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Evolution of breeding systems: conflict and cooperation

Doctor of Science Dissertation

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Male Kentish plover attending a chick (credit: Su-shyue Liao)

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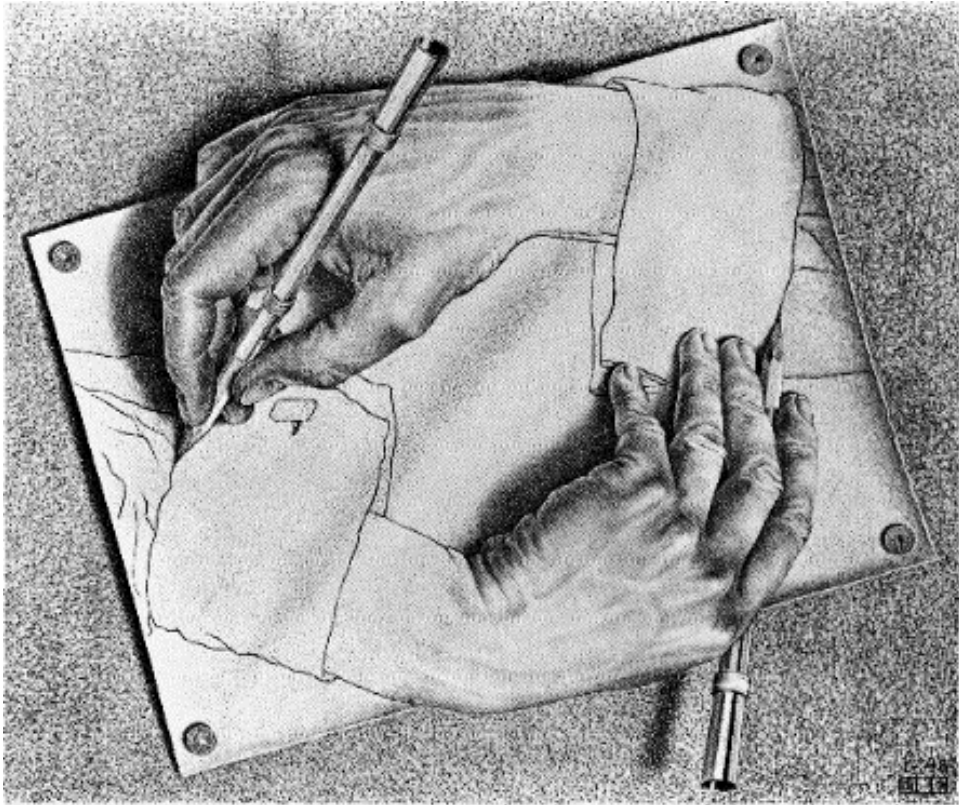
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Chapter 1. Introduction



Drawing hands (M.C. Escher, 1948)

Discovery consists of seeing what everybody has seen, and thinking what nobody has thought
(Albert Szent-Györgyi)

The evolution of mating systems and parental care came to the forefront of evolutionary biology via behavioural ecology research. The seminal ideas of Darwin (1871) on sexual selection in the evolution of animals and humans were only ignited much interest for well over a hundred years after their conception. Darwin summarised vast amount of information on sexual dimorphism in insects, birds and mammals, and argued that many of these flamboyant traits should have evolved not via natural selection (since it does not seem to increase the survival of the bearer), rather by sexual selection (providing advantage in reproduction). Darwin has recognised two types of sexual selection: intrasexual selection that is largely taking place between members of the same sex (usually among males), and intersexual selection that is takes place between sexes, often labelled as female choice.

Since the 1960'ies researchers re-discovered Darwin's long neglected ideas, and they gradually embraced them. For example, Orians (1969) used New World blackbirds to gain insight into sexual selection and Lack (1968) summarised much knowledge on mating system evolution and its link to ecology in birds. These research programmes eventually morphed into what we now call behavioural ecology and they benefitted three major advances: (1) modelling of male-female interactions in an explicit mathematical framework, (2) molecular ecology especially in DNA fingerprinting that allows establishing the genetic (as opposed to social) mating system, and (3) comparative analyses that tests adaptation using multi-species comparisons in an explicit phylogenetic framework building upon John Crook's work on weaverbirds (Crook 1964).

Behavioural ecology (or as often labelled, sociobiology) is by now an integral part of biological science. The former terminology (i.e., behavioural ecology) is usually used in England and Europe following the influential textbooks by John Krebs and Nicholas Davies, whereas the latter was made popular by E. O. Wilson's controversial tome on social behaviour (Wilson 1975). It is hard to imagine the uproar Wilson's innocent science-focused book has evoked: Wilson only extended the socio-behavioural scientific approach to humans and using these tools he dissected the social behaviour of *Homo sapiens*. This daring approach by a zoologist

this not bode too well with philosophers, social scientists and psychologist who traditionally view themselves as the ones responsible for understanding human behaviour.

A major player in the development of theory of reproductive strategies is Robert Trivers who published a series of influential papers on parental investment (Trivers 1972), conflicts between parents and offspring (Trivers 1974) and on condition-dependent sex allocation (Trivers-Willard 1973). Trivers' models generated immense interests on both sides of the Atlantic – they are among the most cited papers in evolutionary biology, and have been the source of both criticisms and appraisals (Houston et al. 2013).

Since early 1970'ies research on reproductive strategies run in roughly two main threads. On the one hand, researchers used Trivers (1972) parental investment model that provided a theoretical framework for Angus Bateman's experiments. Bateman (1948) worked with fruit flies (*Drosophila melanogaster*) and he wondered what may limit the reproductive success of males and females. He showed that the number of female mates limits the reproductive success of males whereas the number of male mates does not do so for the reproductive success of females (Bateman principle). The logic of Bateman & Trivers have been further advanced by Emlen & Oring (1977) and Davies (1992) by arguing that given the disparity of parental investment between males and females, more intense sexual selection is expected on males than on females.

On the other hand, Maynard Smith (1977) produced an influential model of parental behaviour in which care was an evolutionary response to costs and benefits of care that is partly dependent on the environment. An important component of the environment was mating opportunity, i.e. the chance to find a new mate once terminating parental care (Houston et al. 2013).

These two approaches are complementary since mating systems (and mating opportunities) do influence caring behaviour, and vice versa, parental care influences the type of mating system that evolves (McNamara et al. 2000, Székely et al. 2000). For instance, monogamy is often (but not always) co-occur with biparental care of the young, polygyny tends to be associated with female-only care whereas polyandry is with male-only care. However, which aspects of reproduction is “causing” the other aspects of reproduction is controversial, and probably involve various evolutionary feedback loops (see below).

1.1. Evolution of mating systems and parental care

Mating systems and parental care are among the most diverse social behaviours: courting, mating, pair bonding and various forms of parenting are termed together breeding systems (Reynolds 1996). These behaviours are often associated with morphological differences between males and females: sexual size dimorphism (SSD, Fairbairn et al. 2007). Courtship is especially highly variable between animals: whilst in majority of species the males court (or fight for) females and females are usually the ones that choose mate, in a small number of taxa these traditional sex roles are reversed. For example, in a small shorebird, the Eurasian dotterel *Charadrius morinellus*, the females are more ornamental and aggressive than the males, and they are the ones that court the males (reversed sex roles). In contrast to species with conventional sex roles in which the females look after the young in reversed sex role species (like the dotterel), the males are the ones taking care of the eggs and young. How such a diversity of mating system and parental care have evolved?

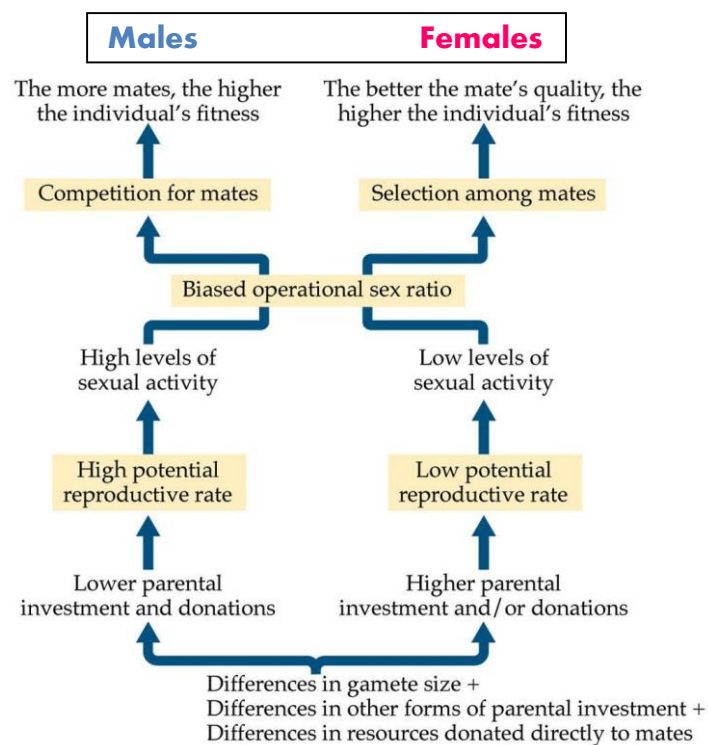


Figure 1.1. Hypothesised pathways that lead to male and female sex roles (Alcock 2009).

Behavioural ecologists usually investigate separately the components of breeding systems since specific research programmes focus on courtships, pair bonding and parenting. The specialisation of this field is reflected on the structures of behavioural ecology and animal

behaviour textbooks since specific chapters discuss mate choice and sexual selection, mating systems and parental care (Alcock 2009, Davies et al. 2012). Nevertheless, the logic of the whole field is reflected by Figure 1.1: the size difference between gametes leads to a sex difference in parental care, and the latter induces sexual selection and diverse mating and parenting strategies (Alcock 2009).

However, there are problems with this concept. First, recently we tested whether gamete investment predicts sex role in parental care using phylogenetic analyses of approximately 700 bird species. However, our analyses found no evidence that gametic investment (e.g. gamete size difference between males and females or reproductive organ size) would predict division of parental care between males and females (Liker et al. 2015). These empirical results are consistent with theoretical arguments that the presumed difference in male-female gametic investment should not explain the differences in sex roles (Jennions & Kokko 2010). Second, the connections appear to be unidirectional: there are causes and consequences. As I've mentioned above, the causality is ambiguous since positive and negative feedbacks may well work between different components of breeding systems. For example, the extent of parental care may be influenced by mating opportunity (Székely et al. 2000, Parra et al. 2014): this relationship happens to be in the opposite direction as shown on Figure 1.1. Third, the differences are exclusively led by the conflicting interests by males and females. As I argue in this dissertation, cooperation between parents also needs to be taken into account since parental cooperation may also shape breeding systems. Nevertheless, new theoretical analyses allow dynamic relationships between different breeding system components so interacting effects between different components can be analysed simultaneously (Kokko & Jennions 2008, Klug et al. 2010, Barta et al. 2014) – some of this has a cooperative nature.

1.2. Sexual conflict

Geoff Parker made major contribution to behavioural ecology by watching dung flies (*Scatophaga spp*) not only by discovering marginal value theory independently from Eric Charnov, but also by recognising the generality of Bateman's (1948) experiments: the evolutionary interests of males and females are often divergent since the reproductive success of males typically increases with the number of their mates whereas there is no (or weak) relationship between the reproductive success of females and the number of their mates.

Parker (1979) has termed the divergent male and female interest over reproduction as sexual conflict.

Research in sexual conflict has accelerated since 1980 once many researchers recognised that sexual conflict can lead to specific adaptations and thus to rapid speciation, for instance to diversification of clasping and anti-clasping apparatus in water striders (*Gerris spp*), or to diversification of male and female genitalia among closely related dragonflies, damselflies and seed beetles (Arnqvist & Rowe 2005). Although the precise roles of hooks and spines on the penis of these insects are debated, their existence on male penis does seem to increase male fertilisation success by removing the sperm deposited by previous males from the female reproductive track - even though some of these spikes and hooks evoke injuries to the female's internal organs (Arnqvist & Rowe 2005). Recent studies suggest that females are often harmed during copulation in various species: such traumatic consequence of copulation has been demonstrated in mammals including humans (Reinhardt et al. 2014).

The mating system of the dunnock *Prunella modularis* is one of the best illustration of sexual conflict between males and females (Davies 1992). In a dunnock population several mating strategies may occur simultaneously: monogamy, polygyny, polyandry and mixture of these. Using a clever combination of behavioural observation and molecular genetic approach Nick Davies showed that the reproductive success of male dunnock's increases (as one may expect based on Bateman Principle) by copulating with multiple females. Interestingly however, female reproductive success is also increasing with the number of mates since more males can provide more food for her offspring. Therefore, male dunnocks attempt to shift their mating system toward their favoured solution (i.e., polygyny), whereas female dunnocks are selected to shift to their favoured solution (i.e., polyandry). An outcome of this tug of war is the existence of multi-male and multi-female breeding territories (i.e., polygynandry) where it seems neither males nor females "win" the conflict.

The aforementioned examples of sexual conflict referred to the pre-fertilisation stage of sexual conflict (i.e., pre-zygotic sexual conflict). However, the conflict between males and females may not ceases at conception, since male and female's interest may remain antagonistic post-zygotic stage, e.g., over offspring killing (infanticide) which has been reported from primates, carnivores, horses and rodents (Palombit 2014).

A well-known example of post-zygotic sexual conflict is conflict between parents. The latter emerges from the divergent interest of male and female parents over care. Whereas both biological parents gain evolutionary benefit from providing care for their young, caring is costly (i.e., takes time and energy, and caring parents can be predated). Therefore, from an individual parent's perspective the optimal solution is if the other parent spends time & energy on looking after the young. A well-known example of the conflict between parents is Eurasian penduline tit *Remiz pendulinus*. In this small passerine bird either the male or the female parent provides full care for the eggs and chicks. We showed that the reproductive interests of male and female penduline tits are different, since both males and females gain by abandoning the nest and seeking new mates. However, when their mate abandons the nest, this harms the interests of both males and females (Szentirmai et al. 2007). Taken together, the examples of dunnoek and penduline tits suggest that if males are contributing to offspring survival, the Bateman Principle may not work.

1.3. Parental cooperation

A definitive feature of social behaviour is cooperation. Cooperation between members of the same species is investigated for a long time: one of the landmark studies was published by Piotr Kropotkin (1902), a Russian prince who happened to be an anarchist and an evolutionary biologist at the same time. Following Kropotkin numerous eminent evolutionary biologists dealt with cooperation including Ronald Fisher, William D Hamilton, J. Maynard Smith and E. O Wilson (West et al. 2007). Note that the precise modelling framework to understand cooperation, especially in social insects, is debated largely due to the polarized views of inclusive fitness theory and multi-level selection (Wenseeler et al. 2010).

Within the framework of breeding systems, cooperation is much less controversial since the male and female parents are rarely kin-related and it is fairly straightforward that they gain direct benefits by producing and looking after their offspring. To model parental cooperation behavioural ecologists usually use game theoretic models that seek the evolutionarily stable strategies (ESS) whereby no individual can increase his (or her) fitness by changing behaviour. At the ESS level of care there can be no care by either parent, full care by both parents or outcomes between these two extremes, depending on parameter condition (Maynard Smith 1977, Webb et al. 1999, Barta et al. 2002, Barta et al. 2014).

Most game-theoretic analysis of parental behaviour assumes that care is a single type of behaviour although in reality care may have numerous components, for instance the parents may provide food, shelter or protection for the young. Once the uni-dimensionality assumption of parental care is relaxed, each parent can specialise on a different type of care, e.g., one parent feeds the young whereas the other defends them. Using a game-theoretic analysis, we showed that such role division in care and task specialisation can maintain parental cooperation (Barta et al. 2014).

1.4. Adult sex ratio

Whilst behavioural ecologies traditionally focus on ambient environment, it is increasingly recognised that the social environment also plays a role influencing various behaviours. For example, we behave differently when we are on our own as opposed to have somebody in our company. The composition of social environment (e.g., potential mates, relatives, competitors) may also influence behaviour. Although most sociobiologist would agree with these notions, investigation of social environment appears to be less widespread than the investigation of abiotic environment. For example, whilst numerous studies explored how parental care is influenced by abiotic factors, studies that explored the effects of social environment on parental care or on mating systems are scant (Székely et al. 2014b). A convenient proxy representing social environment is adult (or population) sex ratio (ASR) that is usually expressed as the proportion of males in the adult population.

Ernst Mayr (1939) appears to be the first evolutionary biologist who recognised the link between ASR and breeding systems. Although Mayr did not specify the nature of the relationship between ASR and breeding systems, by using various avian examples he argued that the two are related. Specifically, Mayr thought that deviations from even population sex ratio seems to produce “unusual” mating systems, e.g., polygyny and polyandry.

Mayr’s notion was followed up after a 30 year gap by Robert Trivers who realised that ASR in many vertebrates deviate from even, and he tried to work out the cause of these deviations. Following Fisher (1930) evolutionary biologists often argue that negative frequency dependent selection should produce balanced sex ratios in wild populations. However, Fisher (1930) clearly stated that if sex difference mortality takes place after the offspring are no

longer controlled by their parents, then the logic of frequency dependence may not apply. Therefore, ASR may deviate from even as it seems to be the case (Székely et al. 2014b).

