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Evolution of breeding systems: conflict and cooperation

Doctor of Science Theses

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

2015

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

1. Introduction

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 takes place between sexes, often labelled as female choice.

Since the 1960's 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's 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). 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?

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: 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).

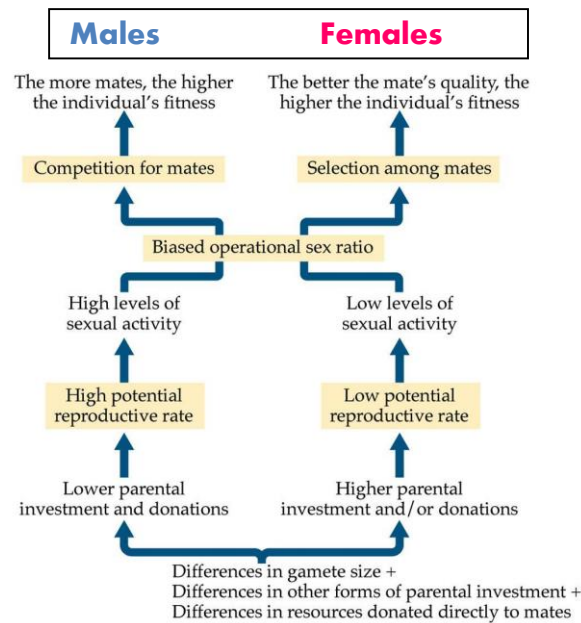


Fig 1. Hypothesised pathways that lead to male and female sex roles (Alcock 2009).

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. Evolution, provisionally accepted). 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 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 Fig 1. Third, the differences are exclusively lead by the conflicting interests by males and females. As I argue in this dissertation, cooperation between parents also need 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-know 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 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 dunnock 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 Pjotr 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. 2014). 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 (Szekely et al. 2014).

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 my studies on breeding system evolution in relation to ASR.

2. Theses

I made various contributions to the field of breeding system evolution, and in this dissertation I wish to focus on three major contributions:

- (i) implications of breeding systems for sexual size dimorphism (**Papers 1 – 2**);
- (ii) the significance of conflict and cooperation for breeding systems (**Papers 3 – 8**);
- (iii) causes and implications of adult sex ratio for breeding system evolution (**Papers 9 – 12**).

Papers

Paper 1. 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

Sexual size dimorphism shows a remarkably widespread relationship to body size in the animal kingdom: within lineages, it decreases with size when females are the larger sex, but it increases with size when males are the larger sex. Here we demonstrate that this pattern, termed Rensch's rule, exists in shorebirds and allies (Charadriiides), 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. 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.

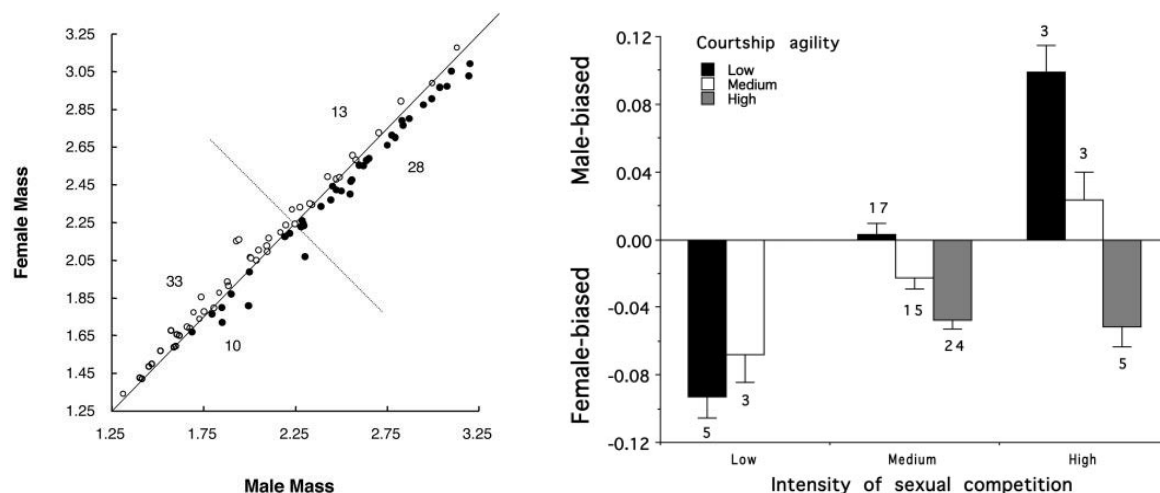


Fig 1.1. (left) Rensch's rule in shorebirds and allies. $\log_{10}(\text{female mass})$ is plotted against $\log_{10}(\text{male mass})$: species in which females are larger than males are shown by open circles, and species in which males are larger than females are shown by solid circles. The numbers 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.

Significance

This study was the first demonstration that the allometric relationship known Rensch's rule is driven by sexual selection. The work also showed that agility in display behaviour predicts small males relative to female: a somehow counterintuitive influence of sexual selection acting on male size.

