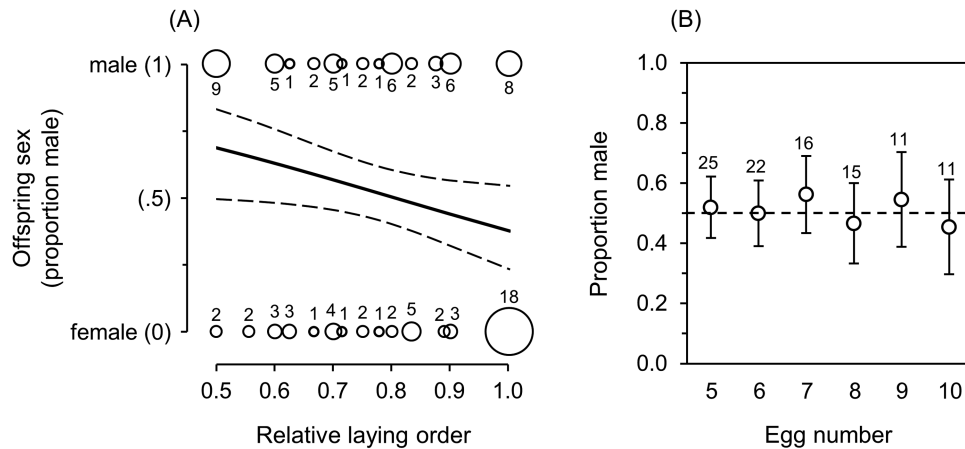


Figure 2

(A) The sex of individual eggs in relation to their laying order relative to the rest of the clutch (last-laid eggs have a relative laying order of 1.0; see text for details). Bubble sizes reflect the number of overlapping data points, which are given, and the solid curve represents the probability of producing a son \pm 95% confidence limits. (B) Mean proportion of male offspring \pm SE in relation to absolute egg number (numbers above points are sample sizes).

(Cichoń et al. 2003; Johnson et al. 2005; Ležalová et al. 2005; Bowers et al. 2011, 2013a).

Egg size represents an important source of maternal investment, as it positively predicts offspring size and other fitness-related traits after hatching (Styrsky et al. 1999, 2000; Krist 2009, 2011; Love and Williams 2011); thus, we predicted that large eggs would more likely contain sons and smaller eggs would more likely contain daughters (Cordero et al. 2000, 2001; Martyka et al. 2010). The lack of a correlation between egg mass and offspring sex may be attributable to constraints on the ability of females to allocate egg size differentially to sons and daughters. Because offspring sex is determined immediately prior to ovulation, it is unlikely that mothers can appreciably alter their allocation to individual oocytes during the brief window of time between meiosis and ovulation; in contrast, the maturation of premeiotic follicles provides ample time for ecological cues to influence allocation to oocytes prior to meiosis (Young and Badyaev 2004; Badyaev et al. 2005, 2006, 2008). Consequently, the yolk environment may influence offspring sex prior to ovulation or oviposition (Rutkowska and Badyaev 2008; Tagirov and Rutkowska 2013). Thus, the potential for sex-specific allocation within the egg remains (see also Chin et al. 2012), but this would seem more likely to be manifested by adjusting offspring sex in response to egg constituents rather than adjusting allocation of resources to eggs in response to offspring sex (but see Saino et al. 2010).

Notwithstanding the potential constraints to adjusting egg size in response to offspring sex, the order in which eggs form prior to oviposition, and the maternally derived compounds they contain, may account for the biased sex ratios we have observed across the laying sequence (see, Pike and Petrie 2003; Alonso-Alvarez 2006; Sockman et al. 2006; Rutkowska and Badyaev 2008). Variation in maternally derived hormone concentrations has been shown to influence the formation of cytological morphology in dividing cells, which can create non-Mendelian segregation of sex chromosomes during meiosis (Rutkowska and Badyaev 2008). Alternatively, differences in the growth rate of follicles within an ovary prior to ovulation could cause sex-specific ovulation order (Badyaev et al. 2005), which is consistent with the notion that sons and daughters frequently differ in their sensitivity to early environmental or hormonal conditions (Myers 1978; Sockman et al. 2006, 2008). Significant sex-ratio bias within clutches from day to day, without gaps in egg laying, may suggest sex-ratio adjustment prior to ovulation, but a recent

hypothesis posits that maternally derived hormones could influence the sex of embryos after meiosis and ovulation but before oviposition via sex-specific growth of early chimeric embryos (Tagirov and Rutkowska 2013). According to this hypothesis, the hormonal milieu experienced by the zygote can promote the retention of the first polar body formed during meiosis and, then, with polyspermic fertilization, create ZZ- and ZW-bearing cells within a single blastodisc/embryo. Variation in the hormonal profile of the yolk could then cause the female or male cells to divide at an unequal rate such that cell division for 1 sex eventually ceases while the other sex's cells proliferate and form the embryo (Tagirov and Rutkowska 2013). This novel hypothesis assumes that segregation can be random and that follicles are ovulated in their traditionally assumed early hierarchical order; this hypothesis is also consistent with the notion that sons and daughters frequently differ in their sensitivity to the hormonal milieu of the yolk (see also Sockman et al. 2006, 2008).

Whether vertebrate mothers allocate the sexes according to prediction remains controversial (Wheelwright and Seabury 2003; Uller 2006), contributing to sustained interest in vertebrate sex allocation. Given that many factors influence optimal allocation to sons and daughters (Leimar 1996; Hewison and Gaillard 1999; Hewison et al. 2005; Wild and West 2007), the context dependence of sex adjustment can cause sex ratios to vary widely in time and space (see also Forsman, Hjernquist et al. 2008; Hjernquist et al. 2009; Taff et al. 2011; Baeta et al. 2012; Michler et al. 2013). Further work integrating ecological conditions with maternal physiology may shed light on the mechanism(s) by which sons and daughters are produced with changes in maternal quality (see also Bowden et al. 2000; Love et al. 2005; Sockman et al. 2006; Bonier et al. 2007).

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