Skewed sex ratios favour the underrepresented sex in the population since the rare sex has an advantage, for instance in finding a new mate. For example, if there are fewer females in the population than males, then females find it easier to find a new mate. One of the early models investigated the role of ASR in parental decisions (McNamara et al. 2000) and showed consistently with Mayr's argument that deviations from even ASR increased the frequency of polygamy and uniparental care in the population. In spite of numerous theoretical and empirical advances in studies of ASR in recent years (Donald 2007, Liker et al. 2014), Kokko & Jennions (2008)'s notion is still valid: *“Some researchers have suggested that the ASR is a major factor in sex role evolution, but their ideas have not been incorporated into mainstream theory.”* The lack of research in ASRs has stimulated some of our studies on breeding system evolution in relation to ASR (Liker et al. 2015, Pipoly et al. 2015, Remes et al. 2015).

1.5. Dissertation structure

This dissertation is focused on the evolution of mating systems and parental care in regards to three topics where most of my research has concentrated: sexual size dimorphism (Chapter 2), conflict and cooperation (Chapter 3) and adult sex ratios (Chapter 4). I will synthesise the main findings of these chapters in the Conclusions (Chapter 5).

Chapter 2. Sexual size dimorphism in birds



A pair of African fish eagle (credit: Áron Székely)

This chapter is based upon the following publications:

1. Székely, T., J. D. Reynolds & J. Figuerola. 2000. Sexual size dimorphism in shorebirds, gulls and alcids: the influence of sexual and natural selection. *Evolution* 54: 1404-1413.
2. Raihani, G, T. Székely, M. A. Serrano-Meneses, C. Pitra & P. Goriup. 2006. The influence of sexual selection and male agility on sexual size dimorphism in bustards (Otididae). *Animal Behaviour* 71: 833-838.
3. Székely, T., R. P. Freckleton & J. D. Reynolds. 2004. Sexual selection explains Rensch's rule of size dimorphism in shorebirds. *Proceedings of The National Academy of Sciences US* 101: 12224 – 12227.
4. Székely, T., T. Lislevand & J. Figuerola. 2007. Sexual size dimorphism in birds. IN: Fairbairn, D., W. Blanckenhorn & T. Székely (eds). *Sex, size and gender roles. Evolutionary studies of sexual size dimorphism.* Oxford University Press, 27-37.

'The males of many birds are larger than the females, and this no doubt is the result of the advantage gained by the larger and stronger males over their rivals during many generations.'

(Darwin 1871)

2.1. Introduction

Body size and its components are the target of several selective processes (Andersson 1994, Abouheif and Fairbairn 1997, Fairbairn et al. 2007, Székely et al. 2007). Thus there are advantages of being large (eg contests over mates or resources, mate preference by the opposite sex, resilience to temporary food shortage), or small (eg early maturation with shorter generation time and more rapid reproduction, higher success in scrambles). Sexual size dimorphism (SSD) is expected to evolve if some of these selective processes are stronger in one sex than in the other. Given that the reproductive physiology and breeding ecology of sexes are often different, we would expect extensive SSD in many bird species.

Our research has focused on four major functional hypotheses of SSD evolution. First, the *Mating competition hypothesis* predicts increasing SSD, as measured by $\log(\text{male size}) - \log(\text{female size})$ with more intense male-male competition. This is because when males contest over females, sheer size is often advantageous. Second, the *Display agility hypothesis* predicts decreasing SSD with more agile male displays (Payne 1984, Jehl and Murray 1986, Figuerola 1999). This hypothesis is likely to be relevant if females prefer males with acrobatic displays. Since manoeuvrability in the air often increases with small size, selection for producing small males are expected by female choice (Andersson and Norberg 1981). Third, the *Resource division hypothesis* predicts increasing SSD with the potential for overall resource use. Thus to avoid exploiting the same resources when males and females forage together and use the same territory, one may expect enhanced SSD. Since resource division may emerge either *via* large males and small females or *vice versa*, we calculated the absolute difference between the sizes of males and females (ie $|\log(\text{male size}) - \log(\text{female size})|$), and used these absolute sizes as a response variable. Finally, the *Fecundity hypothesis* predicts increasing female size with clutch size, and we tested this idea by relating SSD to clutch size.

In addition, we also investigate an allometric relationship in body size termed Rensch's rule (Fairbairn et al. 2007). Bernhard Rensch (1950) noted in numerous animal groups that when the male is larger than the female, SSD increases with body size, but it decreases with body size in groups in which the male is smaller than the female. Rensch's rule is a pervasive

macroecological pattern that has been observed in a wide range of taxa, including mites, water striders, lizards, snakes, turtles, hummingbirds, songbirds, and primates (Abouheif & Fairbairn 1997, Fairbairn et al. 2007).

2.2. Methods

Body size and its components are the target of several selective processes (Andersson 1994, Fairbairn et al. 2007). Thus there are advantages of being large (eg contests over mates or To test these propositions, we collected data from handbooks that included Birds of the Western Palearctic, Birds of Africa, Birds of North America Online, and Handbook of Birds of New Zealand and Australia (Lislevand et al. 2007). Morphometric data of adult birds, preferably taken during breeding season, were compiled. As a proxy variable for the intensity of sexual selection, scores of mating competition were taken from Dunn et al. (2001), or from handbooks using the following scheme: (1) polyandry; (2) monogamy (<5% polygyny); (3) mostly monogamy, but occasional polygyny (5–15% polygyny); (4) mostly polygyny (> 15% polygyny) and (5) lek or promiscuous. This scoring reflects the notion that the intensity of male-male competition increases from one to five. To test the agility hypothesis, descriptions of male display behaviours were taken from textbooks (Lislevand et al. 2007), and these descriptions were scored on a five point scale: (1) Ground displays only that included displays on trees and bushes; (2) Ground displays with occasional jumps/leaps into the air; (3) Both ground and non-acrobatic flight displays; (4) Mainly aerial displays, non-acrobatic; (5) Mainly aerial displays, acrobatic. To investigate the influence of resource sharing on the relative sizes of sexes, we collected information on territorial behaviour and whether the birds feed on, or away from, their territories. Verbal descriptions of territorial behaviour and feeding locations on (or away from) the territory were taken from the literature (Lislevand et al. 2007), and these descriptions were scored on a three point scale: (0) males and females don't share resources and they feed away from their breeding territory; (1) males and females share resources on their territory only during breeding season; (2) males and females share resources on their territory all year round. As with male displays, three observers scored the descriptions blindly to the identity of species. See further details in Székely et al. (2000, 2004, 2007) and Raihani et al. (2006).

2.3. Results

2.3.1. Testing functional hypotheses of SSD variation

Shorebirds. SSD in shorebirds supported both the Mating competition and the Display agility hypotheses (Székely et al. 2000) in both body mass (Figure 2.1., Wilcoxon matched pairs tests, mass dimorphism: $z = 2.291$, $n = 14$, $P < 0.022$) and wing dimorphism ($z = 2.627$, $n = 17$, $P < 0.009$).

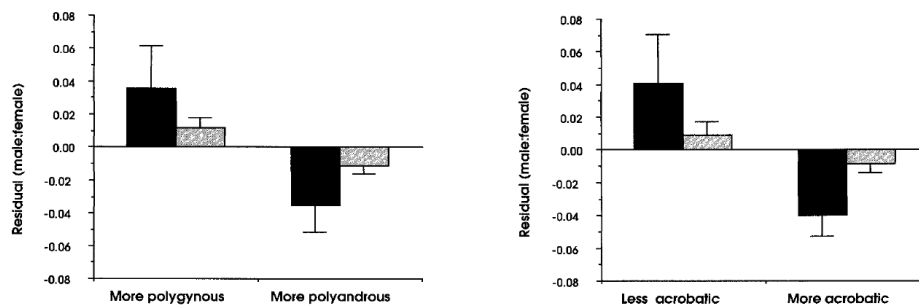


Figure 2.1. Paired comparisons of sexual dimorphism between more polygynous and more polyandrous shorebirds (left), and between taxa where males are more or less acrobatic (right) using residuals from regressions of male contrasts versus female contrasts in body mass (black) and wing length (gray, Székely et al. 2000).

Bustards. Consistently with shorebirds, SSD in bustards also supported both the Mating competition and the Display agility hypotheses (Figure 2.2.). In the multivariate model ($r^2 = 0.431$, $F_{2,22} = 8.342$, $P < 0.002$), both the intensity of mating competition and male agility were associated with SSD. Evolutionary changes towards larger males relative to females were associated with both intensified mating competition ($r_p = 0.563$, $F_{1,22} = 10.197$, $P < 0.004$) and reduced agility of male displays ($r_p = 0.533$, $F_{1,22} = 8.749$, $P < 0.007$).

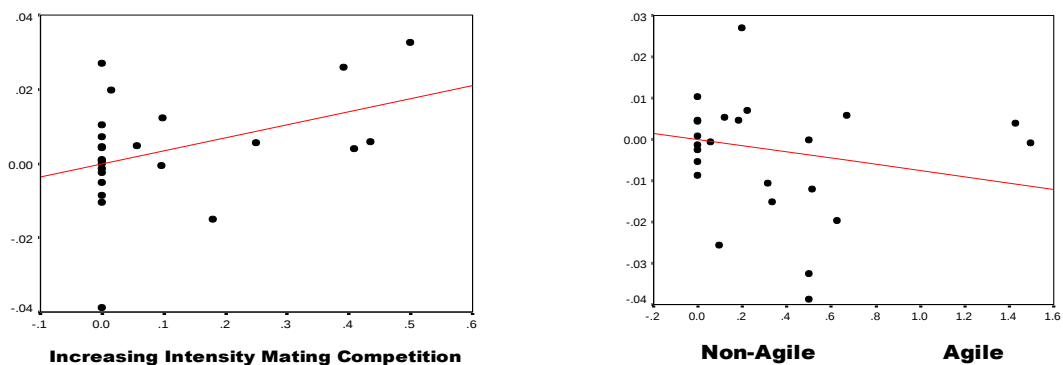


Figure 2.2. Phylogenetically independent contrasts in sexual size dimorphism (SSD) in bustards and (left) the intensity of mating competition ($r = 0.453$, $F_{1,23} = 5.934$, $P < 0.023$) and (right) male agility ($r = 0.409$, $F_{1,23} = 4.634$, $P < 0.042$). Regressions were forced through the origin (Raihani et al. 2006).

Birds. As part of a major overview of SSD in birds, we tested four major hypotheses of SSD separately for each family by calculating Spearman rank correlations between SSD and putative explanatory variables (Székely et al. 2007). Then we tested whether the distribution of correlation coefficients is different from zero.

Overall, there was a strong support for the Mating competition hypothesis, and a somehow weaker support for the Display agility one (Table 2.1). However, there were no clear patterns in regards to the Resource use and Fecundity.

Morphometric trait	Functional hypothesis				No. of species (families)	Reference
	Mating competition	Display agility	Resource division	Fecundity		
Wing length	Yes	N/A	N/A	N/A	341 (12)	Payne (1984)
Body mass	Yes	N/A	N/A	N/A	73 (30)	Owens and Hartley (1998)
Body mass, tail length, wing length	Yes	N/A	N/A	No	1031 (91)	Dunn <i>et al.</i> (2001)
Body mass, wing length, tarsus length, bill length, tail length	Yes	Yes	No	No	3767 (125)	This work

Table 2.1. Summary of functional analyses of sexual size dimorphism in birds (Székely et al. 2007). Only broad-scale studies are listed that used several avian families. N/A indicates that a hypothesis was not tested, and Yes and No show whether a specific hypothesis was supported or not.

2.3.2. Rensch's rule

Bustards. The patterns of SSD results are consistent with Rensch's rule since male biased SSD was greater in large bustards than in small ones, and the 99% confidence intervals did not include one (Figure 2.3). These results remained statistically significant when we used phylogenetically independent contrasts (Figure 2.3).

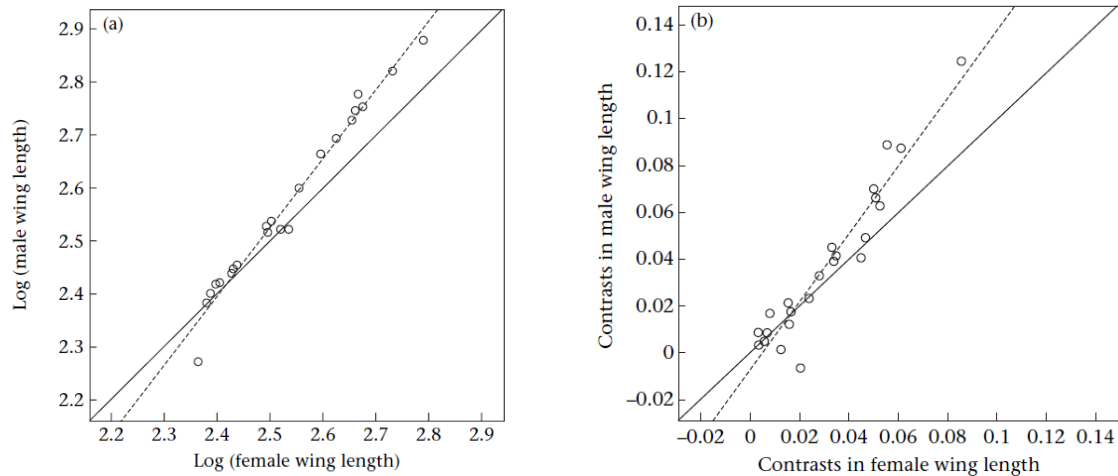


Figure 2.3. Rensch's rule in bustards (Raihani et al. 2006). The continuous line indicates the isometric relation and the dotted line represents the fitted relation between male size and female size by major axis regression for (left) species ($b = 1.311$, 99% confidence intervals 1.204–1.430, $N = 25$ species) and (right) phylogenetic contrasts ($b = 1.542$, 99% confidence intervals 1.218–1.846, $N = 24$ contrasts).

Shorebirds. The Rensch's rule also exists in shorebirds and allies (Charadriides, Figure 2.4), and it is determined by two components of sexual selection: the intensity of sexual selection acting on males and the agility of the males' display (Székely et al. 2004). These effects are interactive so that the effect of sexual selection on size dimorphism depends on male agility. As a control, we also examine dimorphism in bill length, which is a functionally selected trait. As such, dimorphism in bill length neither exhibits Rensch's rule nor is associated with sexual selection and display. Our results show that variation among taxa in the direction and magnitude of sexual size dimorphism, as manifested as Rensch's rule, can be explained by the interaction between the form and strength of sexual selection acting on each sex in relation to body size.

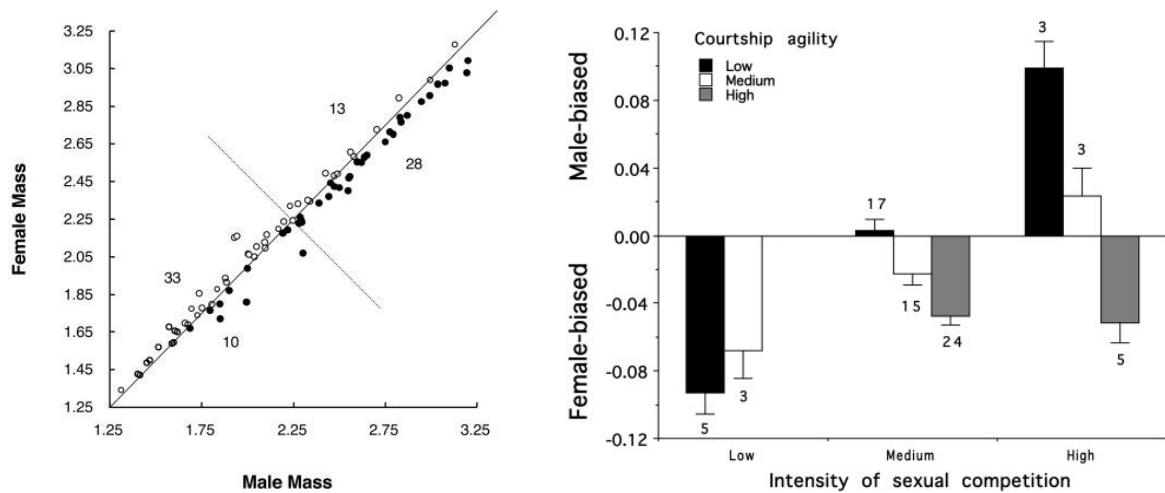


Figure 2.4. (left) Rensch's rule in shorebirds and allies (Székely et al. 2004). $\log_{10}(\text{female mass})$ is plotted against $\log_{10}(\text{male mass})$: species in which females are larger than males are shown by open circles, and species in which males are larger than females are shown by solid circles. The numbers of species are given in each of the four quadrants delimited by the line of equality and its tangent. If Rensch's rule were false, these numbers would be approximately equal. (right) Sexual dimorphism in body mass [mean $\pm$ SE $\log_{10}(\text{male mass}) - \log_{10}(\text{female mass})$] in relation to the intensity of sexual competition and male agility. The numbers of species are given below (or above) each bar.

Birds. Consistently with bustards and shorebirds, avian families also exhibit the allometric relationship (Figure 2.5), although the extent of allometry varies between families.