Paper 2. Fairbairn, D., W. Blanckenhorn & T. Székely (eds). 2007. Sex, size and gender roles. Evolutionary studies of sexual size dimorphism. Oxford University Press, 1-266

Sex, size, and gender roles is the first book to investigate the genetic, developmental, and physiological basis of sexual size dimorphism found within and among the major taxonomic groups of animals. Carefully edited by a team of world-renowned specialists in the field to ensure a coherence of style and approach between chapters, it presents a compendium of studies into the evolution, adaptive significance, and developmental basis of gender differences in body size and morphology. Adaptive hypotheses allude to gender-specific reproductive roles and associated differences in trophic ecologies, life history strategies, and sexual selection. This 'adaptationist' approach is balanced by more mechanistic studies of the genetic, developmental, and physiological basis of sexual size dimorphism to provide a comprehensive and authoritative overview of the subject. Throughout the volume the emphasis is on sexual dimorphism in overall size; however, the scope of enquiry encompasses gender differences in body shape, the size and structure of secondary sexual characteristics, patterns of growth (ontogeny), and patterns of gene regulation. This advanced, research level text is suitable for graduate level students and researchers in the fields of evolutionary biology, behavioural ecology, physiology, developmental biology, and genetics. It will also be of relevance and use to non-biologists from fields such as anthropology and gender studies.

A chapter in this book (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):

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. 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.

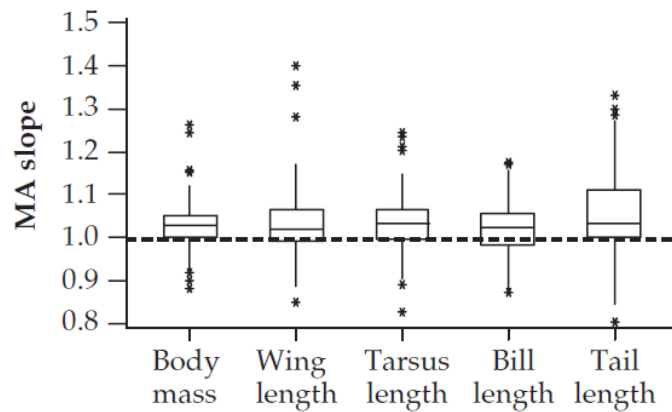


Figure 2.1. Rensch's rule in birds. The principal axis of major-axis (MA) regression $\log_{10}(\text{male size}) : \log_{10}(\text{female size})$ was calculated separately for each family with data from at least five species. The median slope is significantly larger than 1.0 in all traits (Wilcoxon 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.

Significance

This book was (and still is) the most comprehensive evaluation of sexual size dimorphism across a broad range of taxa. The chapter I co-authored with Terje Lislevand and Jordi Figuerola showed that the pattern we reported from shorebirds (Székely et al. 2004) holds as general explanation across avian taxa.

Paper 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. *Journal of Evolutionary Biology* 20: 1739-1744

A fundamental tenet of sexual conflict theory is that one sex may increase its reproductive success (RS) even if this harms the other sex. Several studies supported this principle by showing that males benefit from reduced paternal care whereas females suffer from it. By investigating penduline tits *Remiz pendulinus* in nature, we show that parental conflict may be symmetric between sexes. In this small passerine a single female (or male) cares for the offspring, whereas about 30% of clutches are deserted by both parents. Deserting parents enhance their RS by obtaining multiple mates, and they reduce the RS of their mates due to increased nest failure. Unlike most other species, however, the antagonistic interests are symmetric in penduline tits, because both sexes enhance their own RS by deserting, whilst harming the RS of their mates. We argue that the strong antagonistic interests of sexes explain the high frequency of biparental desertion.

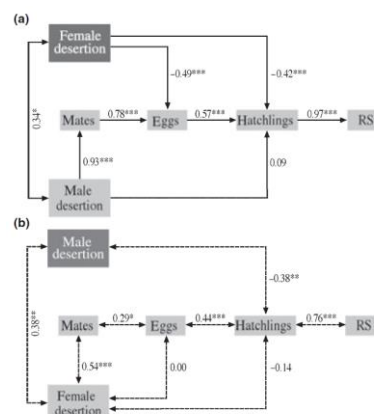


Figure 3.1. (left) Penduline tit pair at the nest (credit: Csaba Daroczi). (right) Clutch desertion in relationship to reproductive success (RS) of (a) male and (b) female penduline tits. (a) Path diagram of male RS. Arrows indicate direct linear relationships between explanatory and response variables, 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. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Significance

This paper presents the best estimates to date on the fitness components of various parenting options. It shows that male and female interests are antagonistic over brood desertion, and argues that the high frequency of biparentally deserted nests book (about 30%) is the outcome of parental conflict.

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, pp 245-263

The focus of this book chapter is to overview studies of sexual conflict between parents. To illustrate the results of such studies, I used the Kentish Plover investigations as an example:

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 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 4.1).

