



## Variation in female mate choice and mating success is affected by sex ratio experienced during early life



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Females vary in their mate choice and consequent fitness outcomes. Individual differences may be explained by conditions experienced early in life. We tested whether the sex ratio at which young pheasants, *Phasianus colchicus*, were reared affected their adult sexual behaviour. Females reared in equal sex ratios discriminated strongly between males of differing attractiveness in choice tests and had the lowest variance in mating success. Conversely, females reared in female-biased sex ratios showed little discrimination between males based on their attractiveness, and exhibited highly skewed mating success with the majority gaining no copulations, but a quarter each gaining more copulations than any other female in the study. Early life environmental determination of variation in female choice could explain the lack of uniformity in mate choice and hence maintain variation in male traits in the face of directional sexual selection.

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Individual females typically differ from one another in their mating preferences (Jennions & Petrie 1997). Differences in their preferences may be driven by external factors that exert their effects early in life, with consequences only seen as individuals become sexually mature (Lindström 1999). Components of an individual's early social environment affect mate preference functions. These can include the presence of adults of one sex (Adkins-Regan & Krakauer 2000), tickling and play (Paredes-Ramos et al. 2011, 2012) and being reared in groups of single-sex young (Mansukhani et al. 1996).

One component of the early social environment likely to affect adult sexual behaviour is the sex ratio at rearing. This may act directly by affecting the process of sexual imprinting (ten Cate & Vos 1999). In extreme cases, individuals reared in single-sex groups switch their sexual preferences to exhibit homosexuality (Field & Waite 2004). Alternatively, or in addition, the sex ratio early in life may act indirectly on mate preference, modulating the individual's hormone profiles by altering the levels of intrasexual and intersexual competition that an individual experiences (Dhondt 1970; Oddie 2000) leading to differential hormonal levels

being experienced during development (Hirschenhauser & Oliveira 2006). Steroid hormone levels early in development affect development of partner choice in mammals (Henley et al. 2011) and birds (Burley & Foster 2004).

Pheasants, *Phasianus colchicus*, operate a polygynous, nonresource-based mating system in which males defend a harem of females. Females appear to make free choices among males, probably based on male morphology (Göransson et al. 1990; Mateos & Carranza 1995), courtship behaviours (Mateos & Carranza 1999) or complementary MHC (Baratti et al. 2012). Despite the opportunity for free choice, and males being able to hold a harem of five or more females, the distribution of females between males reveals that few individual males have especially large harems; instead, many have just one or two females (Ridley & Hill 1987). Clutches comprise an average of 13 eggs, but occasionally include over 25 eggs (Hill & Robertson 1988). Pheasant broods typically have an even sex ratio on hatching (Rodgers 1984), but this can vary (Latham 1947; Dale 1952). Chicks are precocial and remain with their mother for 7–8 weeks (Hill & Robertson 1988). During this period around a third of the brood will die, often from predation, farming machinery or exposure (Riley et al. 1998). Such stochastic events can lead to biases in the sex ratio of the remaining brood. We tested how three different early sex ratios (male biased, female biased and equal) experienced by pheasants in the first 7 weeks of

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life affected their patterns of mate choice and subsequent mating success as adults, 10 months later.

## METHODS

### *Rearing Birds at Different Sex Ratios*

Nine hundred 1-day-old pheasant chicks were obtained in June 2010 from a commercial hatchery and were sexed using wattle presence as a cue (Woehler & Gates 1970). Our accuracy of sexing birds, confirmed by comparing their putative sex at 1 day old with their sex determined on release at 7 weeks old when adult plumage was well established and visual sexing uncontroversial, was high: we misclassified 38/888 (4.3%) birds that survived to 7 weeks. All individuals were marked using numbered plastic patagial wing tags (Roxan Ltd, Selkirk, U.K., [www.roxan.co.uk](http://www.roxan.co.uk)). Individuals were allocated randomly to one of three rearing treatments in which they remained for the first 7 weeks: a male-biased sex ratio, with 20 males and 10 females per pen; an equal sex ratio, with 15 males and 15 females per pen; and a female-biased sex ratio, with 10 males and 20 females per pen. Each treatment had 10 replicates in visual, but not auditory isolation from the other replicates. For the first 2 weeks, chicks were confined to an enclosed, heated shed (130 × 130 cm). After 2 weeks they were allowed access to an open grass run (130 × 680 cm), as well as the shed. All treatments were supplied with identical diets (commercial, age-appropriate feeder pellets provided ad libitum in standard plastic feeders, and water supplied ad libitum through standard plastic drinkers) and tended by staff at the game farm who were naïve to the hypotheses being tested. Any birds that died during rearing were replaced by a sex-matched individual drawn from a pool of replacement birds that were reared at approximately equal sex ratio. A total of 75 birds died during rearing. These deaths were spread fairly evenly across treatments (27 male bias, 19 female bias and 29 equal), with nine male bias replicates, eight female bias replicates and 10 equal-sex replicates containing replacement birds. These replacement birds were simply there to maintain the experimental rearing ratios and were individually marked. They were excluded from our subsequent analyses because they had not spent all their early rearing in the experimental treatments. The work was approved by the University of Exeter Psychology Ethics Committee (Approval 2007/015).