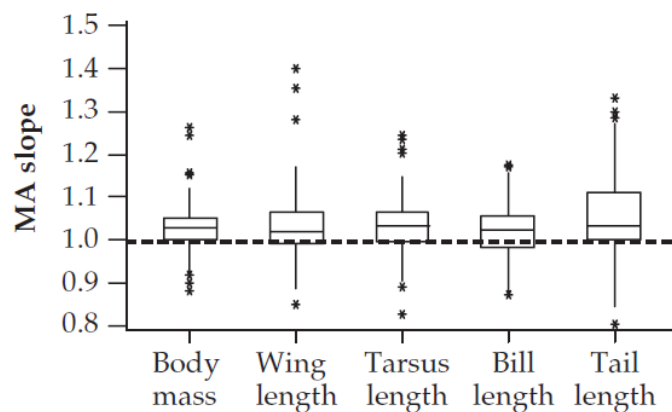


Figure 2.5. Rensch's rule in birds (Székely et al. 2007). The principal axis of major-axis (MA) regression $\log_{10}(\text{male size}) : \log_{10}(\text{female size})$ was calculated separately for each family with data from at least five species. The median slope is significantly larger than 1.0 in all traits (Wilcoxon one-sample tests, body mass $P < 0.001$; wing length $P < 0.002$; tarsus length $P < 0.001$; bill length $P < 0.003$; tail length $P < 0.001$). Asterisks indicate outliers.

2.4. Discussion

Our results in bustards, shorebirds and across birds as whole are consistent with the assertion of Darwin (1871) and previous comparative works that intense mating competition between males predicts male-biased SSD (Webster 1992, Winquist and Lemon 1994, Raihani et al. 2006; but see Oakes 1992, Björklund 1990). We also showed that the relationship between sexual selection and SSD is more complex than usually acknowledged, since display agility, a functional explanation that is often considered of minor importance, related to reduced size in males relative to females. The latter effect, however, was weaker than the effect of mating competition on SSD. One potential explanation for the difference between the predictive powers of mating competition and display agility may be data quality. Breeding system, a proxy we used for mating competition, is often better described in the literature than display agility for which we used scores based upon verbal descriptions. Interestingly, mating competition is not only likely to select for large size in the sex competing more intensively for mates, but can also promote changes towards small size when small size is favoured during displays. To what degree these results in birds elucidate the processes in other taxa - is not yet known. We conjecture that male agility should influence SSD in many more taxa in which males display to and/or fight over females; for instance bats, primates and pinnipeds.

We found no support for *Fecundity* and *Resource division hypotheses*. There may be good reasons why these hypotheses may only work in certain avian taxa (Selander 1972, Shine 1989, Temeles and Kress 2003). In sum, we agree with Andersson (1994) that discounting the latter hypotheses would be premature since differences between species in foraging ecology, parental roles, and demands imposed by egg production may also affect sexual size dimorphism. To advance further tests of these hypotheses (and lots of others we have not considered here, see Andersson 1994, Blanckenhorn 2000) one needs further comparative analyses, perhaps by using higher-quality data from those groups that exhibit unusually large ranges of SSD.

We propose that future tests of functional hypotheses in avian SSD should use a two-pronged approach. First, to select a group of species for detailed quantitative description of selective forces in regards to major functional hypotheses. This may include observational or experimental tests of specific hypotheses. Second, use the comparative approach for these observational (or experimental) data for establishing which (if any) hypotheses predict SSD across species and traits. Note that functional explanations may have integrated effects, and

there may be statistical interactions between these effects (Székely et al. 2004). Powerful statistical analyses of cross-species effects thus require precise data and good number of species. Thus integrating the results of within-species and across-species approach is likely to reveal a comprehensive picture of functional explanations of SSD.

Our analyses strongly suggest that Rensch's rule occurs across a broad range of avian taxa, and the rule appears to be exhibited in all five morphometric traits. These results expand previous works that show existence of Rensch's rule among Passeriformes, Pelecaniformes, Procellariiformes (Fairbairn 1997), Galliformes (Sæther and Andersen 1988, Fairbairn 1997), hummingbirds (Fairbairn 1997, Colwell 2002), bustards (Payne 1984, Raihani et al. 2006), grouse (Payne 1984) and shorebirds (Székely et al. 2004). No evidence of allometry consistent with the Rensch's rule was found in Falconiformes, Strigiformes, Anseriformes, Charadriiformes (Fairbairn 1997) and seabirds (Serrano-Meneses and Székely 2006).

The discrepancy between some of the previous studies of Rensch's rule, however, raises two important questions. First, what is the correct way of testing Rensch' rule. As Fairbairn (1997) argues, major axis regression using phylogenetic control is desirable. Phylogenetic correction, however, can be carried out in a variety of ways (Freckleton et al. 2002), and the phylogenies themselves are prone to errors. Second, what is the correct taxonomic level of analyses: species, genera or families? Rensch (1959, p 159) suggests that '*This rule, however, applies only to subspecies of a species, to related species of a genus, or to related genera of a family*'. Note that Rensch himself is inconsistent illustrating his rule using three species of Scarabaeidae that represent three different genera (Rensch 1959: Figure 50, p 160). In our view, the answer to both issues requires simulation studies to explore the sensitivity of allometric relationship to phylogeny, comparative methods and taxonomic level of analyses.

Chapter 3. Sexual conflict and parental cooperation



A pair of Eurasian penduline tits building a nest (credit: Csaba Daróczy)

This chapter is based upon the following publications:

1. Houston, A. I., T. Székely & J. M. McNamara. 2005. Conflict over parental care. *Trends Ecol Evol* 20: 33-38.
2. Thomas, G. H., T. Székely & J. D. Reynolds. 2007. Sexual conflict and the evolution of breeding systems in shorebirds. *Advances in the Study of Behavior* 37: 277-340.
3. Szentirmai, I., T. Székely & J. Komdeur. 2007. Sexual conflict over care: antagonistic effects of clutch desertion on reproductive success of male and female penduline tits. *J Evolutionary Biology* 20: 1739-1744.
4. Székely, T. 2014. Sexual conflict between parents: offspring desertion and asymmetrical parental care. IN: Gavrillets, S. & W. Rice (eds). *Sexual Conflict*. Cold Spring Harbor.
5. Parra, J E, M. Beltrán, S. Zefania, N. dos Remedios, T Székely. 2014. Experimental assessment of mating opportunities in three shorebird species. *Animal Behaviour* 90: 83-90.
6. Harrison, F., Z. Barta, I C Cuthill & T. Székely. 2009. Conflict and cooperation between parents over care: a meta-analysis. *J Evolutionary Biology* 22: 1800-1812.

3.1. Introduction

Sexual conflict over care is a type of evolutionary conflicts that emerges from the different interests of males and females in regards to parental care (Trivers 1972; Clutton-Brock 1991; Chapman et al. 2003; Arnqvist & Rowe 2005). The conflict arises when the young benefit from the effort of either parent but each parent pays only the cost of its own effort, so that each parent would have higher fitness if the other parent provides more care (Houston et al. 2005; Lessells 2006; Klug et al. 2012). Conflict refers to the way selection acts on the two sexes that have different optimum value in parental provisioning; between the two optima sexually antagonistic selection operates (Lessells 2012). Sexual conflict over care can be seen as tug-of-war since each parent is tempted to pull out of care leaving the other parent to provision more care for the young (Székely et al. 1996; Arnqvist & Rowe 2005; Lessells 2012).

Sexual conflict over care seems to be the rule rather than the exception. The conflict may be resolved by one (or both) parents failing to adopt the optimal parenting for their mate and nonetheless remaining in conflict, or by both parents adopting the optima that suit their mate (i.e. exhibit the maximum provisioning possible). Examples of the latter conflict resolution (whereby the conflict is completely wiped out) are exceedingly rare, and seem to be limited to three scenarios. First, conflict over care is not expected in obligate monogamy by both males and females so that the life-time reproductive successes of both parents are identical. This may occur in semelparous organisms (i.e. both the male and the female put their resources into a single breeding event), or in iteroparous organisms with life-long exclusive monogamy. Second, males and females might be genetically identical, so even though one (or both) sexes are polygamous, polygamy would benefit the same genome whether it is in the male or the female phenotype. Third, if parental care is cost-free and thus parents provide maximum level of care (Smiseth pers comm). However, few (if any) organisms fitting these restrictive assumptions, and thus conflict-free parenting seems exceedingly rare in nature: (i) some level of polygamy (by males, females or both sexes) appears to be widespread, (ii) the reproduction by genetically identical individuals (clones) as separate sexes (males and females) seems unlikely, and (iii) care provisioning, as far as we are aware, do have costs that discourages parents to provide their absolute maxima for a given batch of offspring.

Parents may have conflicting interest over caring or deserting the young, the amount of care provided for each young, the number of simultaneous mates, the size and sex ratio of their

brood, and the synchronization of birth for a clutch or litter of young (Westneat & Sargent 1996; Houston et al. 2005; Klug et al. 2012; Lessells 2012). Conflict between parents over care is usually labelled as a post-zygotic conflict (although resources had been already allocated into the gametes prior to fertilization as part of parental provisioning, Clutton-Brock 1991); other examples of post-zygotic conflicts include infanticide and genomic imprinting (Chapman et al. 2003; Tregenza et al. 2006; Lessells 2012).

Studies of conflict over care are fascinating for at least four major reasons. First, parental care is diverse: there is great variation both between and within species in the types of care provided, duration of care, and the sex of the care-providing parent (Wilson 1975; Clutton-Brock 1991; McGraw et al. 2010; Royle et al. 2012). Sexual conflict is thought to be one of the main drivers of this diversity. Second, parental care is one of the core themes in breeding systems and sex role evolution, and it is increasingly evident that parental care can only be understood by dissecting the entangled relationships between ecological and life-history settings, and the variety of mating and parenting behaviour (Székely et al. 2000; Wedell et al. 2006; Jennions & Kokko 2010; Klug et al. 2012). Third, parental care was (and is) one of the test-beds of evolutionary game theory. Numerous models have been developed to understand how parents interact with each other and with their offspring (Trivers 1972; Maynard Smith 1977; Houston & Davies 1985; Balshine-Earn & Earn 1998; McNamara et al. 1999; Johnstone & Hinde 2006). Parental care research is one field where empiricists are extensively testing the predictions of evolutionary game theoretic models both in the laboratory and wild populations (Harrison et al. 2009; Lessells 2012; Klug et al. 2012), although the congruence between theoretical and empirical work is not as tight as often assumed (Houston et al. 2013). Finally, parental care – wherever it occurs – is a major component of fitness, since whether the offspring are cared for or abandoned has a large impact on their survival, maturation and reproduction (Smiseth et al. 2012). Therefore, parental care (or the lack of it) has an impact on population productivity and population growth, and influences the resilience of populations to various threats (Bessa-Gomes et al. 2004; Veran & Beissinger 2009). Thus understanding the behavioural interactions between parents, and the fitness implications of these interactions are highly relevant for population dynamics and biodiversity conservation (Alonzo & Sheldon 2010; Blumstein 2010).

Sexual conflict over care has been reviewed recently (van Dijk & Székely 2008; Lessells 2012). Here I focus on three issues that have not been extensively covered by previous

reviews: why sexual conflict over care occurs, how can one detect it, and what are its implications. I will also point out that both conflict over care and parental cooperation may mould caring behaviour. I view causes and implications of care primarily from empirical perspectives, since there are excellent reviews on the rich theoretical literature (Lessells 2006; Lessells 2012; Klug et al. 2012; Houston et al. 2013). My intention is not be comprehensive, instead I use selected examples to illustrate salient features of conflict over care. I focus on ecological and evolutionary aspects; for a discussion of the genetic and neuro-endocrine bases of parental care, see Adkins-Regan (2005), McGraw et al. (2010) and Champagne & Curley (2012). I prefer to use the term ‘parental care’ instead of ‘parental investment’, because the latter, as admitted by Trivers (1985), is extremely difficult to estimate empirically and thus has a limited use in empirical studies (Mock & Parker 1997; McGraw et al. 2010). The term ‘parental investment’ can be deceptive, if used without directly demonstrating the full costs of care. The term ‘parental care’ is less restrictive, since it refers to any form of parental behaviour that appears to increase the fitness of an offspring and is likely to have evolved for this function (Clutton-Brock 1991; Smiseth et al. 2012). In this review I focus on families in the narrow sense (i.e. two parents and their offspring), although in numerous organisms the families are more extensive and may include several generations of offspring living together and/or unrelated individuals that assist the parents rearing the young.

3.2. Sexual conflict and parental behaviour

Conflict between parents may occur in species with identical sex roles, or with different sex roles driven by the different cost and benefits of care for males and females arising from the sex differences in physiology, ecology and life history (Fairbairn et al. 2007; King et al. 2013). Conflict may occur in organisms that have no parental care, assuming that at least some parental care (by the male, the female or both parents) would improve offspring survival and thus parental fitness. Conflict may also occur in organisms in which only the male, the female or both parents provide care. I start this section by emphasizing the diversity parental care strategies, and then explore how conflict over care could influence the emergence and maintenance of this diversity.

3.2.1. Diversity of care strategies

Parental care is one of the most diverse social behaviours (Wilson 1975; Reynolds et al. 2002; McGraw et al 2010; Smiseth et al. 2012): the type of care, the duration of care, and the involvement of one of both parents in various care activities are all highly variable both within and between animal taxa (Figure 3.1.). Conflicts between parents and the resolution of these conflicts offer powerful approaches to understand this diversity (Trivers 1972; Maynard Smith 1977; Lessells 2012). Whilst the majority of invertebrates and many vertebrates do not provide any care for the fertilized embryo beyond supplying the eggs with nutrients, the species that do exhibit care have amazing adaptations. There are excellent recent reviews on parental care in both vertebrates and invertebrates (Balshine 2012; Trumbo 2012), and thus here I focus on selected examples that illustrate some of this variation, and note their relevance to the study of sexual conflict.

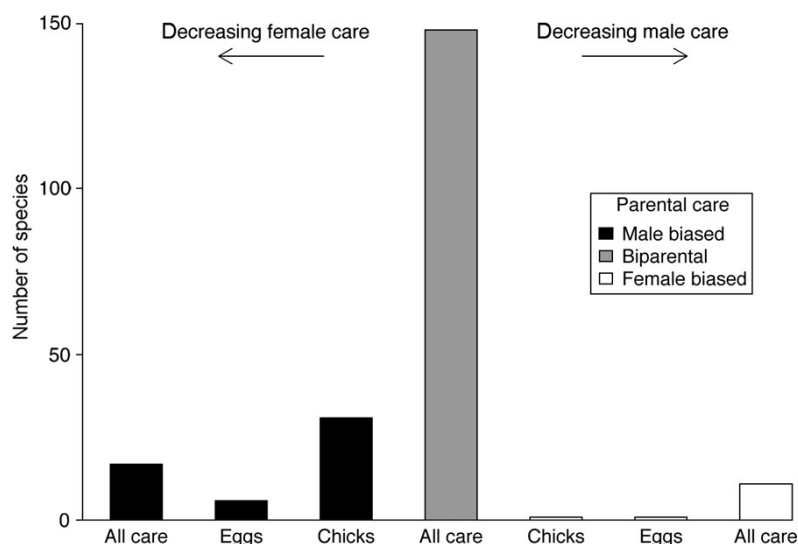


Figure 3.1. Distribution of parental care in shorebirds. “Male biased” means that the male contributes all care either until the chick fledge (“All care”), or the majority of care with females deserting before hatching (“Eggs”), or before fledging (“Chicks”). The same terminology applies to “Female -biased” care. In biparental taxa both parents provide care until the chicks fledge (Thomas et al. 2007).

Recent studies have discovered an immense variety of care strategies, and discoveries of novel forms and types of parental care are still being made. For instance, tropical frogs have some of the most diverse reproductive and parental care systems among animals (Wells 2007), and parental care is thought to have evolved independently at least 41 times (Balshine

2012). Some species of frogs prepare a foam nest for their eggs, whereas others attend the eggs laid on leaves that overhang streams, or are viviparous and give birth to small froglets. Parents in other frog species brood the eggs on their back, in their vocal sac or in their stomach, transport the tadpoles and froglets, or urinate on the eggs to prevent from desiccating (Summers et al. 2006). Parental care can be a major occupation for male and female frogs for substantial periods of time when they regularly check the development of tadpoles, and the female may lay trophic eggs to nourish the tadpoles (Brown et al. 2010). Parents may also seek out pools that are free from competitor larvae and cannibalistic tadpoles, and move their own tadpoles to predator-free pools if necessary (Summers et al. 2006; Brown et al. 2010).

Since the reproduction of vast number of species has not been studied in detail, especially those that live in difficult-to-access habitats such as tropical forest canopies, the deep sea, or in caves or soil, new forms of parental care are waiting to be discovered. For example, in caecilians, a little-studied sub-terrestrial amphibian group, it was not known until recently that mothers incubate their eggs in underground burrows, and that the altricial hatchlings feed for an extended period of time upon the modified and lipid-rich outer layer of the skin of their mother using specialized dentition (Kupfer 2005; Wilkinson et al. 2013).

Care can be provided for a long time not only in whales, elephants and primates including humans in which it may last up to several decades (de Waal & Tyack 2005; Mitani et al. 2012), but also in invertebrates: mother whip spiders *Phrynus marginemaculatus* protect their young for at least 11 months (Trumbo 2012). During such an extended period, the parent-infant relationship that is initially driven by offspring demand and the parents' readiness to provide care, may shift toward an alliance between the parent(s) and the siblings. For instance in scorpions, groups of young can help the mother to subdue large preys (Trumbo 2012).