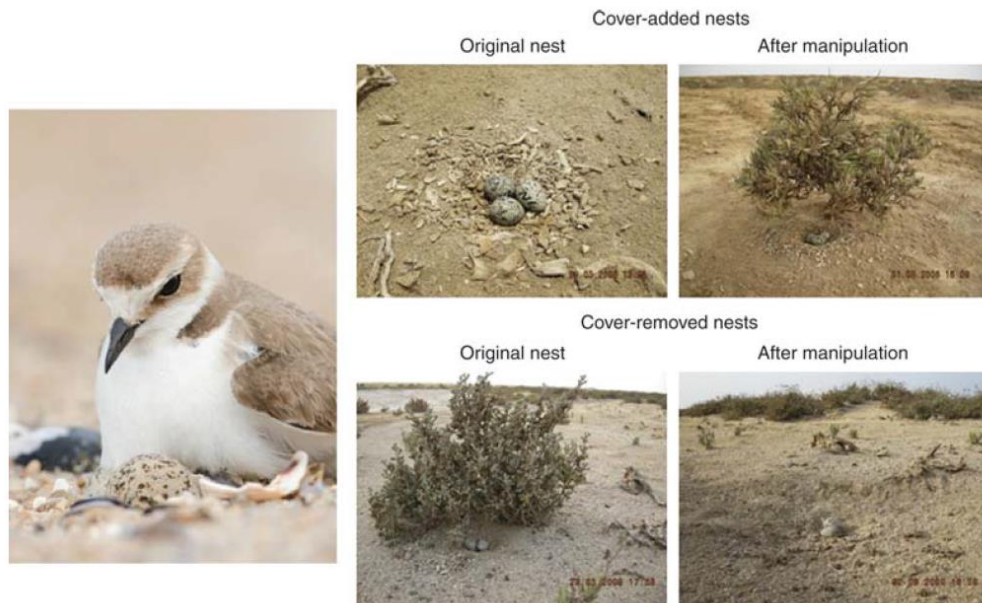


Figure 4.1. Female Kentish plover incubating the eggs (left) and experimental manipulation of nest cover (right).

	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 4.1. Different components of parental care in the Kentish plover. 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.

Significance

This review summarises what we know and we do not know about sexual conflicts between parents. The Kentish plover overview illustrates the need to evaluate the fitness implications of both conflict and cooperation. Taken together, this chapter linked the parental care research to sexual conflict theory.

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

Mating opportunities may differ between closely related species, although the evidence for such variation is scant. Here we compared remating opportunities and courtship behaviour between three shorebird species: the Kentish plover, *Charadrius alexandrinus*, the Kittlitz's plover, *Charadrius pecuarius*, and the white-fronted plover, *Charadrius marginatus*, using data and an experimental approach from a previous study of the Kentish plover. By experimentally creating unmated males and females, we found that remating opportunities differed between these closely related plover species: remating times were shorter for females than males in a Kentish plover population that had a male-

biased adult sex ratio, and in which most brood care after hatching was carried out by males. In contrast, remating times were male-biased in the uniparental Kittlitz's plover and unbiased in the biparental white-fronted plover. Male Kentish plovers spent significantly more time on courtship than females, whereas courtship behaviour was not sex biased in the other two plover species. The mate removal experiments also provided insights into pair bond stability. In the Kittlitz's plover, all 16 newly formed pairs remained together after the release of their former mates from captivity, whereas newly established pairs were replaced by their former mates upon release in all 12 white-fronted plover pairs. Taken together, these results are important in highlighting interspecific variation in mating activities, and suggest that both operational sex ratio and pair bond stability may differ between closely related species. These variations, in turn, may influence mating systems and parental care.

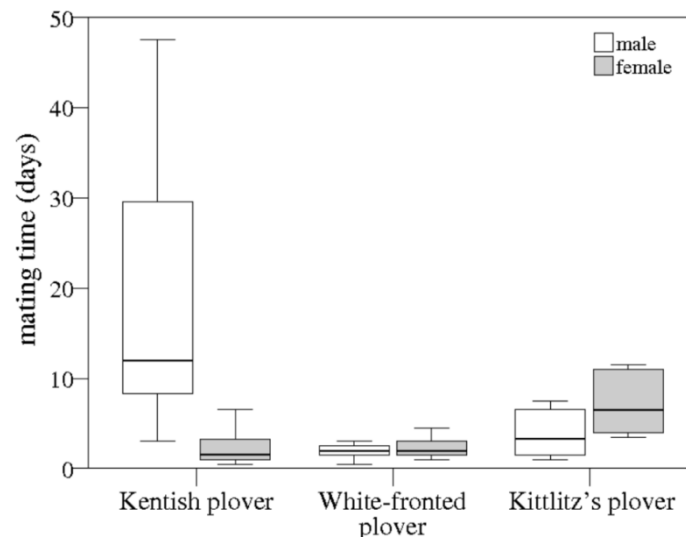


Figure 5.1. Remating times in three plover species. The lower and upper borders of the box are lower and upper quartiles, respectively, the horizontal bar is the median and whiskers represent the lowest and highest observations.

Significance

Experimental evidence for different mating opportunities among closely related species is rare. This study shows that male and female mating times may vary even among closely related species. It suggests that adult sex ratios may differ between the species: a hypothesis that is currently tested using demographic modelling in all three plover species.

