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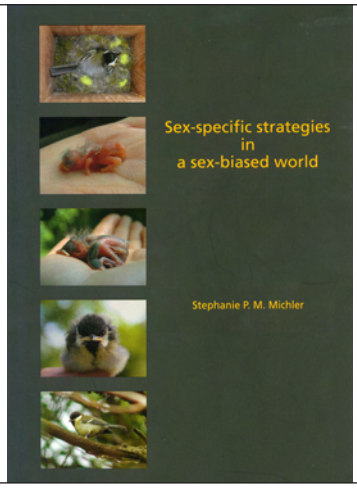
Michler S.P.M. 2009. Sex-specific strategies in a sex-biased world. PhD thesis, University of Groningen, The Netherlands. ISBN: 978-90-367-4175-0, paperback, 200 pp. Available at http://irs.ub.rug.nl/ppn/323869076.



The evolution of sex allocation has generated a wealth of empirical and theoretical studies, yet we are still unable to predict the direction of sex-ratio bias in many species. In part, this has been attributed to environmental heterogeneity leading to spatial and temporal variation in selective pressures, such that male-biased allocation may evolve in one environment but female-biased in another. To complicate this further, these selective pressures may affect males and females differently (leading to conflict between the sexes over sex allocation). It is therefore vital that the local environment is taken into consideration when studying sex allocation. Stephanie Michler's thesis elegantly tackles this important research field using a combination of experimental and statistical techniques to unravel the effects that sex-biased natal dispersal, and sex-biased competitive abilities over resources, have on sex allocation.

Michler's thesis contains five data chapters and four boxes, which are structured into three parts. The first part investigates whether parental provisioning is a mechanism through which parents manipulate sex allocation, and the extent to which parental provisioning is influenced by sibling competition. The second part moves on to examine how environmental heterogeneity, primarily in terms of the local population sex-ratio, influences juvenile survival and post-fledging dispersal. The third part then asks whether females facultatively vary their brood sex-ratio according to the local environment.

Michler's first data chapter, Chapter 2, asks whether parents alter their provisioning behaviour in relation to sex, at both the brood and offspring level. This was possible due to a large-scale manipulation of the sex ratio of the first broods of Great Tits *Parus major*, in four plots in 2004 in the Lauwersmeer area, in the northeast of The Netherlands. These manipulations largely enabled separation of the potentially confounding effects of environmental or genetic variation in quality in relation to brood sex-ratio. Michler concluded, in accordance with other studies, that both parents provisioned male and female offspring at the same rate. The real insight however, was gained in the finding that although the overall amount of food provisioned did not differ with brood sex-ratio manipulation, male-biased broods were fed larger prey, less frequently. Male Great Tits are slightly larger than females and have been shown to have a competitive advantage over females under certain conditions. Altering the frequency and prey load of provisions may therefore represent a mechanism through which parents can influence the level of intra-brood competition.

The second part of the thesis takes the experiment to an impressively large scale, this time manipulating the sex-ratio and juvenile density of 12 plots, over three years, to investigate their effects on fledgling dispersal, and adult and juvenile survival. Importantly, Michler first confirms that the manipulations of brood sex-ratio in the first two years lead to sex-biases at the plot (local) scale up to five months after fledging. She also

shows that the effects of the juvenile density manipulations were much weaker. Chapter 3 analyses the manipulations in 2005 and 2006 and represents the first experimental study within a natural population to show an effect of local sex-ratio on the fitness component of apparent juvenile post-fledging survival, using mark-recapture models. Apparent and not real survival was estimated because emigration could not be ruled out, due the open nature of the study site. Michler predicts that male-biased plots should experience increased competition (due to the sexual dimorphism) and that this should lead to decreased juvenile survival. Although this trend was apparent in the first year, the opposite trend was observed in the second year and no sex-specific effect was detected. Michler suggests that although the sex-ratio of the local population affects apparent juvenile survival of both sexes, context dependent factors may shape the direction of this selection pressure.

The same experimental approach was then used in Chapter 4 to investigate whether local sex-ratio and juvenile density affect post-fledging dispersal, and whether there are differential effects on the sexes. Female fledglings dispersed further from male-biased plots, and male fledglings dispersed further from plots that had a high density of nestlings before manipulations. This is the first experimental study in a system of wild-living birds to demonstrate that the local social environment can play a role in differentially shaping the post-fledging dispersal patterns of males and females. The costs and benefits of dispersal are central to the evolution of social behaviour; these findings therefore have widespread implication. Furthermore, this is a nice finding as it suggests that the difference in apparent survival of juveniles according to sex-ratio treatment (Chapter 3) was not due to differential emigration rates, given that no sex-bias in apparent juvenile survival was detected (and assuming that no sex-biased long-distance dispersal occurs outside of the study area).

Chapter 5 asks whether the survival of juveniles and adults are affected by local sex-specific competition, using manipulations over three years. Due to competitive asymmetries in size and age, it was expected that adults versus juveniles and males versus females would show differences in survival in relation to manipulations of local juvenile sex-ratio and juvenile density. For example, male survival may be negatively affected by an increased density of juvenile males. However, no negative effects were detected in adults or juveniles as a result of increased density of same or opposite sex juveniles. Unexpectedly Michler found that juvenile survival increased with the density of same-sex fledglings, which she proposes may be due to behavioural or physiological changes that improve sex-specific juvenile competitive ability. An additional explanation in males is that higher densities of males may increase pressure on adult males to decrease their territory size, increasing the areas available for males to settle in.

The final part of the thesis focuses upon sex allocation, starting with Box C: An investigation of the error associated with the sexing of unhatched eggs. DNA was extracted and sexed from only ca. 60% of the unhatched eggs versus over 95% of the dead hatchlings, suggesting degradation of DNA in the unhatched eggs. No sex-bias was observed in dead hatchlings, but an apparent male bias occurred in unhatched eggs, however, this is likely to be an artefact of poor quality DNA – running a positive control within each sample would confirm this. This simple analysis highlights the importance of methodological rigour and calculation of error rates.

In the last data chapter, Michler shows that both first-year and experienced female breeders biased their broods towards females after experiencing a high nestling-density plot in the previous year (natural density for the first-year birds, experimental density for the experienced birds). This is in line with predictions from the Local Resource Competition hypothesis. The experiment demonstrates that sex-specific competition in the local environment is important in shaping sex allocation, which is the central theme of this thesis. By experimentally manipulating the level of local competition, Michler provides insight into the fitness consequences of the resulting patterns of sex allocation, in terms of the dispersal and survival patterns. She also highlights future research avenues, emphasising that more studies are required to understand the exact nature of local resource competition in female Great Tits (Box D), and whether sex allocation decisions lead to realised fecundity benefits.

Stephanie Michler's thesis is a lovely example of how carefully designed experiments can unravel subtle yet biologically important effects. Her findings have widespread application, for example, showing how provisioning should be analysed at both the level of the quantity and frequency of prey delivery. Her findings also highlight the importance of scientific rigour, and of long-term analyses to control for year-to-year variation. Overall this thesis represents a sound piece of evolutionary research that adds substantial knowledge to our understanding of how the local environment can shape sex allocation.

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