Usually assumed that the transitions in duration of care or type of care are driven by sex-specific costs and benefits and thus due to changes in ecology and life-history of males, females or both sexes. However, it is plausible that some of these transitions are largely (or entirely) due to changes in male and/or female behaviour as they are trying to resolve the conflict. First, for a given set of costs and benefits, multiple patterns of care may occur in a population; this may be due to mixed evolutionarily stable strategies (ESSs, Webb et al. 1999), to different behavioural interactions between parents (McNamara et al. 1999), or to social interactions between parents and other members of a population that can stabilize

different ESSs in a coevolutionary process that involve mate choice, mating behaviour and parental care (McNamara et al. 2000). Second, an important insight from evolutionary game theory is that as males (or females) attempt to attain their respective fitness optima, they may change the cost and benefit functions for their mates, and thus the fitness landscape for the opposite sex (McNamara & Weissing 2010). Although it is not known whether the first or the second processes are involved generating multiple care patterns in wild populations, it seems likely that conflict resolution either at ecological or evolutionary time scales are involved by influencing the transitions between different parenting behaviour.

3.2.2. Why (not) care?

Sexually antagonistic selection is one of the theories that behavioural ecologists use to understand the emergence and maintenance of diverse care patterns (Trivers 1972; Maynard Smith 1977; Houston et al. 2005; Lessells 2012): as each sex is moving toward its parental care optima, it elicits a response from the other parent and *vice versa*. Selection may operate on these changes: actions and responses that lead to higher reproductive success are likely retained in the population. However, similarly to other types of sexual conflict, it is difficult to infer conflict from behavioural patterns alone, since the parental behaviour exhibited by the sexes does not tell anything the difference between the optima of males and females (Lessells 2012). Therefore, observations that one parent deserts and all care is provided by the other parent, or that both parents share care equally, do not tell too much about the extent of conflict. Furthermore, since sexual conflict refers to selection process, conflict may not have behavioural signs, e.g. aggressive behaviour.

The direct evidence for sexual conflict over care is scarce, since few studies have estimated the fitness outcomes of parenting behaviour from the perspectives of both the male and the female (see Detecting conflict over care). The hedonistic breeding systems of Eurasian penduline tits (*Remiz pendulinus*) may illustrate fitness consequences of various parenting options (Figure 3.2.). In this small passerine bird either the male or the female abandons the clutch, and re-nests with a new mate shortly after desertion. Re-mating is common: both males and females may have up to 5 different mates in a single breeding season (Persson & Öhrström 1989). A puzzling aspect of penduline tit breeding biology is the large number of deserted clutches: about 30-40% of clutches are abandoned by both parents. High frequencies

of biparental desertion have been observed in all studied population to date, so most likely it is part of their natural breeding behaviour (van Dijk et al. 2010a). Whereas in many animal populations predation of eggs or young is the major sources of breeding failure, in penduline tits biparental desertion is a substantially more common cause of breeding failure than predation of eggs or young.

Szentirmai et al. (2007) estimated the reproductive success separately for caring and deserting penduline tits using data from an intensely studied population in Hungary.

Deserting the clutch increased the reproductive success of the deserting males, since many of these males found a new mate and re-nested. Desertion, however, was costly to deserted females, since they either deserted the clutch themselves and thus doomed the offspring to death, or stayed with the offspring for about one month and cared for them till they became independent (Szentirmai et al. 2007; van Dijk et al. 2012). The fitness consequences of desertion and caring in males are mirrored by fitness consequences in females: deserting the clutch increases a female's own reproductive success but reduces her mate's reproductive success. Once they were abandoned, male and female penduline tits provide comparable offspring care (Pogány et al. 2012). Although extra-pair paternity does occur in penduline tits (van Dijk et al. 2010b), the frequency of extra-pair young (EPY) is comparable between male-cared and male-deserted young suggesting that EPY does not bias the estimated reproductive success of deserted *versus* cared nests.

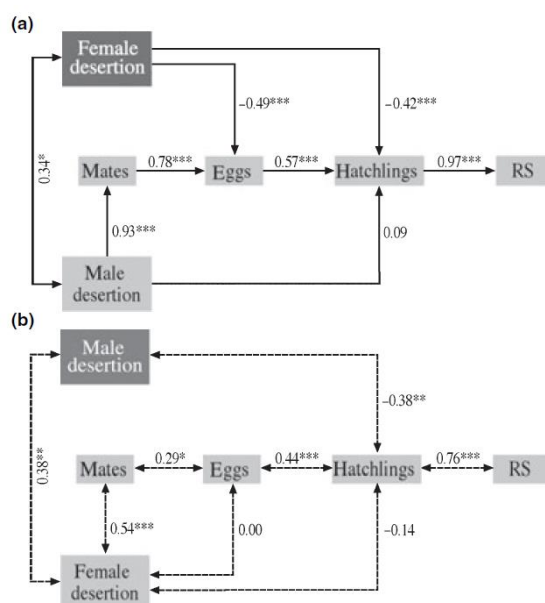


Figure 3.2. Clutch desertion in relationship to reproductive success (RS) in Eurasian penduline tits. (a) Path diagram of male. Arrows indicate direct linear relationships between explanatory and response variables, and standardized path coefficients are shown next to the paths. (b) Correlations between female RS, male desertion and female desertion. Double headed arrows with dashed lines indicate correlations between variables, and Spearman rank correlation coefficients are shown next to the arrows. In both diagrams variables of the focal sex (a: male; b: female) are shown in light grey boxes and desertion of their mate in dark grey boxes. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Species with variable care patterns, like penduline tits, offer great opportunities to quantify fitness implications of care and desertion, and assess the extent of sexual conflict. Similarly, the highly variable care patterns (both within and between species) in assassin bugs, cichlid fishes, poison dart frogs, tinamous and shorebirds may emerge via conflict over care whereby a shift in costs and benefits of care for one sex (or for both sexes) can flip from one pattern of care to another. Whilst different costs and benefits of care for male and female, and thus difference in sex roles, are not essential for sexual conflict over care, these taxa offer biological systems where the fitness implications can be evaluated. Since selection is expected to produce male behaviour that is the best responses to female parental behaviour, the changes in cost and/or benefits of care in one sex likely to induce change in parental behaviour of the other sex, somehow analogous to the sexually antagonistic pre-zygotic selection.

Theoretical models suggest that social behaviour itself can generate shifts: there are situations in which both uniparental care and biparental care are evolutionarily stable strategies (ESSs), and they can co-exist in a population (McNamara et al. 2000; Kokko & Jennions 2008; Klug et al. 2012). The presence of several care patterns in a single population is consistent with theoretical results (see *Diversity of care strategies*), although alternative explanations of co-existing caring strategies are also possible e.g. age-dependent care strategies, and/or temporal or spatial variation in costs and benefits of care for different members of the population.

Parental care, however, is a complex trait even though theoretical models and comparative studies often reduce care to a single (or a few) variables. Representing care as a single trait is problematic, since parents may provide different types of care and these different components can evolve independently from each other (Smiseth et al. 2012; Székely et al. 2013). Parents may also divide the tasks so that each parent specializes on particular tasks; male dung beetles for instance excavate the ground under the dung ball, whereas the female covers it with soil (Trumbo 2012). Such specialization can reduce conflict between males and females, and maintain biparental care (Lessells 2012; Barta et al. 2014).

3.2.3. Manipulation and parental tactics

Males and females may use a variety of tactics to entice (or coerce) their mate to increase their care. In biparental species a female may attempt to monopolize the parental care of its

mate (Chapman et al. 2003). Females may solicit superfluous copulations from their mates (Eens & Pinxten 1996), or interfere with their mate to prevent them from attracting new females (Slagsvold & Lifjeld 1994). Female burying beetles *Nicrophorus defodiens* bite and attempt to push the male off his signaling perch and interfere with the male's attempt to release pheromones attracting additional mates in order to impose monogamy on him (Arnqvist & Rowe 2005). Similarly, females may be hostile toward other females so as to keep their mate's care provisioning for their own offspring (Liker & Székely 1999; Sandell & Smith 2005). Males, however, can counteract female strategies by attracting females away from their existing mates, or intervening directly by keeping peace between females (Walter & Trillmich 1994).

Parents may manipulate their mates' behaviour to extract more care using two strategies. First, paternally imprinted genes in placental mammals may facilitate embryonic growth so that the developing embryos extract more resources from the mother than would be optimal for her (genomic imprinting). An analogous manipulation has been proposed for birds: females are hypothesized to deposit elevated levels of androgens in the eggs to increase chick begging behaviour, so that the chicks extract more care from the male (Schwabl 1996; Groothuis et al. 2005). The latter hypothesis has been tested by several studies, and currently little evidence supports it (Lessells 2006; Laaksonen et al. 2011). Instead of improving offspring viability, elevated androgen level appears to reduce offspring viability in the long term (Ruuskanen et al. 2012).

Second, parents may strategically handicap themselves to extract more care from their mate (Barta et al. 2002). By reducing their own body condition, females can put their mate in a difficult situation: if the male abandons, then the female alone cannot rear the young so the brood would die ('credible threat', Barta et al. 2002). Although body condition has been shown to relate to parental care, e.g. males in low body condition reduce their care (Steinegger & Taborsky 2007), the existence of strategic handicapping by lowering body condition, has not been demonstrated.

Although the larger individuals in a pair can 'force' the smaller parent to care, reports of physical coercion are rare (Awata & Kohda 2004). There may be three reasons for this. Firstly, harmful behaviour, coercion and manipulation are expected to be weaker in conflict over care than in conflict over mating (Lessells 2006), because in the former a harmful behaviour to a mate would not only reduce the mate's reproductive success but also the

actor's reproductive success. Secondly, enforcing a complex behaviour such as care that may be tuned to the specific age and demand of the offspring seems exceedingly difficult. In contrast to other forms of coercion that seem straightforward (e.g. keeping another animal away from a resource, e.g. food, water, or forcing another individual to copulate) because specific behaviours have evolved to achieve this objective (e.g. aggression), by forcing an animal to carry out a fine-tuned behaviour such as care seems less likely. Third, the manipulated parent could retaliate and harm (or eat) the offspring, and thus defeat the objective of the manipulation in the first place.

3.3. Detecting sexual conflict over care

Since sexual conflict may involve adaptation and counteradaptation, it is thought that these processes and their results will be difficult to observe (Chapman et al. 2003; Arnqvist & Rowe 2005). Theoretically, the extent of conflict can be estimated in two ways: (i) by quantifying the parental optima for males and females, and then estimating the difference between the two optima (the conflict 'battleground', Godfray 1995), or (ii) by estimating the fitness reduction in males, females or both sexes due to conflict ('conflict load', Lessells 2006). Ideally, both battleground and conflict load should be estimated simultaneously to reveal both the behavioural differences due to conflict and their fitness implications; however, no study appears to have done both. Much of our current knowledge is based on either of these estimates, or on indirect inferences of the conflict.

3.3.1. Observations

Fitness implications of caring and deserting can be established by studying wild or laboratory populations. Studies have compared the reproductive success of different care patterns (for instance male-cared *versus* female-cared, uniparental *versus* biparental families, no care *versus* care, Clutton-Brock 1991; Eldegard & Sonnerud 2009; Pogány et al. 2012), assuming that a difference between the two estimates indicates the lost reproductive success due to unwillingness of one (or both) parents to provide care.

Offspring desertion by the male, female or both parents is a common behavioural strategy that occurs in wide range of taxa (insects, fish, frogs, birds and mammals, Clutton-Brock

1991; Székely et al. 1996; Korpimäki et al. 2011), and studies suggest conflict over care is involved (Houston et al. 2005; Griggio et al. 2008; King et al. 2013). The social environment may modulate the benefit of desertion: high density of potential mates expected to favour desertion whereas low density may temper desertion (Owens 2002). Social environment, however, may offer biased mating opportunities: adult sex ratio (ASR) is biased in numerous organisms (Donald 2007; Hirst et al. 2010), and the biased ASR favour one sex over the other. For instance, male-biased ASR was thought to explain female-biased desertion (Box 3.1., Kosztolányi et al. 2011). Furthermore, the benefit of desertion may differ between the sexes, if one sex needs longer time to recover from breeding than the other (Gubernick et al. 1993; Balshine-Earn & Earn 1998).

In principle, comparing the two strands of benefits (care *versus* desertion) should indicate the fitness consequences for males and females, and thus tells what extent these fitness peaks differ between males and females (the ‘battleground’). However, there are caveats. First, comparing the fitness consequences of caring and deserting for a selected group of animals may not represent the population as a whole. Thus the best fathers may decide to care, whereas the most attractive fathers may decide to desert and find another mate. Similarly, a single parent may be able to provision the young on a territory with abundant food, whereas both parents may be needed to feed the young on a poor territory (Eldegard & Sonnerud 2009). Second, the benefit for a given parent, let us say the male, from deserting depends on his mate’s response: will she continue rearing the offspring or desert herself? Therefore, estimating the fitness consequences of caring and deserting should be done at various response levels of the other parent. This is rarely feasible, since wild populations rarely exhibit all behavioural strategies. Third, the benefits of caring and deserting may manifest over a long time period, whereas studies usually estimate short-term fitness consequences (van Dijk et al. 2012). One may need to investigate several generations to reveal the full scale of costs and benefits. This can be challenging in long-lived animals or in polygamous species where the number of mates may proliferate into an extensive network of breeders for which reproductive success estimates are required.

How males and females play out these conflicts are rarely studied in detail. Unlike divorce in humans that can be an extended and convoluted process, desertion in non-human animals can be rapid (van Dijk et al. 2012). Studies are needed to work out on behavioural scale how parents interact: whether they may escalate or converge in response to each other behaviour.

3.3.2. Experiments

To overcome the limitations of observational studies, two kinds of manipulations were used to perturb parental behaviour, and seek the consequences of perturbation on parental behaviour and reproductive success. First, experimenters manipulated the benefits of matings, e.g. making males (or females) more attractive to the opposite sex (Smith 1996; Griggio et al. 2010). For example, by setting up an additional nest box close to a pair of common starlings (*Sturnus vulgaris*), male starlings reduced their involvement in care and sang to attract a new mate (Smith 1996).

Second, researchers manipulated parental attendance (e.g. by removing or handicapping one parent) to investigate the consequent changes in partner's behaviour and fitness (Harrison et al. 2009). By experimentally removing one parent, and creating uniparental and biparental broods in zebra finches *Taeniopygia guttata*, male chicks reared by a single parent was more attractive to females than males reared by two parents suggesting that the conflict between male and female parents may result in lower quality offspring (Royle et al. 2002).

Males (or females) were handicapped (or removed) in various biparental organisms (insects: Rauter & Moore 2004; Smiseth et al. 2005; Suzuki & Nagano 2009; fish: Mrowka 1982; Itzkowitz et al. 2001; birds: Sanz et al. 2000; Harrison et al. 2009; mammals: Wynne-Edwards & Lisk 1989; Gubernick & Teferi 2000). There are two overall conclusions of these experiments. First, although there is large variation between species in response to manipulation of parents, mates of handicapped parents tend to compensate, although the compensation is usually not complete (Harrison et al. 2009; but see Mrowka 1982). This is consistent with theoretical arguments: partial compensation is necessary to maintain biparental care (McNamara et al. 2002; Lessells 2012). Second, whilst parental care tends to be asymmetric in that females usually take a larger share than males (Queller 1997), across the species compensatory responses of males and females are not different (Harrison et al. 2009). This is in contrast with three species of *Nicrophorus* beetles where the males but not females compensated for the lost care of their mate (Lessells 2012). Presumably, in the latter species the females are already working close to their maximum capacity whilst they are still attended by their mate, and once their mate removed they can't improve their workload (Lessells 2012).

In burying beetles desertion by the male may be actually beneficial for the female, since staying males eat some of the carcass that would be available for the larvae (Boncoraglio & Kilner 2013). Therefore, females may have co-evolved to anticipate desertion by their partner so that they now benefit from the male's absence. However, in wild population the male presence may be beneficial by helping to protect both the carcass and the developing larvae from intruding males that may kill the offspring (Trumbo 2007).

Whilst these experimental studies have intrinsic advantages over observational studies, they suffer from drawbacks. First, manipulations of a focal sex (let us say, males) should be designed to reveal the fitness implications at various levels of response (here, by the female). Existing experiments, however, usually manipulate one sex, and estimate fitness implications at the self-selected level care of its mate. Since parents cannot be forced to care, manipulating systematically the care of both parents seem exceedingly difficult. Second, complex mating patterns (such as the one exhibited by Eurasian penduline tits) exacerbate this difficulty, because full exploration of parental behaviour and their fitness implications would mean experimental manipulation not only in one family, but in all subsequent families of the focal individuals. Therefore, the best empirical system for experimental evaluation of battleground and conflict load would be short lived largely monogamous animals that only breed a few times throughout their life.