6. 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

We argue that sexual conflict theory is an excellent conceptual framework for understanding the diversity of breeding systems. In this review we focus on shorebirds (Charadriiformes), although the theoretical framework should be applicable beyond this clade. Shorebirds are an excellent group to understand breeding system evolution, because they exhibit unusual ranges of mating systems and parental care among birds. First, we review cases in which the interests of males and females are different over mating. This includes mate choice, female–female competition, and infanticide. Second, we review experimental and phylogenetic studies that suggest conflict between males and females over parental care. The latter studies, along with game-theoretic models, suggest that conflict resolution over care has implications for mating behaviour. In turn, the resolution of mating conflict may have implications for parental behaviour. Thus a key element of sexual conflict theory, unlike traditional sexual selection theory, is the dynamic view of mating and parental behaviours. To test the predictions and implications of sexual conflict theory, we need thorough experiments in the field or aviary, and advanced phylogenetic comparative analyses. We anticipate that shorebirds will continue providing challenges and solutions to central issues of evolutionary biology, such as breeding systems.

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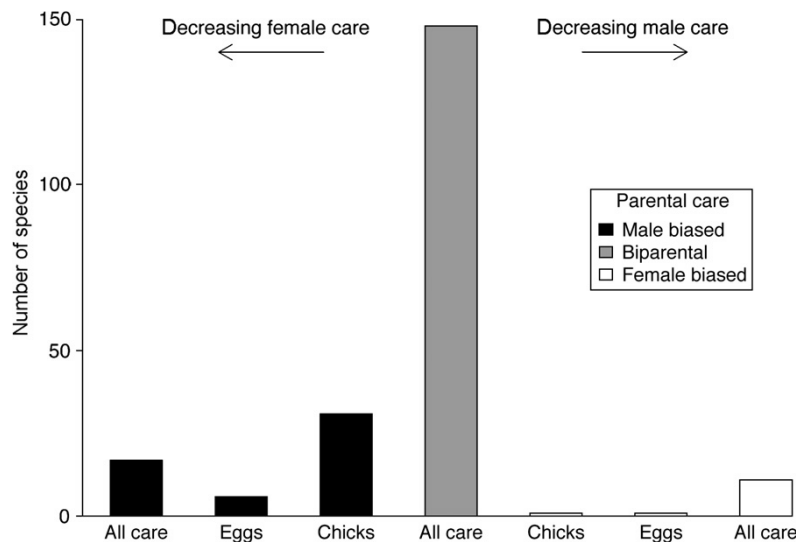


Fig. 6.1. Distribution of parental care in shorebirds. “Male biased” means that the male contributes all care either until the chick fledge (“All care”), or the majority of care with females deserting before hatching (“Eggs”), or before fledging (“Chicks”). The same terminology applies to “Female -biased” care. In biparental taxa both parents provide care until the chicks fledge.

Significance

This review provides the background for one of the major concepts underpinning breeding systems evolution: sexual conflict. It uses shorebirds as ecological model organisms to evaluate various components of sexual conflict. The great diversity of breeding system variation shorebirds offer unparalleled opportunities to test hypothesised components of sexual conflict.

7. Houston, A. I., T. Székely & J. M. McNamara. 2005. Conflict over parental care. *Trends in Ecol Evol* 20: 33-38

Conflict between parents over care of young arises when the young benefit from the effort of both parents, but each parent suffers a reduction in future reproductive success as a consequence of its own effort. Here, we review existing models and argue that they fail to capture many important components of parental conflict. For example, we lack adequate models of how a parent should compensate for a reduction in the effort of its mate. These models should incorporate the process by which decisions are reached. Recent theory suggests that a parent benefits by handicapping itself, and more experimental and theoretical work on this topic could be fruitful. We also need more theoretical work on attractiveness that incorporates consistent interactions between males and females.

Significance

This well-cited invited review evaluate key (largely theoretical) advances in the study of sexual conflict between parents. It argues that new theoretical advances are necessary to dissect the various components of conflict, and proposes specific processes that have not been theoretically explored.

8. Harrison, F., Z. Barta, I C Cuthill & T. Székely. 2009. Conflict and cooperation between parents over care: a meta-analysis. *Journal of Evolutionary Biology* 22: 1800-1812

Biparental care of offspring is both a form of cooperation and a source of conflict. Parents face a trade-off between current and future reproduction: caring less for the current brood allows individuals to maintain energy reserves and increase their chances of remating. How can selection maintain biparental care, given this temptation to defect? The answer lies in how parents respond to changes in each other’s effort. Game-theoretical models predict that biparental care is evolutionarily stable when

reduced care by one parent leads its partner to increase care, but not so much that it completely compensates for the lost input. Experiments designed to reveal responses to reduced partner effort have mainly focused on birds. We present a meta-analysis of 54 such studies, and conclude that the mean response was indeed partial compensation. Males and females responded differently and this was in part mediated by the type of manipulation used.