### *Releasing and Recapturing Birds*

At 7 weeks, the birds from all of the treatments and replicates were mixed together and placed in a large (ca. 70 × 60 m) open-topped pen in woodland in mid-Devon, U.K. The pen contained feeders and drinkers that provided ad libitum access to food and water, along with natural and artificial shelter. Birds could disperse from or re-enter the pen at will by flying over the fence or using gates in the fence.

Birds were recaptured by the gamekeeper at the end of the shooting season 2011 using large walk-in traps (3 × 3 m and 1.2 m high), baited with grain and containing food, water and natural cover. The traps were visited each day by the gamekeeper. These birds were taken to a commercial game farm for breeding in the forthcoming year.

Thirty of our experimental adult females were captured and used by the gamekeeper for breeding the following season. These comprised 12 hens from the female-biased treatment, and nine from each of the equal and male-biased treatments. At the end of March 2011, females were placed in laying pens measuring 4 × 12 m, which were roofed with netting, had a grass floor and contained perch sites and shelters. Each pen contained six hens

comprising two hens from the female-biased treatment, one hen that had not been in any of our treatments, and either one or two hens from the equal and male-biased treatments; three pens had two hens from the equal treatment and one from the male-biased treatment and three pens had two hens from the male-biased treatment and one from the equal treatment. A cock pheasant was introduced to the pen on 1 April. All pens were supplied throughout the observation period with commercial poultry food ad libitum, as well as water and ground shells to provide a calcium and nutrient source during egg production. All birds were returned to the wild by the gamekeeper at the end of May 2011.

### *Observing Adult Mating Behaviour*

We conducted a series of 12 observation periods on each pen, each lasting 30 min, between 20 April 2011 and 13 May 2011, at the peak of the mating and egg-laying period. One set of observations was collected from each pen on the same day, between 0830 and 1600 hours with the times and order in which pens were observed being randomized between days. During these observation periods, we recorded a total of 49 copulations with our treatment females. These were highly conspicuous, typified by the cock pheasant performing a display and then jumping on the hen's back, and beating his wings vigorously as he copulated, followed by his descent from the female to crow and in some cases attacking the female (pecking at her) as she stood shaking her wings. Females could escape this male harassment by moving to other areas of the pen. We did not observe any injuries arising from these interactions.

### *Measuring Mate Choice by Adult Hens*

We exposed six hens from each treatment group to binary mate choice tests on 15 April 2011. Each hen was placed in a central choice chamber (400 × 150 cm). At either end was a male, separated from the female by plastic mesh, so that she could see both males simultaneously. The choice chamber was divided, by external markings on the frame, into three equal-sized areas, with one corresponding to each male and the central area reflecting a zone of indecision. The males had not encountered the test females in the previous 4 months, although as they had been caught from the same shooting estate we cannot be certain that they had not encountered the females previously. Each hen was given 5 min to acclimatize and then observed for a further 5 min; the time that she spent in each of the three areas was recorded. We used three different pairs of males, with two females from each treatment being tested with each pair.

Within each pair of males, we assigned one as the preferred male and one as the nonpreferred male. Our assignment was based on two methods. Prior to testing, we collected morphometrics from each male and compared them between males. As female choice of pheasants is based on multiple morphometric and behavioural elements (Göransson et al. 1990; Mateos & Carranza 1995, 1999; Baratti et al. 2012) we considered three measures that were simple to collect from live birds and have previously been correlated with mating success: mass, spur length and wattle height. We corrected for body size for the spur length and wattle height by dividing each of these measures by the male's tarsus length. We did not measure tail length as four of six males had broken tails. We designated the preferred male as the one that was larger, had longer spurs and a larger wattle. In one pairing, one male was larger than the other in all three measures, while in the other two pairs, one male was larger than the other in two of the three measures. Following testing, we compared the total amounts of time across all females that were spent next to each male during the test and designated as

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