3.3.3. Comparative analyses

Phylogenetic comparative analyses have been used to detect the tug-of-war between males and females. In shorebirds which exhibit an unusually diverse parental care strategies ranging from male-only care to biparental and female-only care, the duration of male care is traded off against the duration of female care (Reynolds & Székely 1996), so that evolutionary increases in male care were associated with decreases in female care and *vice versa*. Although the duration of care is not necessarily a good indicator of parental effort, the implication is that male and female do adjust their care to the care of their mate, consistent with experimental manipulations (Kosztolányi et al. 2009; Harrison et al. 2009; Trumbo 2012).

Whether the tug-up-war over care occurs may depend on phylogenetic plasticity. Webb et al. (2010) showed that care strategies are more variable in species with short rather than long

development time. Furthermore, taxa with high variation in care duration exhibit variable care patterns, since male involvement in care is associated with an extensive period of parental care (Webb et al. 2010).

Artificial selection and experimental evolution are powerful approaches to investigate causes and implications of pre-zygotic sexual conflict (Holland & Rice 1999; Chapman et al. 2003; Rowe & Day 2005), although no study seems to have used this approach for conflict over care. There may be two reasons for this. First, fast breeding laboratory species often do not exhibit care (e.g. fruit flies, *Caenorhabditis elegans*), or if they do have some care like in mice (*Mus musculus*), there is little flexibility in the male and female involvement that would capture the variation seen in nature. Second, although care-related behaviours have been artificially selected in poultry (e.g. Champagne & Curley 2012), such work usually targets one sex, the female, so it is not straightforward extrapolate to both sexes.

3.4. The implications of sexual conflict over care for macroevolution

Sexual conflict over care, similarly to other types of sexual conflict, is expected to facilitate diversification; speciation and rapid evolution. Although the specific theory for conflict over care has not been developed, the sexually antagonistic selection - the adaptations and counter-adaptations to increase male or female fitness - are thought to influence care strategies, somehow analogous to pre-zygotic sexual conflict (Chapman et al. 2003). For instance, the diverse reproductive modes in frogs and fish are related to parental care (Goodwin et al. 1998; Gomez-Mestre et al. 2012). However, a caveat is that it is extremely difficult to nail down whether speciation (or diversification) is largely (or exclusively) due to conflict over care, since phylogenetic studies are correlational and they don't identify causation. The most convincing approach would seem experimental evolution, although as I note above, this approach has not been used in studies of conflict over care.

Conversely, offspring desertion and uniparental care can reduce productivity of the population (Holman & Kokko 2013). As an extreme example, the 30-40% loss in Eurasian penduline tits due to conflict (Szentirmai et al. 2007) likely to impact on population productivity and increase the risk of population decline, and/or extinction. Reduced productivity due to reluctance of males to provide care appears to be costly, since female-

only care led to a 20 % reduction of productivity compared with other types of care in birds (Sibly et al. 2012).

3.5. Ecology of conflict and cooperation

Although theory tells us that family life is rife with conflicts, the intricate pair-bonding ceremonies and tender (often affectionate) relationships between males and females observed in some insects, fish, birds and mammals leave no doubt that males and females coordinate their behaviour, and they do cooperate not only to copulate but often beyond. Studies of cooperation have a venerable history (Hamilton 1964; Wilson 1975; West et al. 2007; Székely et al. 2010), and one may view parental behaviour as a balance between factors that facilitate conflict, and those that facilitate cooperation (see below). The various costs and benefits of care can be translated into that of the former or the latter. Since there are excellent reviews on the costs and benefits of care (Clutton-Brock 1991; Reichard & Boesch 2003; Wedell et al. 2006; Royle et al. 2012), here I focus on one issue: how conflict and cooperation may balance each other in ecological settings.

On the one hand, parents tend to cooperate in rearing the young in a harsh physical environment (for example, extreme cold or heat, very humid or dry, Wilson 1975; Clutton-Brock 1991), although convincing evidence is scarce because manipulating the physical environment can be challenging. One of the few experimental studies manipulated the exposure of parents and their eggs in a desert environment by shading some nests, or removing the shade from other nests (AlRashidi et al. 2011). The results were consistent with the harsh environment hypothesis: at the experimentally exposed nests parental cooperation increased whereas at shaded nests parental cooperation was reduced. The need of the young may also influence parental cooperation: when substantial parental resources are needed (e.g. food or protection), biparental care tends to evolve (Thomas et al. 2005; Brown et al. 2010).

Different skills of the parents may also facilitate parental cooperation (parental role specialization, Lessells 2012; Trumbo 2012): if one parent specializes in providing one type of care (e.g. feeding the young) whereas the other parent specializes on a different task (e.g. defending the offspring), this stabilizes biparental care (Barta et al. 2014). Finally, long life span and durable pair bonds correlate with biparental care of the young (Ens et al. 1996; Port

& Cant 2013), suggesting that in long-lived animals retaining the mate for future breeding is beneficial.

On the other hand, high mating opportunities and promiscuity tend to destabilize parental cooperation, and reduce the incentive to provide care in one or both parents. Adult sex ratios are often unbalanced, and in female-biased populations like in many mammals, males are at an advantage in finding a new mate (Donald 2007; Kokko & Jennions 2008). When one sex has higher mating opportunity than the other, the favoured sex tends to capitalize from the opportunity to leave the other parent to look after the young (Balshine-Earn & Earn 1998; Pilastro et al. 2001; Kosztolányi et al. 2011). In addition, promiscuity tends to temper the males willingness to provide care, although caring for somebody else's offspring may still be the best option if finding a new mate is difficult, or if the male can somehow selectively assist his own offspring (Møller & Cuervo 2000; Kamel & Grosberg 2012).

The breeding system of a ground nesting small shorebird, the Kentish plover, illustrates how conflicts and cooperation may interactively influence parental care (Box 3.1.). In Kentish plovers, as in most shorebirds, both parents incubate the eggs and biparental care of the eggs for substantial part of incubation seems essential for any young to hatch. Since hatchlings are precocial and capable of feeding themselves, after hatching the demand for care is reduced so that one parent (the male or the female) may desert the family. Brood desertion benefits only the deserting parent, because the deserting parent typically re-mates and re-nests with a new mate, whereas the deserted parent stays with the chicks until the chicks die or fledge at about 4 weeks of age. Desertion is costly for both parents since brood survival is lower after desertion than before desertion (Székely & Williams 1994). On top of this, the deserted parent can be killed by predators whilst defends its young, and he/she loses mating opportunities.

Box 3.1. CONFLICT AND COOPERATION BETWEEN KENTISH PLOVER PARENTS

The Kentish plover, *Charadrius alexandrinus*, is a small shorebird (body mass of 40–44 g) that exhibits a variable mating system and parental care. Two to three eggs are laid in a small scrape on the ground. Both parents incubate the eggs, although, after hatching, one of the parents usually abandons the brood and renests with a new mate. Thus, in a single population, three types of brood care (biparental, male-only, and female-only) and three types of mating system (social monogamy, sequential polygamy by the male, and sequential polygamy by the female) are observed. DNA fingerprinting shows that extra-pair paternity is rare (4% of chicks); and, thus, the social mating

system reflects genetic mating system. A series of experiments and observational studies have been performed in the natural habitat to clarify the roles of environmental and life-history variables that may influence the extent of conflict and parental cooperation (Table 3.1.).

Kentish plovers live in temperate and subtropical habitats, and their breeding habitat includes salt flats around Mediterranean lakes and deserts in which ground surface temperature may exceed 50°C. Preventing the eggs from overheating is a major challenge, and we hypothesized that exposure to heat may select for biparental incubation. To test this hypothesis, they experimentally manipulated the exposure of eggs to sun by shading the nest with a small bush. The results were consistent with the hypothesis, because the extent of biparental incubation was reduced in the shaded nests.

To compare the benefits of deserting for male and female plovers, unmated plovers were experimentally created, and the time they took to find a new mate was observed. Unmated females remated after a substantially shorter time than unmated males, suggesting that mating opportunities are significantly better for female than male plovers. This experimental result is consistent with a demographic study that estimated a heavily male-biased adult sex ratio (Table 3.1).

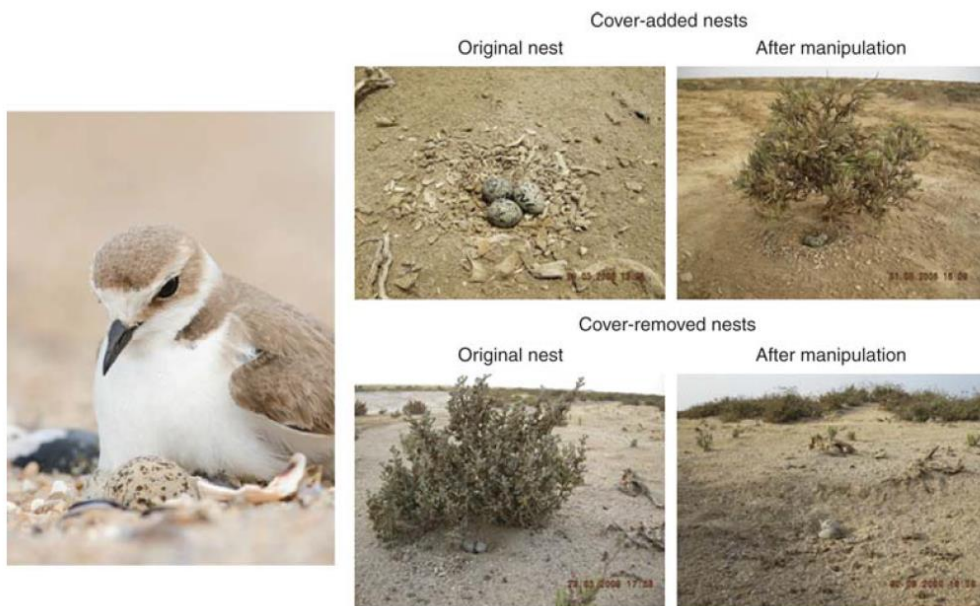


Figure 3.3. Female Kentish plover incubating the eggs (left; credit: Hugo Amador) and experimental manipulation of nest cover (right, AlRashidi et al. 2011).

	Uniparental care	Biparental care	Type of evidence	Reference
Life history				
Family size	Small	Large	Experiment	Székely and Cuthill 2000
Timing of breeding	Early	Late	Observation	Székely and Cuthill 2000
Ambient environment				
Environmental harshness	Mild	Harsh	Experiment	Al-Rashidi et al. 2011
Food abundance	Poor	Rich	Observation	Kosztolányi et al. 2006
Predation rate	Low	High	Observation	Amat et al. 1999
Social environment				
Adult sex ratio	Strongly biased	Less biased	Observation	Kosztolányi et al. 2011

Table 3.1. Different components of parental care in the Kentish plover (Székely 2014). Both parents cooperate in incubating the eggs, although after hatching, most broods are cared for by a single parent (either the male or the female). Desertion is beneficial only for the deserting parent and costly to its mate.

The fitness implications of Kentish plover parental care may illustrate two points (Box 3.1.). First, the costs and benefits of care are often complex, and they may vary between different populations and over the breeding season. To reveal these costs and benefits, one needs to combine observations with experiments to expose the full magnitude of fitness implications.

Second, the conflict and cooperation between parents are played out in a breeding population where breeding and non-breeding individuals interact, and thus it is important to understand how parenting decisions relate to mate choice, competition for mates and pair bonding. Thus conflict over care needs to be approached as influencing (and being influenced) by other aspects of breeding behaviour (Houston et al. 2005; Jennions & Kokko 2010; Alonzo & Sheldon 2010).

3.6. Future directions

Whilst immense progress has been made recently in studies of conflict over care, certain areas are ripe for major advances. First, care is a complex and multidimensional social behaviour, and analyzing the implications of the different components is likely to give novel insights into conflicts over care and conflict resolution in regards to both parental strategies (battleground) and fitness (conflict load). Theoretical, experimental and phylogenetic analyses of this multidimensionality are long overdue.

Second, parental conflict is played out in a population, and it is essential to reveal the interactions between a focal pair (or family), and the rest of the population. Since behavioural

actions have demographic consequences (e.g. maturation, reproduction, mortalities), rolling up the complex relationships between sexual selection, cost of care, sex-specific mortalities and breeding system dynamics seem especially important. The causes of parenting behaviour and their consequences at population level are likely to be complex, although detailed studies of populations that are monitored for long time now offer the opportunities to tease apart these feedback relationships (Székely et al. 2000; Klug et al. 2012).

Third, although studies established some of the genetic, hormonal and neuro-endocrine causes of parental care, much remains to be discovered about the mechanisms of care and parental interactions. (i) New advances in genomics and neuroscience are offering unparalleled insights into the genetic, genomic and neural causes of parental behaviour (McGraw et al. 2010; O'Connell & Hoffman 2012), and using these approaches one may work out how each sex is attempting to maximize its own reproductive success and/or how they influence (or manipulate) their mate's behaviour. (ii) Learning aspects of parental care should receive more attention, for instance when, how and why young animals learn to be a parent. Learning and genetic mechanisms of care are probably interwoven in a complex way (Székely et al. 2010), and revealing these interdependencies will establish the pathways how males and females may respond to each other's behaviour. (iii) Male and female parents may monitor each other's behaviour, and alter their own strategy in response to the other parent. Such repeated interactions ('negotiation', Lessells 2012) have received much theoretical attention, although how these interactions play out in nature is not known in detail. (iv) Parents may manipulate their mate's behaviour or take on self-imposed handicaps. Experimental studies are needed to test these theoretical scenarios.

Fourth, whilst various studies provide behavioural evidence of conflict over care, few studies have quantified the magnitude of conflict in terms of reproductive outcomes for both males and females. (i) Studies are needed that contrast the expected *versus* observed behaviour and reproductive success of males and females. Also, detailed studies are needed to work out the fitness implications (costs & benefits) of care. For instance, a common assumption of theoretical models is that the benefit of care follows a saturating curve while the cost function is accelerating (Houston & Davies 1985; Lessells 2012). Whilst these assumptions seem perfectly plausible, I am not aware any empirical study that has estimated the shape of these functions over a range of realistic parameter values. This may be important because theoretical predictions may depend on the shape of the cost and benefit functions. Using behavioural norms may be one approach to quantify these (Westneat et al. 2011). (ii)

Artificial selection and experimental evolution are powerful approaches, although no study seems to use these approaches for sexual conflict over care. (iii) Furthermore, theoretical, comparative and experimental studies are needed to work out the potential implications of sexual conflict over care for speciation and extinction, somehow analogous to comparable works in pre-zygotic conflict.

Finally, parental care has been investigated in detail less than 1% of animal species that populate the planet, and our knowledge is biased toward taxa that are readily studied (McGraw et al. 2010; Balshine 2012; Trumbo 2012). The parental care of organisms living in extreme environments (e.g. deep sea, extreme heat or freezing) deserve further attention. Information from a wider range of organisms coupled with recent advances in phylogenies and phylogenetic comparative analyses are likely to reveal novel aspects of conflict over care.

3.7. Concluding remarks

Conflict over care is central to the understanding of sex roles and breeding systems. Research in this field is rapidly advancing due to the tractability of many biological systems to experimental manipulations, long-term field studies and phylogenetic comparative analyses. Parental care is also one of the well-known examples of evolutionary game theory, and empiricists are making laudable efforts to match theoretical predictions with experimental results.

Research on parental care and on its implication is making a fundamental contribution to evolutionary biology as exemplified by Trivers' (1972) study of parental investment that ignited a paradigm shift, and became one of the most cited studies produced in this broad field. Parental care research will further benefit from new theoretical advances, methods and techniques, and are likely to be productive.

Chapter 4. Adult sex ratios and breeding systems



Painted snipe pair: female on the left and male on the right (credit: Dan Smith)

This chapter is based upon the following publications:

1. Liker, A., R. P. Freckleton & T. Székely. 2013. The evolution of sex roles in birds is related to adult sex ratio. *Nature Communications* 4: 1587.
2. Liker, András, R. P. Freckleton, & T. Székely. 2014. Divorce and infidelity are associated with skewed adult sex ratios in birds. *Current Biology* 24: 880-884.
3. Székely, T., A Liker, R. P. Freckleton, C. Fichtel & P. M. Kappeler. 2014. Sex-biased survival predicts adult sex ratio variation in wild birds. *Proc Roy Soc London B* 281, article number: 20140342.
4. Székely, T., F. J. Weissing & J. Komdeur. 2014. Adult sex ratio variation: implications for breeding system evolution. *Journal of Evolutionary Biology* 27: 1500-1512.

The great importance of the adult sex ratio has long been recognized by the student of human populations, but it has not received as much attention from the animal biologist as it deserves. (Mayr 1939)

4.1. Introduction

Sex ratios and sex allocation are fundamental concepts in evolutionary biology (Hardy 2002, West 2009). The ratios of males to females at conception, at birth and during adult life (termed primary, secondary and adult sex ratio, respectively) have pervasive influences on ecology, behaviour and life-histories. Primary sex ratio (PSR) plays a central role in sex ratio theory, since selection on PSR is negatively frequency dependent, and there are clear equilibrium predictions for a variety of scenarios, including differential costs in raising male and female offspring, differential effects of parental condition on the reproductive values of male and female offspring, and local mate competition (Trivers 1985, West 2009). However, PSR rarely translates directly into ASR, since various ecological, life-history and demographic processes modulate the transition from PSR to ASR (see below). Consequently, the causes and implications of ASR variation may depend on numerous ecological and evolutionary processes.