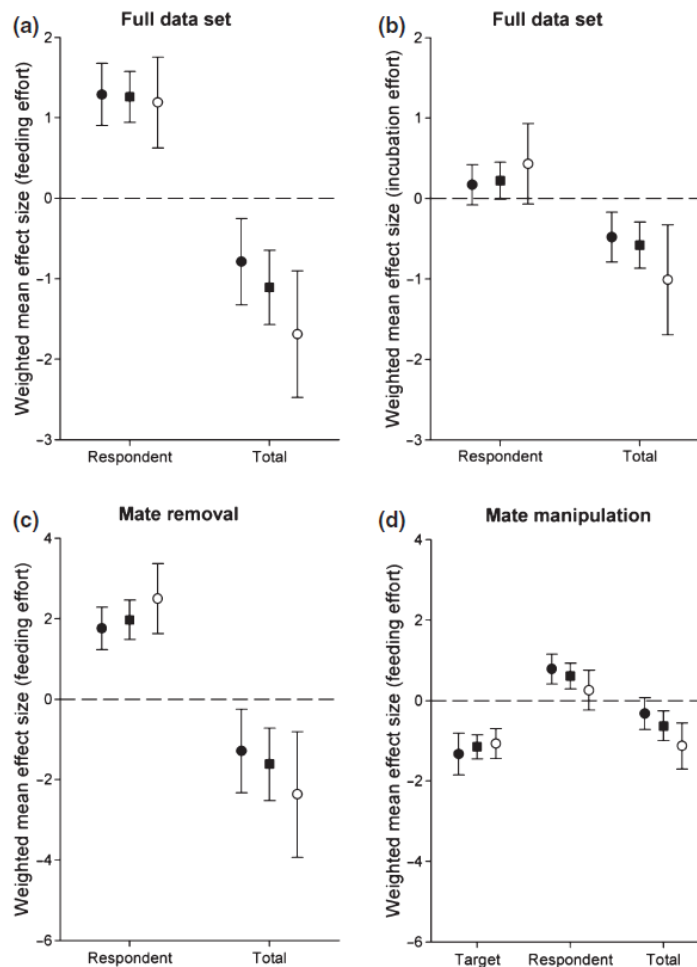


Figure 8.1. Weighted mean effect sizes (Cohen's d) computed from our data set. In all graphs, squares show mean across both sexes, black circles show mean for females and white circle mean for males. Error bars show 95% confidence intervals. (a) Effect sizes for changes in feeding effort calculated from the full data set. (b) Effect sizes for changes in incubation or brooding effort calculated from the full data set. (c) Effect sizes for changes in feeding effort calculated from mate removal studies only. (d) Effect sizes for changes in feeding effort calculated from mate manipulation studies only.

Significance

The seminal experiment of Wright and Cuthill (1988) has sparked much interest among behavioural ecologists so that numerous studies have carried out experimental manipulations that targeted one parent and also reported the responses of the targeted parent's mate. We pulled together these studies, and using meta-analytic techniques show that partial compensation is the most typical response to manipulation. This well-cited study shows that parental cooperation could be maintained by partial compensation although other hypothesised causes of biparental care have remained untested.

9. 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

Sex-role reversal represents a formidable challenge for evolutionary biologists, since it is not clear which ecological, life-history or social factors facilitated conventional sex roles (female care and

male-male competition for mates) to be reversed (male care and female-female competition). Classic theories suggested ecological or life-history predictors of role reversal, but most studies failed to support these hypotheses. Recent theory however predicts that sex-role reversal should be driven by male-biased adult sex ratio (ASR). Here we test this prediction for the first time using phylogenetic comparative analyses. Consistent with theory, both mating system and parental care are strongly related to ASR in shorebirds: conventional sex roles are exhibited by species with female-biased ASR, whereas sex-role reversal is associated with male-biased ASR. These results suggest that social environment has a strong influence on breeding systems and therefore revealing the causes of ASR variation in wild populations is essential for understanding sex role evolution.

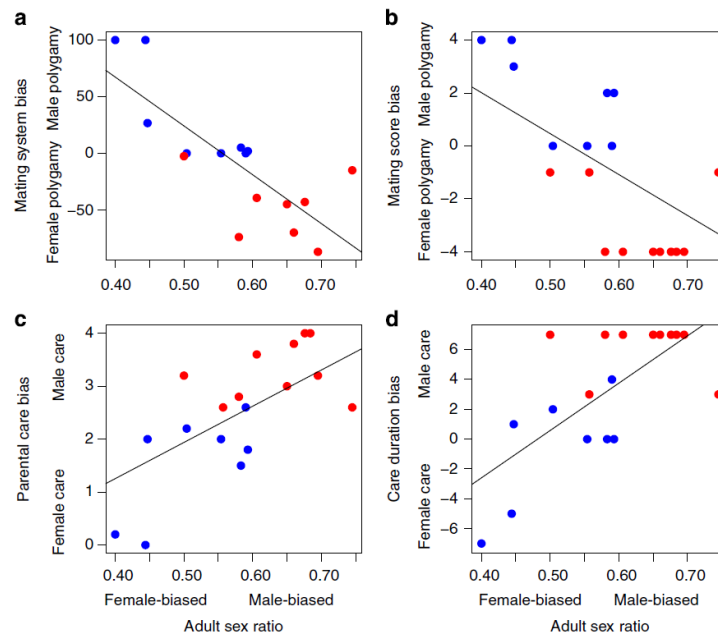


Figure 9.1. Relationships between adult sex ratio and components of sex roles in shorebirds. Adult sex ratio (number of adult males / (number of adult males plus females)) is associated with (a) mating system bias ($r = -0.79$, $P < 0.001$), (b) mating score bias ($r = -0.69$, $P = 0.001$), (c) parental 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.

Significance

This paper has opened a series of comparative analyses that addressed the causes and implications of sex ratio variation. Sex role reversal caused headaches to evolutionary biologists ever since Charles Darwin spotted that dotterels, phalaropes and painted snipes appear to exhibit the reversal of normal sexual roles. Numerous ecological hypotheses have been proposed, but empirical data were not consistent with any of these explanations. Here we show that adult sex ratio explains a high percentage of interspecific variation in sex roles in shorebirds. This explanation is still the best supported hypothesis of sex role reversal.

10. 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

Adult sex ratio (ASR) is a fundamental concept in population demography, and recent theory suggests that ASR plays a central role in social behaviour, mating systems, and parental care. Unbalanced ASRs are predicted to influence pair bond and mating behaviour, since the rarer sex in the population has more potential partners to mate with than the more common sex. Here we use phylogenetic comparative analyses to test whether ASR is related to three major aspects of mating behaviour: divorce, social polygamy, and pair-bond infidelity. ASR is strongly correlated with long term pair bonds, since the divorce rate is higher in species with a female-biased sex ratio, indicating that mate change by pair members and/or breaking of pair bonds by unmated individuals is more frequent when

females outnumber males. Short-term pair bonds are also associated with unbalanced ASRs: males are more commonly polygamous when females outnumber males, and conversely, females are more polygamous when males outnumber females. Furthermore, infidelity increases with male-biased ASR in socially monogamous birds, suggesting that male coercion and/or female willingness to cheat the partner are facilitated by male-biased ASR. Our results provide the first comprehensive support for the proposition that ASR influences multiple aspects of pair-bond and mating behaviour in wild populations.

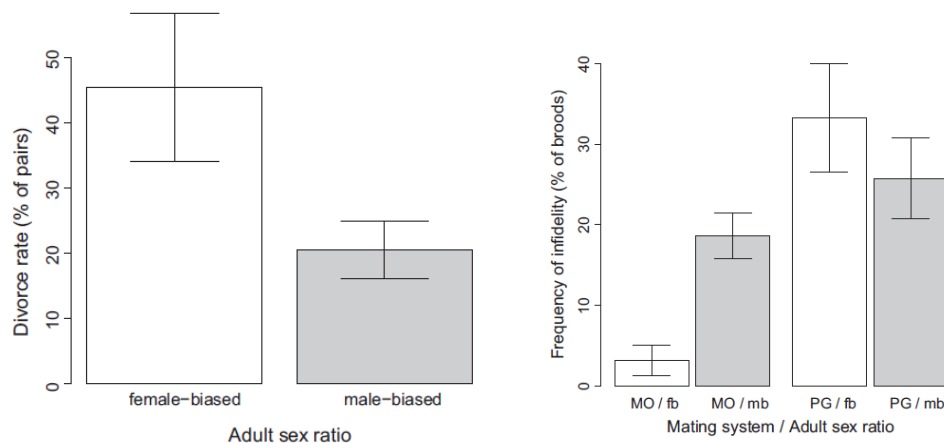


Figure 10.1. (left) Divorce Rates in Wild Bird Populations Exhibiting Male-Biased or Female-Biased Adult Sex Ratios. Divorce rate (mean $\pm$ 1 SE% of pairs that divorce from one year to the next) is higher in birds with female-biased adult sex ratio (ASR) (proportion of adult males in all adults < 0.5 , white bar) than in male-biased species (ASR > 0.5 , gray bar). (right) Adult Sex Ratio, Mating System, and Pair-Bond Infidelity In monogamous bird species ($< 1\%$ polygyny, MO), pair-bond infidelity (estimated by the frequency of broods with extrapair paternity) is higher under male-biased ASR (mb, gray bar) than under female-biased ASR (fb, white bar). In polygamous species ($> 1\%$ polygyny, PG), the frequency of infidelity does not differ significantly between female-biased and male-biased species.

Significance

Although it seems fairly trivial, Divorce, pair bonding and extra-pair paternities have never been investigated from the perspectives of social environment. Here we reported the results of the first investigation by showing that both short-term and long-term pair bonds relate to adult sex ratio. Although the precise causes of these patterns remained elusive, this work represent a major step towards revealing the complex relationships between population sex ratio and social behaviour.

11. 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

Adult sex ratio (ASR) is a central concept in population demography and breeding system evolution, and has implications for population viability and biodiversity conservation. ASR exhibits immense interspecific variation in wild populations, although the causes of this variation have remained elusive. Using phylogenetic analyses of 187 avian species from 59 families, we show that neither hatching sex ratios nor fledging sex ratios correlate with ASR. However, sex-biased adult mortality is a significant predictor of ASR, and this relationship is robust to 100 alternative phylogenetic hypotheses, and potential ecological and life-history confounds. A significant component of adult mortality bias is sexual selection acting on males, whereas increased reproductive output predicts higher mortality in females. These results provide the most comprehensive insights into ASR variation to date, and suggest that ASR is an outcome of selective processes operating differentially on adult males and females. Therefore, revealing the causes of ASR variation in wild populations is essential for understanding breeding systems and population dynamics.