Although many animals spend a substantial part of their life as adults, most research in evolutionary ecology of sex ratios has been directed to pre-adult sex ratios. This bias is striking for three reasons. Firstly, since the lack of direct frequency-dependent selection on the ASR means there is no guarantee that ASR biases remain insignificant, one would expect intense research to uncover the processes that create biased ASRs. Secondly, the ASR may affect mate choice, mating system and parental care (Mayr 1939, Trivers 1972, Breitwisch 1989), and therefore, ASR appears to make a substantial, yet not fully understood, impact on breeding system evolution. Thirdly, the ASR in part *via* the number of females, impacts on population growth, and therefore, has implications for population dynamics, risk of extinctions and biodiversity conservation (Bessa-Gomes et al. 2004, Veran & Beissinger 2009, Wedekind et al. 2013). However, no recent review evaluates ASR variation across a broad range of organisms, and the implications of this variation for breeding systems and population demography – in contrast to numerous reviews on primary and secondary sex ratios (e.g., Charnov 1982, Trivers 1985, Hardy 2002, West 2009, Komdeur 2012).

At first sight, one might imagine the ASR to be easier to determine than PSR because in many species sexing adults is easier than of newborn individuals. However, whilst establishing the ratio of male and female offspring in a litter or brood (secondary SR or offspring SR) may be a simple task facilitated by DNA-based sexing, doing the same for adults can be challenging in wild populations, since non-breeding adults (e.g. floaters) often have non-conspicuous lifestyles and remain unnoticed, adult males and females may have different detectabilities due to sex-difference in behaviour and ecology, and adults may form sex-specific aggregations during breeding and/or non-breeding periods. Therefore, reliable ASR estimates often require capture-recapture estimates and demographic modelling (Veran and Beissinger 2008, Kosztolányi et al. 2011).

Here we investigate the processes that may produce ASR bias, and highlight some of the striking examples of ASR variation in natural populations. The term ‘adult’ refers to an animal (male or female) that is physiologically capable of producing offspring. ASRs are often expressed as proportion of males in the adult population. We do not cover simultaneous hermaphrodites or sex-changing organisms (i.e., sequential hermaphrodites). Second, we discuss the implications of the ASR for breeding system evolution, and argue that the ASR and operational sex ratio (OSR, ratio of sexually active males to females, see below) have a dynamic relationship. Understanding the OSR does not necessarily reveal much about the ASR, and *vice versa*. Thirdly, we propose three topics for further research. Future studies in these areas are likely to provide new insights into breeding systems and sex role evolution. Although we do not explore humans or plants here, we note that the ASR may also have relevance for human behaviour, demography and economic decisions (Trent & South 2011, Griskevicius et al. 2012, Schacht et al. 2014), and for plant breeding systems (Taylor 1999, Medrano et al. 2005, Field et al. 2013).

4.2. Causes of variation in adult sex ratios

Adult sex ratio emerges as the result of sex-specific processes affecting sex ratio at various life cycle stages including primary sex ratio, secondary sex ratio or sex ratio at independence (Figure 4.1.). Various factors can result in biased ASRs: a biased sex ratio at birth, sex-differential mortalities of young and adults, sex-differential maturation times, and sex-differential dispersal and migration patterns (Figure 4.1., Wilson 1975, Bessa-Gomes et al. 2004, Veran & Beissinger 2009). Differences in the maturation times of males and females

are well known in various organisms (Daan et al. 1996, Stamps & Krishan 1997, Donald 2007), although their impact on the ASR is rarely explored (but see Hirst et al. 2012). Sex differences in movement patterns are ubiquitous in the animal kingdom, and they can cause extreme ASR at the local level; at a metapopulation level, however, these local biases may balance out, since if an animal moves out from a population it has to move in another population assuming it remains alive.

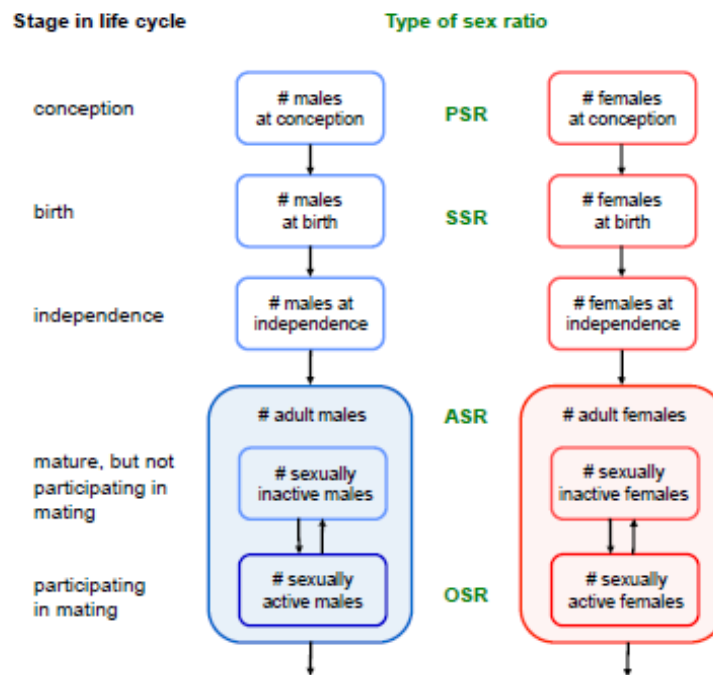


Figure 4.1. A schematic representation of the sex-differential processes affecting sex ratio at various stages in a life cycle: primary sex ratio (PSR), secondary sex ratio (SSR), adult sex ratio (ASR) and operational sex ratio (OSR). A bias in ASR may reflect a bias in PSR, and SSR and/or sex differences in maturation, dispersal and survival. A bias in OSR may reflect a bias in ASR and/or sex differences in behaviours affecting participation in the ‘mating market’ such as sexual receptivity, parental care and post-care recovery (Székely et al. 2014b).

The largest scale study that has been carried out to date tested whether secondary (hatchling) sex ratios, sex ratios at the end of parental care periods (fledgling sex ratios) and/or sex difference in adult survival predicts ASR (Székely et al. 2014a). The study, using data from the avian literature, found that sex bias in adult mortalities predicted ASR (Figure 4.2.) whereas neither hatchling sex ratios nor fledgling sex ratios were related to ASR.

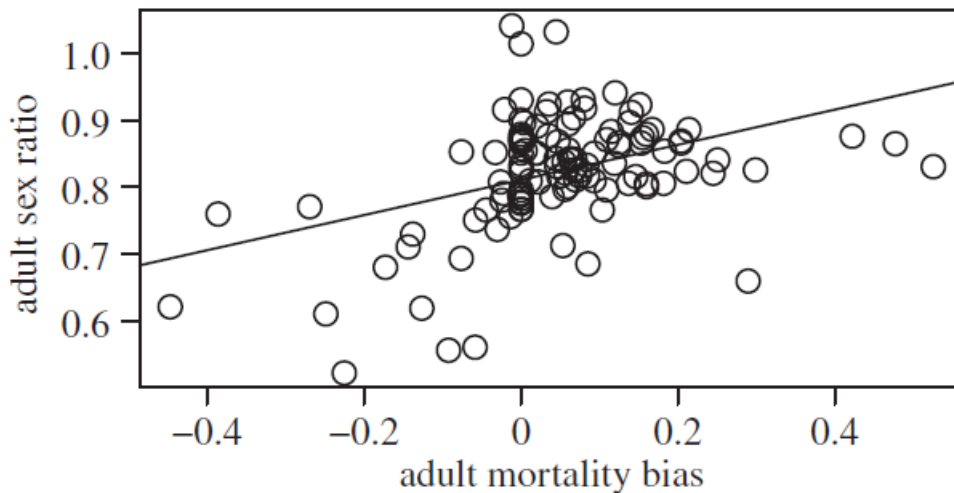


Figure 4.2. Adult sex ratio in relation to adult mortality bias in birds ($(\log(\text{adult female mortality}/\text{adult male mortality}))$, male-biased adult mortality is associated with female-biased ASR whereas female-biased adult mortality is associated with male-biased ASR ($b = 0.263$, $p < 0.001$). ASR is expressed as no. of males/(no. of males + no. of females) and their arcsinesquare-root-transformed values are shown (Székely et al. 2014a).

In contrast to frequency-dependent selection operating on primary sex ratio, there are no similar predictions for adult (or tertiary) sex ratios, since in sexually reproducing diploid organisms the total reproductive value of all adult males equals the total reproductive value of all adult females irrespective of the sex ratio. As a consequence, sex ratio biases in adults are not directly selected against by a compensating adjustment of the PSR, since any increase in the abundance of, say, males is exactly compensated by a reduction in the average reproductive value of individual males. However, as discussed below, a bias in the ASR can initiate numerous ecological and evolutionary processes that indirectly feedback on this bias.

4.2.1. Offspring sex ratios

Sex ratios are already biased early in life (i.e., at conception or at birth) in numerous organisms which can be adaptive, for instance if the cost (or benefit) of care differs for male and female offspring (e.g., in mammals sons may drink more milk than daughters, sons may compete locally for the access to daughters, maternal condition may influence differentially the reproductive success of sons and daughters, Clutton-Brock 1991, Trivers 1985, West 2009). Hatchling sex ratios are often biased in species with environmental sex determination,

for instance hatchling sex ratios are temperature-dependent in numerous fishes and reptiles (Pen et al. 2010). Biased secondary sex ratios can be either enhanced (or diminished) by sex-differential juvenile mortality leading to biased sex ratio at maturation. In sexually dimorphic birds and mammals sex-biased mortality often reflects the direction of sexual size dimorphism: male mortality is higher when males are the larger sex, and female mortality is higher when females are larger than males (Clutton-Brock 1991, Kalmbach and Benito 2007). These differences are attributed to the larger sex either being more sensitive to food shortages (Clutton-Brock 1986, Kalmbach & Benito 2007), or shifted away from its ecological optimum, if size dimorphism is induced by sexual selection (Andersson 1994).

Biased juvenile mortality also occurs in sexually monomorphic species, although the cause of these biases is often obscure. In common eiders *Somateria mollissima* the hatching sex ratio does not deviate from parity, but a male-biased sex ratio soon becomes established due to the higher mortality of female ducklings presumably caused by female-biased predation of chicks (Lehikoinen et al. 2008). In Kentish plover *Charadrius alexandrinus* hatchling mortality is female biased (for unknown reasons), and the sex-difference in juvenile mortalities generates strongly male-biased ASR (Kosztolányi et al. 2011).

4.2.2. Sex difference in the age of maturation

Maturation rates may differ between the sexes (Ancona et al. in prep). Sex-differences in the age of maturation may produce a biased ASR, as seems to be the case in fruit flies, fishes, salamanders and turtles (Kusano & Inoue 2011, Lovich & Gibbons 1990, Osmundson 2006, Pitnick 1993). In common voles *Microtus arvalis*, females mature earlier than males, and therefore, more females than males are recruited to the adult population in early summer (Bryja et al. 2005).

Maturation, in turn, can be influenced by adult mortalities and the ASR. For example, if old and/or large animals are selectively eliminated from the population (for instance, by trophy hunters or a predator specialized on taking large preys), males and/or females may shift toward maturing fast and reproducing at an early age (Roff 2002). In humans, male-biased ASR is associated with early puberty and an increased likelihood that a woman marries before the age of 25, and engages in more premarital and extramarital sexual relationships (Andersson 1994, Trent and South 2011).

4.2.3. Sex difference in adult lifestyles

Adult males and females often have different body sizes and body shapes, behaviour, ornaments and armaments (Arnqvist and Rowe 2005, Fairbairn et al. 2007, Székely et al. 2010), and these sex differences can precipitate into differences in energy consumption, foraging ecology and mortalities - ultimately influencing the ASR. Consistently, in many organisms sex ratio bias only emerges during (or close to) adulthood. For instance, ASR bias in birds and reptiles emerges from even juvenile sex ratios due to sex-biased mortality after reaching adulthood (Donald 2007). Furthermore, the sex ratio in mosquitofish *Gambusia affinis* shifts from an even PSR to a female-biased ASR, since adult males are less resistant to extreme temperatures than females (Krumholz 1948). Temperature-dependent mortality appears to induce a large shift in fish ASR (Wedekind et al. 2013), and thus future climatic changes may potentially affect the ASR of fish populations.

Adult males and females often represent different ecotypes with different lifestyles. For example, females are often cryptic whereas males are more exposed to predators, especially when they are seeking mates (Pettersson et al. 2004; Brouwer 2007). Conversely, pregnant, incubating or nursing females are more vulnerable because their fleeing capabilities are reduced, and they need to spend more time feeding to cope with increased energy demands (Clutton-Brock 1991). A strong diurnal pattern in incubation behaviour by males and females may create sex biased mortalities in Seychelles warblers *Acrocephalus sechellensis*, since common mynahs *Acridotheres tristis* predate during the day when females are incubating (Brouwer 2007, van der Woude unpublished data). Sex biased predation may also result if males and females have different nutritional value (e.g. different fat content) causing predators to preferentially hunt the sex with the highest value, or if males force females into habitats that are more exposed to predators (Darden & Croft 2008).

Given these contrasting predictions, is there a systematic pattern in data with predation bias on males or females? Differential predation is a common cause of biased ASR in fishes, frogs, birds and mammals (Magnhagen 1991, Berger & Gompper 1999, Sargeant et al. 2004, Post & Gotmark 2006, Christe et al. 2006). Male-biased predation is 2.3 times more common than female-biased predation in 81 predator-prey species pairs suggesting that predators often have male-biased prey preference, or they encounter males more often than females (Boukal

et al. 2008). Male-biased predation is not only more common, but also reaches more extreme values (Boukal et al. 2008).

Sex biased predation rates may vary between predators. Although males are preyed more often than females in 23 out of 31 ungulate species (Berger & Gompper 1999), in Thomson gazelles *Gazella thomsonii* the odds of getting killed by wild dogs *Lycaon pictus* were six times higher for males than for females, whereas the odds of getting killed by cheetahs *Acinoyx jubatus* was higher for female gazelles (Berger & Gompper 1999). The same predator may induce different sex biases in predation rates in different prey species: when attacked by African lions *Panthera leo* the likelihood of being killed is 7.3 times higher for male than for female African buffalos *Syncerus caffer*, whereas in reedbuck *Redunca redunca* only females are killed (Schaller 1972).

Parasites and diseases may also create sex biased ASR. In mammals infections by arthropods, helminths and unicellular parasites are often male-biased suggesting that males invest less into their immune system (Moore & Wilson 2002), and this correlates with male-biased mortalities (and female-biased ASRs). Differential morbidity may also emerge if one sex is more sensitive to a particular type of parasite (or disease) than the other.

The effect of parasites on the sex ratio of their host may interact with the ecology of the host. For example, the influence of microsporidian parasite *Edhazardia aedis* was studied as a function of larval food availability to its host, the mosquito *Aedes aegypti* (Agnew et al. 1999). The number of infected mosquitoes dying before adulthood increased as larval food availability decreased. However, proportionately more female mosquitoes died as food availability decreased, so that the adult mosquito populations became increasingly male-biased (Agnew et al. 1999).

Anthropogenic sources of mortality can also be sex-dependent, even when there is no explicit aim to influence mortality, e.g. by hunting, in a sex-specific way. For instance, size selective fishing affects sex ratios in salmon (Kendall & Quinn 2013), and female-biased mortality is caused by cutting the hay during incubation in a meadow bird, the whinchat *Saxicola rubetra*, in which only females incubate the eggs (Grubler et al. 2008).

4.2.4. Sex determination, sex distorters and adult sex ratios

Sex determination systems may also influence the ASR. First, one would expect that in organisms with chromosomal sex determination the heterogametic sex (males in mammals; females in birds and butterflies) is more vulnerable since harmful mutations cannot be "masked" in the homogametic sex. In line with this, males tend to have a higher mortality in mammals, while the opposite is reported in birds and butterflies (Berger & Gompper 1999, Liker & Székely 2005, Donald 2007). These patterns are in line with Haldane's rule which states that hybridization leads to reduced vitality and fertility, and increased early mortality especially in the heterogametic sex (Schilthuizen et al. 2011).

Second, besides having a direct effect on sex differential mortality, the mechanism of sex determination has a more subtle effect on selection differentials. The dynamics of genetic variation on sex chromosomes (where genes related to sex differences tend to accumulate) is different between the genes occurring in only one sex (the Y in mammals, the W in birds and butterflies) and the genes that occur in both sexes. As a consequence, theory predicts marked differences in sex roles that are associated with sex chromosomes (Haig 2006). For example, the different sex determining mechanisms in birds and mammals may cause a sex-difference in philopatry (mammals: typically male-biased dispersal; birds: female-biased dispersal, Haig 2006), male-male competition (mammals: strong; birds: relatively weaker) and female choice (mammals: relatively weaker; birds: stronger). It is obvious that philopatry, male-male competition and female choice can potentially influence the ASR.

Third, sex determination can have an effect on the sex ratio at conception (primary sex ratio) and, hence, indirectly affect the ASR. Sex-specific lethality or sex change can be induced by "selfish" genetic elements (often transmitted with the cytoplasm), or microorganisms like *Wolbachia*. Microbes and cytoplasmically inherited symbionts are common in arthropods, and are well known to bias sex ratios of their hosts early in life (Burt & Trivers 2008), and these may precipitate into biased ASRs. Some cytoplasmatic genetic elements (including microorganisms like *Wolbachia*) are vertically transmitted through the female line (since sperm does not contain cytoplasm); accordingly males are a dead-end road for such genetic elements, and they are only interested in female survival and reproduction.