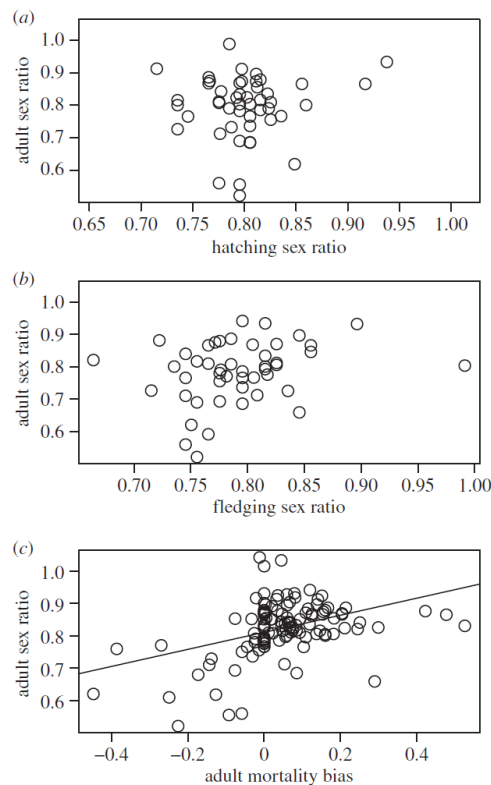


Figure 11.1. ASR in relation to hatching sex ratio, fledging sex ratio and adult mortality bias in birds. (a) Hatching sex ratio ($b = 0.518$, $p = 0.127$), (b) fledging sex ratio ($b = 0.470$, $p = 0.082$) and (c) sex bias in adult mortality ($\log(\text{adult female mortality}/\text{adult male mortality})$, $b = 0.263$, $p < 0.001$). Sex ratios are expressed as no. of males/(no. of males + no. of females), and their arcsine square-root-transformed values are shown.

Significance

This is the first study analysing the causes of ASR variation in a broad range of taxa. By using birds as model organisms, we explored whether birth (or fledgling) sex ratios predict population sex ratios as opposed to mortalities during adulthood. Since the latter seems a lot more important than the former, this raises further questions WHY adult mortalities are sex-biased. In a recent study we advance this topic by comparing ASRs between sex determination systems in tetrapods (Pipoly et al. *Nature*, in press), and show that the heterogametic sex has higher mortality than the homogametic sex; a pattern that is consistent in amphibians, reptiles, birds and mammals.

12. Székely, T., F. J. Weissing & J. Komdeur. 2014. Adult sex ratio variation: implications for breeding system evolution. *Journal of Evolutionary Biology* 27: 1500-1512

Adult sex ratio (ASR) exhibits immense variation in nature, although neither the causes nor the implications of this variation are fully understood. According to theory, the ASR is expected to influence sex roles and breeding systems, as the rarer sex in the population has more potential partners to mate with than the more common sex. Changes in mate choice, mating systems and parental care suggest that the ASR does influence breeding behaviour, although there is a need for more tests, especially experimental ones. In the context of breeding system evolution, the focus is currently on operational sex ratios (OSRs). We argue that the ASR plays a role of similar importance and urge researchers to study the ASR and the OSR side by side. Finally, we plead for a dynamic view of breeding system evolution with feedbacks between mating, parenting, OSR and ASR on both ecological and evolutionary time scales.

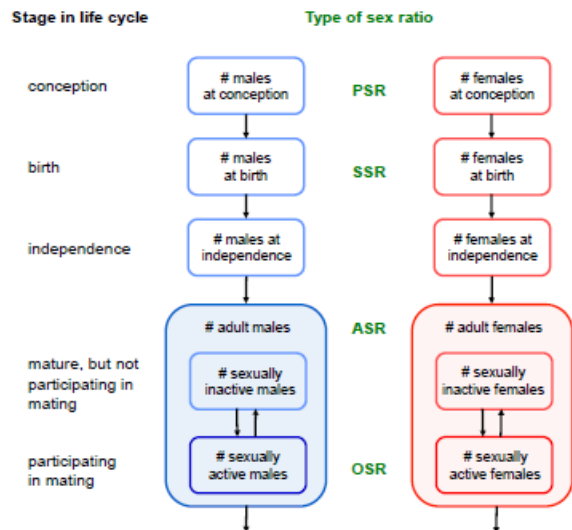


Figure 12.1. A schematic representation of the sex-differential processes affecting sex ratio at various stages in a life cycle: primary sex ratio (PSR), secondary sex ratio (SSR), adult sex ratio (ASR) and operational sex ratio (OSR). A bias in ASR may reflect a bias in PSR, and SSR and/or sex differences 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.

Significance

This review paper is focused on the significance of ASR and its relevance to studies of breeding systems. It argues that ASR and OSR (operational sex ratio, i.e. ratio of sexually active males and females) represent different entities, and call for more studies focusing on ASR. We also emphasize the need to investigate demographic processes, ASR and breeding systems in a coherent theoretical framework, given the complex relationships between these terms and processes

3. Conclusions

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 (Papers 1 & 2). These opposing forces appear to explain a common allometric pattern, the Rensch’s rule (Papers 1 & 2).
2. Breeding systems offer a great model system to investigate selective processes that influence male and female behaviour (Papers 3 & 4). 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. The core of this idea came to me whilst preparing for a workshop in Erice (1998, Italy), so I choose an illustration of Escher (Figure 1), a Dutch painter who spent substantial time in Italy.