As a consequence, these elements come up with a multitude of tricks to shift the sex ratio in favour of females that include male-killing, feminizing males, and making females parthenogenetic. They sometime produce spectacularly female-biased ASRs, such as 100 female to 1 male (e.g. in isopods, fruit flies, butterflies; Engelstadtler & Hurst 2009, Price &

Wedell 2008). Experimental support comes from *Eurema hecabe* butterflies that have female-biased ASR: experimentally treated butterflies with antibiotic reverted to 1:1 ASR after treatment (Narita et al. 2007).

4.3. Spatial and temporal variation in adult sex ratios

The different sources of biases create strikingly diverse ASRs between species and populations. Some patterns appear to exist, although it would be premature to make categorical statements about many animal taxa. For example, copepods and mammals tend to have female-biased ASR, whereas male-biased ASR occurs in *Schistosoma* parasites and birds (Beltran et al. 2009, Donald 2007). Some of the most extreme bias occurs among marsupials (Didelphidae and Dasyuridae): in the dusky antechinus *Antechinus swainsonii* and in eight other marsupials males abruptly die after the mating season and there are times when no adult males are alive, and the entire population is made up of pregnant females (Cockburn et al. 1985).

ASR may vary in time, and in open populations some of this variation is due to dispersal (emigration and immigration), or demographic stochasticity that can cause considerable spatial and temporal fluctuations in the ASR in small populations increasing the risk of extinction (Dale 2001, Bessa-Gomes et al. 2004). Nevertheless, ASR fluctuates even in closed populations due to biases in the primary and/or secondary sex ratios, sex differential mortalities or maturation rates (Donald 2007, Hirst et al. 2010). ASR varies over time, for instance, in the jumping spider *Phidippus clarus*: the males emerge before females so that the ASR is male-biased initially in the breeding season (protandry) shifting toward female bias after the females start emerging (Hoefler 2007). In migratory birds, the more common sex (often males) experiences stronger competition for mates so is predicted to arrive earlier (Kokko et al. 2006).

ASR may also vary between different locations, for instance Trinidad guppy *Poecilia reticulata* populations in some streams exhibit significantly male-biased ASR, whereas others have unbiased or female-biased ASR (Pettersson et al. 2004). Since the sex ratio of juveniles is unbiased in all of these populations, the biased ASR appears to result from sex-differential mortality, which in turn reflects spatial differences in natural and sexual selection (Pettersson et al. 2004, McKellar et al. 2009). Male guppies appear to be more sensitive to

high temperatures than females, and thus temperature differences between sites are expected to impact upon the ASR (Pettersson et al. 2004). In addition, with males being more colourful and active than females, the males are predated more often than the females by one predator (killifish *Rivulus hartii*) but not by another (freshwater prawn *Macrobrachium crenulatum*; McKellar & Hendry 2011). Therefore, variation in predator densities between streams may also contribute to ASR variation (McKellar & Hendry 2011).

However, the aforementioned studies have two major limitations. First, no study has tested comprehensively whether ASR bias is due to biased offspring sex ratio, and/or sex difference in maturation and/or survival of juveniles and adults, and thus integrate over all major processes that produce the ASR. Second, most studies that investigated components of ASR variation were non-experimental. Since the ecology, physiology and behaviour of organisms tend to co-vary, it is difficult to disentangle which aspect of animal's life is causally related to sex-biased mortalities, and thus to ASR biases. As demonstrated by Maly (1970), causal analysis can sometimes be performed using controlled and replicated laboratory experiments. He investigated sex-specific intake rates of three different predators feeding on two species of *Diaptomus* copepods. Tadpoles *Ambystoma tigrinum* ate more female than male copepods, guppies ate more males than females, whereas *Hydra cauliculata* ate equal numbers of male and female copepods. Male copepods are more active than females, and this activity difference coupled with the different hunting style of predators produced the bias in prey composition: tadpoles stalk their prey and they capture primarily slowly moving prey, guppies hunt the faster moving prey, whereas *Hydra* feeding is passive and they eat prey that swim into their tentacles. Remarkably, the copepod ASRs in natural ponds were consistent with the results of the laboratory experiments (Maly 1970).

4.4. Implications of adult sex ratios for mate choice, pair bonds and parental care

Theory suggests that the ASR should influence mate acquisition, mating systems and parental care (McNamara et al. 2000, Székely et al. 2000, Kokko & Jennions 2008). Consistently with theoretical expectations, observational, experimental and comparative studies suggest that the ASR influences (or correlates with) various aspects of breeding behaviour, since the rarer sex in the population has more potential partners to mate with than the more common sex.

4.4.1. Mate acquisition

ASR influences pairing behaviour, male-male, female-female and male-female interactions (Alonzo 2010). Males may move away from male-biased patches (Croft et al. 2003, Stefetten & Dale 2012), or if they stay, they intensify courtship and/or competition for mates, for instance in gobies *Gobiidae* and pipefishes *Syngnathidae* (Kvarnemo et al. 1995, Forsgren et al. 2004, Silva et al 2010).

When the ASR is heavily biased, the sex in excess may engage in homosexual pairings or seek mates from a congeneric species. Consistently, female-biased ASR appears to induce female-female pairings in seabirds (Tershy and Croll 2000): Laysan albatross *Phoebastria immutabilis* has a female-biased ASR, and 31% of pairs were female-female pairs (Young et al 2008). Coinciding with strongly female-biased ASR in western gulls *Larus occidentalis*, female-female pairs constituted at least 10% of the breeding population (Hunt et al. 1980). Homosexual pairing has also been observed in captive or domestic birds held in groups with highly skewed sex ratios (Collias and Jahn 1959; Dilger 1960; Sauer 1972). Furthermore, the lack of suitable mating partners has been proposed to lead to hybridisation between different tern species (Whittam 1998).

ASR may influence developmental pathways of juveniles to prepare for mate acquisition as adults. In dung beetles *Onthophagus spp.* male-biased ASR appears to trigger the development of horns that are used as weapons, whereas in populations with female-biased ASR males tend to be hornless (Pomfret and Knell 2008).

4.4.2. Mating system and paternity

Male-biased ASR was associated with higher frequency of polyandry in dunnoek *Prunella modularis* and lesser spotted woodpecker *Picoides minor* (Davies 1992, Rossmanith et al. 2006), whereas in song sparrows *Melospiza melodia* males were monogamous in years when there was an excess of males, but tended towards polygyny when the ASR became female-biased (Smith et al. 1982). Comparative studies support the findings of these single-species studies, at least in birds: polygamy by males is significantly more common at female-biased ASR than at male-biased ASR, whereas polygamy by females is more common at male-biased ASR (Liker et al. 2013, 2014; Figure 4.3). Thus the rarer sex can exploit the

favourable mating opportunities provided by biased ASR, and desert his/her mate and reneest with a new mate (Pilastro et al. 2001).

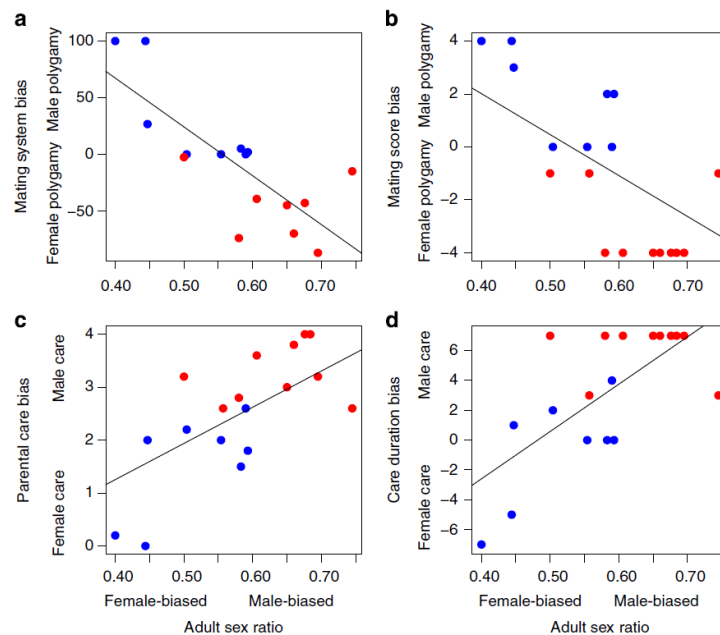


Figure 4.3. Relationships between adult sex ratio and components of sex roles in shorebirds (Liker et al. 2013).

Adult sex ratio (number of adult males / (number of adult males plus females)) is associated with (a) mating system bias ($r = -0.79$, $P < 0.001$), (b) mating score bias ($r = -0.69$, $P = 0.001$), (c) parental care bias ($r = 0.70$, $P = 0.001$), and (d) care duration bias ($r = 0.69$, $P = 0.001$). Red and blue dots refer to species with reversed and conventional sex roles, respectively.

Extra-pair paternity occurs in a wide range of organisms, although we are not aware any theoretical model that would link ASR to mate guarding and paternity. Male-biased ASR may be associated with multiple paternities in two ways. On the one hand, multiple paternity may increase with male-biased ASR since there are more males per female (e.g. in *Rana dalmatina* frogs, Lode et al. 2009). Fruit fly *Drosophila melanogaster* males experimentally kept at male-biased ASR depleted their ejaculates faster than males kept at female-biased ASR (Linklater et al. 2007). Therefore, male reproductive traits appear to have evolved in response to the level of sperm competition, and associated with the rate of ejaculate depletion and the degree of ASR. On the other hand, males may respond to male-biased ASR by intensifying mate-guarding behaviour that reduces multiple paternities (Harts & Kokko 2013). This appears to be the case in frogs, spiders and crustaceans (Fromhage et al. 2005, Takeshita & Henmi 2010, Karlsson et al. 2010).

Intuitively, ASR is expected to influence pair bonds and divorces, although we are not aware of a specific theoretical model. Unbalanced sex ratios may destabilise pair-bonds and induce divorces, although it is not clear whether these effects work through influencing mortality rates (and thus impacting mate availability), or via behaviour for instance one sex harasses (or entice) mated members of the others sex that lead up breaking up existing pair bonds (Liker et al. 2014). Experimentally altered ASR has influenced mating rates (or divorce) in lobsters, fishes and mice (DeLong 1978, Keenleyside 1983, Balshine-Earn & Earn 1998, Debus et al. 1999, Beltran et al. 2009, Karlsson et al. 2010, Silva et al. 2010). An elegant manipulation of the ASR in the endoparasitic trematode *Schistosoma mansoni* showed that male-biased ASR induced more divorce than even or female-biased ASR.

Male-biased ASR was experimentally created in domestic pigeons *Columbia livia* during half of the breeding season, whereas the ASR was reverted to even for the second half of season (Marchesan 2002). During the male-biased period, clutch failure rate increased, and there were more within-pair copulations and a higher proportion of pairs divorcing presumably due to intense male-male harassment. Although the experiment was not fully controlled since male-biased and control ASR were achieved in different parts of the breeding season, the results are consistent with the explanation that surplus of males are detrimental to the breeding population.

4.4.3. Sexual conflict and male harassment

ASR has often been used to induce variation in sexual conflict (Holland & Rice 1999, Arnqvist & Rowe 2005, Wigby & Chapman 2004, Fitze & Le Galliard 2008). Consistently with expectations, female mating rate increased with male-biased ASR in fruit flies *Drosophila melanogaster* (Wigby & Chapman 2004). Furthermore, the duration of mate-guarding, mating duration and mating rate tended to have higher values in male-biased, compared to female-biased adult sex ratios in water striders *Gerris spp.* (Arnqvist & Rowe 2005).

Male-biased ASR (i.e., male skew) may lead to high male aggression and reduced female survival (Hailey and Willemsen 2000, Le Galliard et al. 2005). The excess of males in common lizard *Lacerta vivipara* induces aggression toward females, whose survival and fecundity drop. The ensuing prediction is that male skew should be amplified and total

population size should decline. Numerical projections show that this amplifying effect strongly enhances the risk of population extinction (Bessa-Gomes et al. 2004).

4.4.4. Parental care

Theoretical models predict that male-biased ASR should induce more care by the male, whereas female-biased ASR should induce more care by the female (McNamara et al. 2000, Kokko & Jennions 2008). However, there is mixed support for these predictions (Breitwisch 1989, Keenleyside 1983, Balshine-Earn & Earn 1998). Experimental manipulation of the ASR in cichlid fish *Herotilapia multispinosa* found that brood-guarding males deserted their mates and broods more frequently in the presence of a surplus of females (Keenleyside 1983). However, female parents did not desert their mates, regardless of the sex ratio.

In birds, the evidence for ASR driven parental care is also mixed (Breitwisch 1989). In captive zebra finches, *Taeniopygia guttata* male-biased ASR induced more parental care from males compared to female-biased ASR, but there was no difference in female parental behaviour (Burley & Calkins 1999). In shorebirds, however, parental behaviour of both males and females were related to the ASR: at male-biased ASR male care increased whereas female care decreased, whereas at female-biased ASR the opposite patterns were observed (Liker et al. 2013). Consistently with the shorebird patterns, a recent phylogenetic analysis of parental care found that skewed ASRs (either toward males or females) predicted uniparental care across 659 bird species (Figure 4.4., Remes et al. 2015).

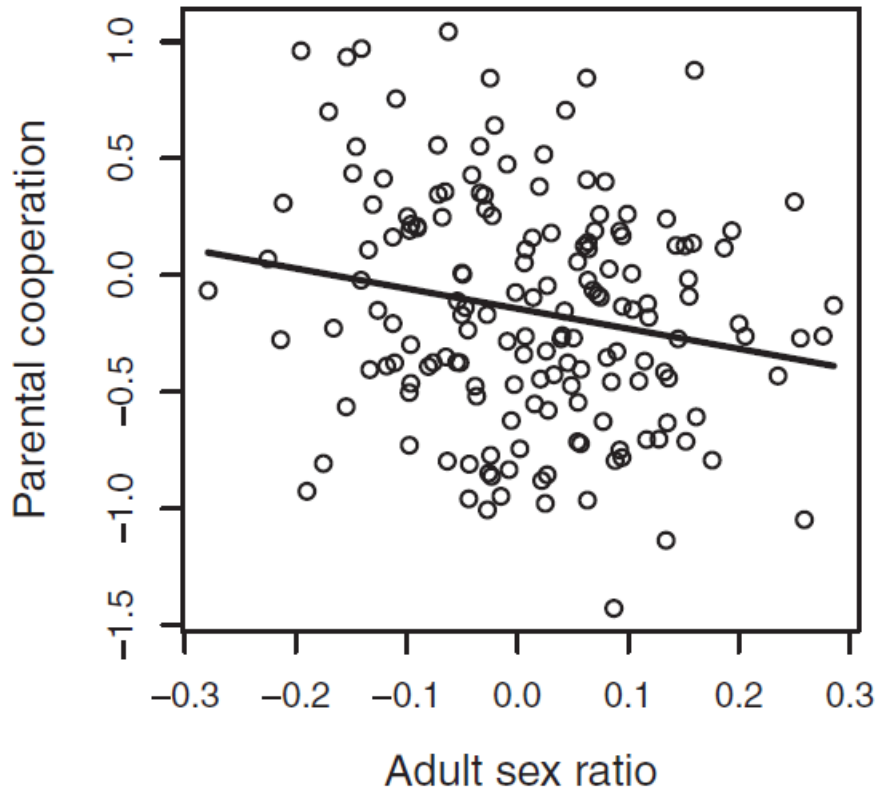


Figure 4.4. Adult sex ratio predicts parental cooperation in birds (Remes et al. 2015). Parental cooperation was statistically adjusted for other predictors in a phylogenetic generalized least squares (PGLS) model and the residuals from statistical models are plotted. Ordinary least squares regression lines are shown.

4.4.5. Strengths and weaknesses of ASR studies for breeding systems

Two major conclusions may emerge from these studies. First, the responses to male-biased and female-biased ASR need not be symmetric. For instance, experimentally altering the ASR toward males increased divorce rate in trematode parasites, whereas female-biased ASRs induced no change in divorce rates (Beltran et al. 2009). The reason for the different responses to male-biased and female-biased ASR appears to be female behaviour: females initiate the divorce, and they only seek divorce when the ASR is male-biased so that they have more options to choose high quality mates (Beltran et al. 2009).

Second, it is often difficult to pin down whether a particular relationship between the ASR, mating and parenting is due to changes in male behaviour, female behaviour or the interaction of both sexes. Mate choice, pair bonds and parenting emerge via social interactions (see below), and the social strategies of individuals are not always directly

visible. For example, unmated individuals (e.g. floaters) should not be ignored when studying mate choice or parenting decisions, since the presence of such individuals may strongly affect the mating (or parenting) decisions of the breeding part of the population, even if they neither mate nor care for the young (Webb et al. 2002).