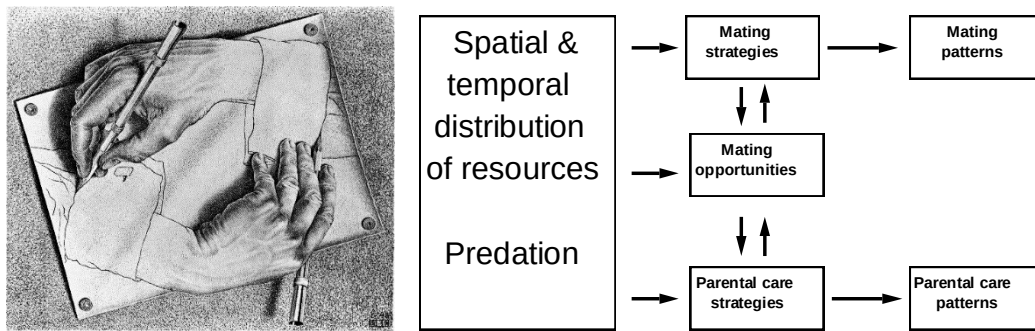


Figure 1. (left) Drawing Hands by M.C. Escher. (right) The proposed framework. Mating strategies refer to the behavioural decisions of unmated animals, such as to accept or reject a mate. Parental care strategies are the behavioural decisions of mated animals, such as to care for a brood or desert them.

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 (Papers 7 & 8). 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 (Paper 4). To illustrate the significance of seeing one pattern and interpreting this pattern from two different perspectives, I chose an illustration of Victor Vasarely (Figure 2).

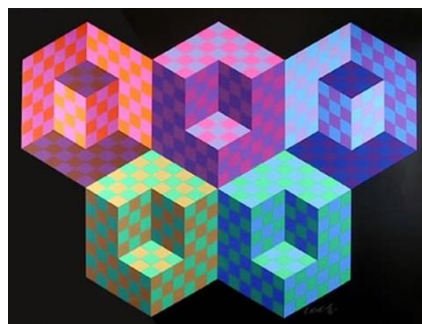


Figure 2. Victor Vasarely: Hexa5. The small cubes on the corner of large cubes can be in 2 positions: sticking out or dipping inside the large cubes.

4. Adult sex ratio (ASR) is an important although somehow neglected component of breeding system evolution (Papers 10 - 12). 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 different 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 3).

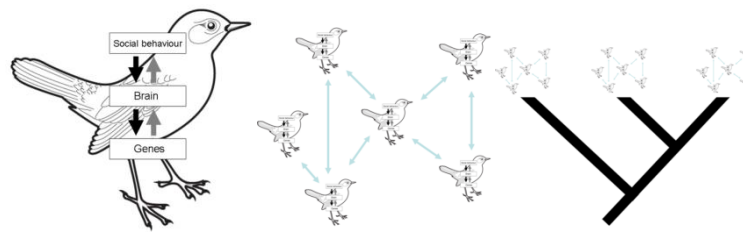


Figure 3. Different levels of sociobiological research. (left) The top-down approach (black arrows) and the bottom-up approach (white arrows). (middle) Increased complexity occurs when there are interactions between individuals within a population. (right) Including phylogenetic information allows a study of social behaviour over evolutionary time, which we call socio-phylogeography (Székely et al. 2010).

Taken together, studies in this dissertation 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.

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Acknowledgements

I am very grateful to my parents for encouraging my intention to become an evolutionary biologist, or as it was known then, an ethologist. My wife and our sons received much of the fallout that comes with research; many month away, and works until late hour and over the weekend. My professors and teachers provided immense support, and I will never forget them: Zoltán Varga, Csaba Aradi, István Précsényi and Pál Jakucs. I was also supported an ever burgeoning group of students: I am very glad to see them flourishing in academia or conservation. Let me just mention some of them: Zoltán Barta, András Liker, Csaba Moskát, Zsolt Végvári, András Kosztolányi, Ákos Pogány, Veronika Bókony, István Szentirmai, Ádám Lendvai and Orsolya Vincze Orsolya. Among the numerous foreign collaborators and students I wish to name Innes Cuthill, John McNamara, Alasdair Houston, Jan

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Komdeur, John Reynolds, Rob Freckleton, Mike Bruford, Oliver Krüger, Peter Kappeler, Clemens Küpper, Gavin Thomas, René van Dijk, Monif Alrashidi and Sama Zefania.

I very appreciate all support I was lucky to receive in various countries: over the last 24 years we worked in at least 24 countries. Let me mention here Toliary University (Madagascar) and Maio Biodiversity Foundation-t (Cape Verde). At least 50 funding agencies have supported our projects including EU (FP6, LIFE), OTKA, Leverhulme Trust, NERC, BBSRC, Humboldt Foundation and DFG. Thank you all.

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