The majority of the aforementioned studies, however, were non-experimental, and it is therefore difficult to disentangle cause and effect. For instance, a correlation between the ASR and mating system may also emerge if food distribution varies between years, and the change in mating system is driven by the spatial distribution of food resources that coincides with ASR shift (Davies & Lundberg 1984, Pröhl 2002). Studies that did manipulate ASR directly and investigated the animals' responses to altered ASR, however, were often carried out in the laboratory so that it is not known how realistic the animals' responses were to the experimentally altered sex ratios. In addition, in laboratory experiments the animals' options are constrained, for instance, as a response to reduced mating opportunities they may not be able to move to a different habitat as they would do in wild populations.

4.5. Operational sex ratio and adult sex ratio

The operational sex ratio (ratio of sexually active males to females, OSR, Kvarnemo & Ahnesjö 1996, Shuster & Wade 2003) has played a central role in the context of sexual selection, mating systems and breeding system research (note that in their seminal paper Emlen & Oring 1977 defined OSR as the ratio of fertilizable females to sexually active males). The OSR, however, has shortcomings: it is often not trivial to judge whether an individual is sexually active or not, for instance if sexual activity does not have a clear visual or olfactory cue, like sexual swellings in female primates. Many males are able to fertilize females even if they are in a pair-bond or caring for young. Sometimes it is tricky to work out who actually counts, for instance in leks there are only a few males the females are interested in mating, whereas there are many males off the lek that are excluded from mating (Bro-Jorgensen 2007). Therefore, lek-based OSR estimates may give a very different OSR from the population-level OSR.

There is a general tendency to equate the ASR and the OSR (Kokko & Jennions 2008, Weir et al. 2011). A possible reason is that in most experimental studies both ratios are manipulated simultaneously using the starting condition where all adults contribute to the

OSR (Kokko pers comm). For example, X mature males and Y mature females are placed in an enclosure, and then the reproductive variable of interest is measured. Variation among enclosures is then attributed to variation in X : Y which is almost always labelled as the OSR rather than the ASR (Alonso-Pimentel & Papaj 1999; Jirotkul 1999; Klemme et al. 2007; but see Fitze & Le Galliard 2008). This may not be correct because the sexual activity of males and females (and thus OSR) may change during the course of the experiment since some of them pair up, look after the young or lose interest in mating.

The ASR and the OSR may substantially differ in wild populations (Figure 4.1.). First, the sexually available periods of males and females are rarely identical, since males and females may need different times to prepare physiologically for breeding, their receptive periods may have different duration, males and females may contribute differentially to parental care and have different post-care recovery periods. Therefore, cases where the OSR and the ASR are identical appear to be the exception, rather than the rule. For example, the OSR is expected to be male-biased both in mammals and birds, although in mammals the male-biased OSR may emerge from female-biased ASR due to females providing offspring care for substantially longer than males, whereas in birds the male-biased OSR may emerge from male-biased ASR *via* monogamous social pair bonds and biparental offspring care.

Second, *time in*-s and *time out*-s (i.e. time periods when an individual is sexually available or unavailable for mating, respectively) can be phenotypically plastic as a response to OSR, since animals may spend more time sexually active when chances of breeding are high (i.e., increased *time in*), whereas high mating opportunity may entice some adults to reduce parental caring periods and seek a new mate (i.e., reduced *time out*, Székely et al. 2000, Parra et al. 2014). Therefore, the correlation between the OSR and the ASR can be weak: longer *time in* (or shorter *time out*) may change the OSR, whilst the ASR remains constant.

As we argued above, ASR is primarily a demographic property of populations that emerges *via* sex differences in mortality, maturation rates and movement patterns (Bessa-Gomes et al. 2004, Le Galliard et al. 2005, Veran & Beissinger 2009). On top of this, the OSR emerges *via* individuals' decisions whether to join the breeding population, and how long to opt out from breeding during (and after) periods of parental care (Clutton-Brock and Parker 1992, Kokko & Jennions 2008). Since the OSR is partly due to short-term changes between mating decisions, parental care and post-care recovery, the OSR by definition is related to mate choice, pair bonds and parental care (Székely et al. 2000, Jennions & Kokko 2010).

Therefore, the OSR can be viewed as both a cause and a consequence of the mating systems and parental care, rather than an external factor that “explains” mating systems (Székely et al. 2000, Donald 2007). To a certain extent, this may also apply to the ASR (see below), since sex differences in mortality, maturation and movement may also reflect reproductive decisions, such as fighting for territories, delaying maturation to become more competitive, and moving to locations with a lower degree of reproductive competition, although given the ASR’s dependence on demographic processes the effect appears to be weaker.

4.6. The dynamics of adult sex ratios, mating system and parental care

The demographic and behavioural processes that generate the ASR and the OSR are only partly independent, and they both interact with breeding behaviours (Figure 4.1.). So far we emphasized the feedbacks between the OSR, mating behaviours and parental care. Here we focus on feedbacks between the ASR and mortality implications of breeding behaviours (Kokko & Jennions 2008, Jennions & Kokko 2010).

The aforementioned empirical studies should be interpreted with bearing in mind that responses to ASR may involve plastic behavioural responses and/or evolutionary responses manifested over phylogenetic time scales. Accordingly, it might be helpful to recognize two kinds of feedbacks: one on the ecological time scale directly affecting contemporary populations, and the other on an evolutionary time scale (Jennions & Kokko 2010, Klug et al. 2012). On an ecological time scale, the movements of animals from and to particular locations can alter the local ASR. Since one cause of animal’s movements is seeking a mate or a suitable breeding territory, the breeding system in one location may impact upon the sex-specific movement decisions, and thus on the ASR. For instance, if in a polygynous species the males are territorial and floating males are expelled from the local population, the resulting female-biased ASR, is in part a consequence of the breeding system.

Feedbacks on an evolutionary time scale can be positive or negative (Lehtonen & Kokko 2012, Liker et al. 2013). On the one hand, biased ASR may elevate the mortality of the more common sex and thus ASR may be self-correcting (Fisher 1930). For instance, if the ASR is heavily male-biased, this may intensify mate competition and as such, increase male mortality. This process could counter-balance the biased ASR producing a more even ASR. Following Fisher’s logic, Trivers (1972) noted that sex-specific mortality patterns tend to

coevolve with sex-specific patterns of parental investment. For example, the male-biased adult mortalities and female-biased ASRs in mammals are often credited to intense male-male competition (Clutton-Brock 1991, Donald 2007).

On the other hand, sexual selection, parenting and ASR may amplify each other via a positive feedback (Jennions and Kokko 2010, Lehtonen & Kokko 2012). Lack (1968) used a bird example to illustrate this logic in the context of sexual selection and enhanced male mortality: *“Hence, once polygynous mating system has evolved, the unusually strong competition for mates will lead to the males evolving brilliant plumage, which will increase their mortality from predation, which will make it disadvantageous for them to breed when one year old, so there will be a surplus of females, which will be forced to be polygynous, which will reinforce these trends.”* Thus populations may be locked into a heavily biased ASR. Whether the feedbacks are negative or positive, it may depend on the mortality costs of different activities such as the competition for mates and parenting.

4.7. Conclusions and future directions

Adult sex ratio is a fundamental, yet somehow under-appreciated, concept in evolutionary biology. Although substantial progress has been made since Mayr (1939), his main message still holds: evolutionary ecologists should put more effort into estimating the ASR, understanding the causes of ASR variation, and exploring the implications of ASR variation for breeding system evolution, sex roles and population dynamics.

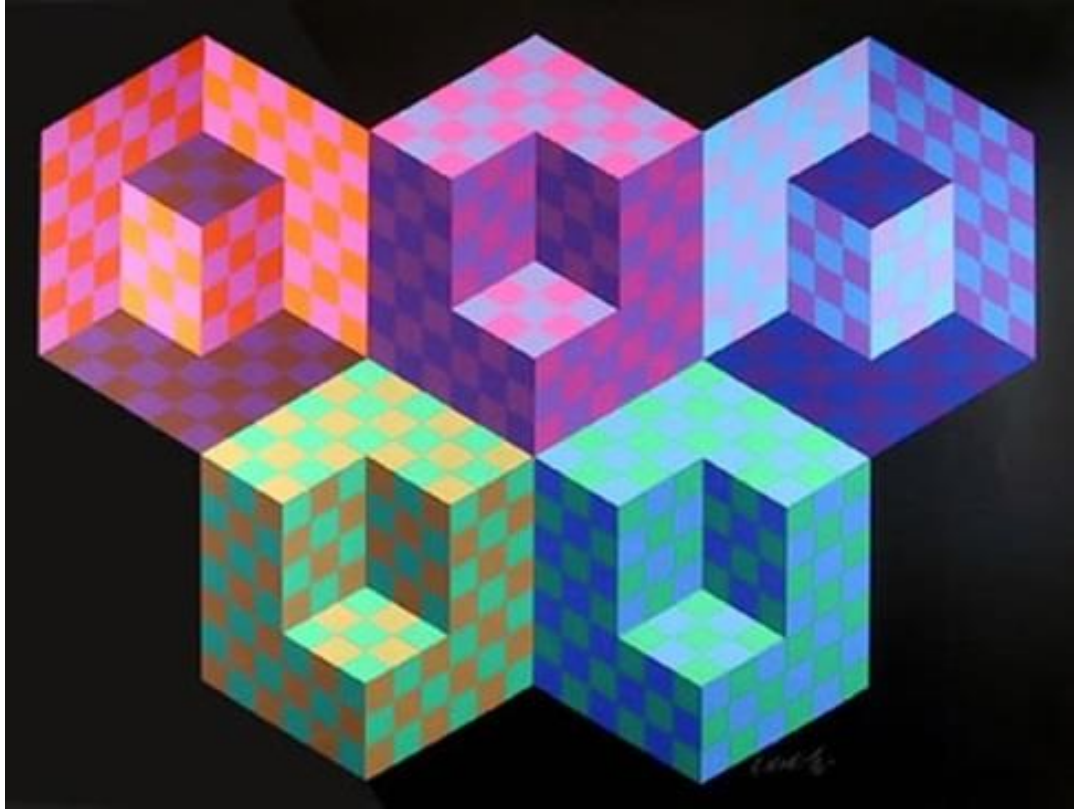
Here we highlights three issues. First, researchers should clearly separate ASR and OSR, and be aware that they may contain different (and often complementary) information. The OSR is a useful term, although it does not replace ASR, since the OSR itself is generated by the mating and parental decisions of animals themselves (Székely et al. 2000, Kokko & Jennions 2008, Alonzo 2010). Biased OSR may emerge from unbiased ASR, and vice versa. Since the ASR and the OSR contain complementary information, separating the effects of the ASR from the OSR would represent an important advance in studies of breeding system evolution.

Second, researchers should be aware of the dynamic nature of relationships with reciprocal causality and a multitude of feedbacks. The ASR and the OSR have effects on sex roles and breeding systems, although sex roles and breeding systems, in turn, may influence individual decisions in a sex-specific manner which will affect the ASR and/or the OSR. Therefore, we

plead for a dynamic view of breeding system evolution, with feedbacks on both ecological and evolutionary time scales.

Third, experimental studies are required to disentangle the thicket of cause and effect relationships. Experiments in laboratory, semi-natural and wild environments can provide novel insights into the complex relationships between populations and individuals that may emerge via sex ratios, breeding behaviour and various selection processes operation on juveniles and adults. Studies are needed to manipulate the ASR and investigate its impact on mate choice, pair bonds and parental care. We hope that in 10 years' time Mayr's quote will be reversed, since the importance of adult sex ratio will have received the much deserved attention from evolutionary biologists.

Chapter 5. Conclusions



Hexa5 (Victor Vasarely, 1988)

Breeding systems exhibit immense variation in animals, and this diversity is the focus of intense evolutionary research. My research made 5 major contribution to this field:

1. Our studies established that sexual selection exhibit disruptive selection on body size: in some organisms large size may be favoured whereas in others small size is an advantage (Chapter 2). These opposing forces appear to explain a common allometric pattern, the Rensch's rule (Chapter 2).
2. Breeding systems offer a great model system to investigate selective processes that influence male and female behaviour (Chapter 3). By considering both the male and the female views of mating and parenting, breeding system research became substantially richer. It is important to consider the costs and benefits for mating, breeding and parenting for both sexes, since evolution is expected to produce strategies that provides the maximum fitness for the individuals (Figure 5.1.). The core of this idea came to me whilst preparing for a workshop in Erice (1998, Italy), so to illustrate this idea I choose the Drawing Hand of Escher, a Dutch painter who spent substantial time in Italy.

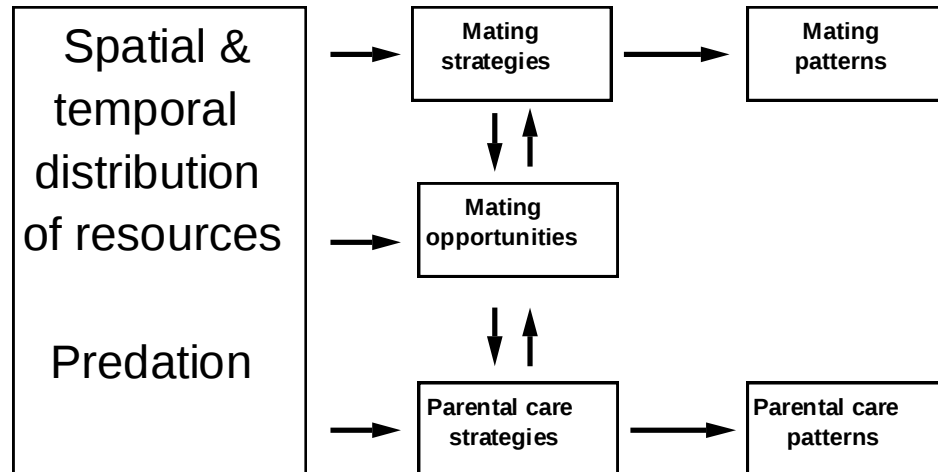


Figure 5.1. The proposed framework for understanding breeding systems (Székely et al. 2000). Mating strategies refer to the behavioural decisions of unmated animals, such as to accept or reject a mate. Parental care strategies are the behavioural decisions of mated animals, such as to care for a brood or desert them. Males and females may have different mating and parental care strategies. The mating and parental care strategies generate the mating patterns (i.e. the distribution of matings in the population, e.g. monogamy, polygyny, polyandry) and the parental care patterns (i.e. the distribution of parental care in the population, e.g. biparental care, female-only care, male-only care).

3. To tease apart the components of breeding systems, it is useful to identify the selection that favours cooperation and the ones that select for conflict (Chapter 3). The strength of these processes may vary over time and can differ between populations. The series of experiments and field studies we carried out in the Kentish plover may illustrate the complexity of natural behaviour whilst teasing apart conflict and cooperation. To illustrate the significance of seeing one pattern and interpreting this pattern from two different perspectives, I chose an illustration of Victor Vasarely: Hexa5: he small cubes on the corner of large cubes can be in two positions: sticking out or dipping inside the large cubes.
4. Adult sex ratio (ASR) is an important although somehow neglected component of breeding system evolution (Chapter 4). ASR offers a straightforward estimate of social environment. Since social behaviours (such as grouping, mating, parenting) may all depend on the social environment, future studies should integrate ASR research into mainstream social behaviour research.
5. Finally, my work may highlight the importance of multi-pronged approach. Whereas most research is reductionist and researchers rarely mixes differ types of research tools due to specialisation, my work benefitted a lot by interaction and collaborating with scientists using very different tools and approaches. Via collaboration it made possible to branch out, benefit from multitudes of tools and skills and integrate these approaches that may have led to new insights in social behaviour (Figure 5.2.).

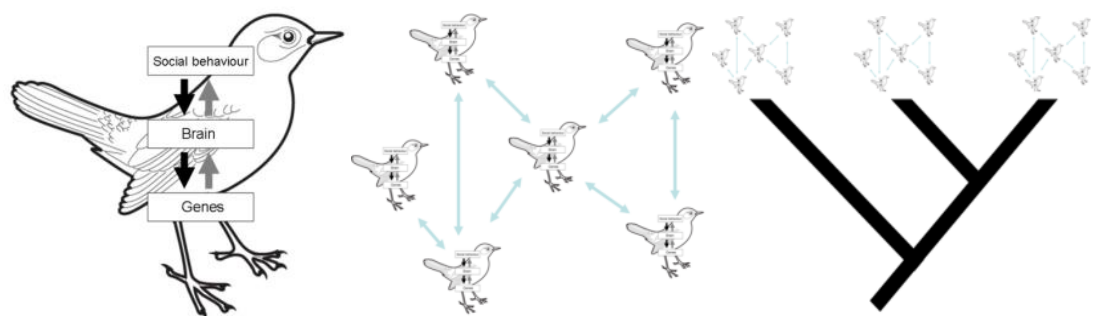


Figure 5.2. Different levels of sociobiological research (Székely et al. 2010). (left) The top-down approach (black arrows) and the bottom-up approach (grey arrows). (middle) Increased complexity occurs when there are interactions between individuals within a population. (right) Including phylogenetic information allows a study of social behaviour over evolutionary time, which we may call socio-phylogeography.

Taken together, studies in this dissertation may suggest that what we can learn from a single population can be investigated across several populations, across multiple species and across a broad range of taxa. In addition, by using a variety of tools such as theoretical modelling, experiments in laboratory or wild and phylogenetic comparisons, we can have a better understanding of social behaviour, and ultimately we gain an integrative view how populations may work in nature. This will not only benefit evolutionary biology but may also impact on social sciences and biodiversity conservation.

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