



Why study plovers? The significance of non-model organisms in avian ecology, behaviour and evolution

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Abstract

Shorebirds (sandpipers, plovers and allies) are some of the most charismatic animals that breed on all continents and inhabit diverse habitats, and their ecology, behaviour and evolution have attracted much attention ever since the work of Charles Darwin. Here I summarise the insights from 30 years of research on shorebird biology to illustrate the contributions of these to four research fields: breeding system evolution, sex ratio research, speciation and biodiversity conservation. Two major conclusions can be drawn from these insights. First, as shorebirds live in a variety of habitats and exhibit puzzling adaptations to their environments, studying their ecology, behaviour and life histories provides novel insights into the emergence and maintenance of organismal diversity. Second, to uncover patterns and processes in evolution, it is both important and stimulating to combine different research methods, and detailed single-species studies with multi-species comparative approach. My main thesis is that curiosity-driven research into the natural history of non-conventional model organisms provides novel insights into fundamental processes in ecology, behaviour and evolution. I also argue that scientific funding should follow the Goldilocks principle: not too little, not too much, just the right amount.

Keywords Shorebird · Mating system · Parental care · Sex ratio · Speciation · Biodiversity

“Discovery consists of seeing what everybody has seen and thinking what nobody has thought.” Albert Szent-Györgyi

Shorebirds: Goldilocks organisms

Naturalists are innately attracted to biodiversity (Wilson 1986). The spectacular variations in orchids, beetles, cichlid fishes and Darwin’s finches have been investigated by

generations of biologists, and given rise to textbook examples of adaptation, natural selection and organismal diversity (Futuyma and Kirkpatrick 2017). The approximately 250 species of shorebirds (or waders; Charadriiformes), including sandpipers, plovers and allies, offer an unparalleled opportunity to unravel how evolution works (Colwell 2010; Gill and Donsker 2018). Although phylogenetically Charadriiformes also include gulls, terns and auks (Hackett et al. 2008; Prum et al. 2015), in this review I focus on the two main groups that are conventionally labelled shorebirds: suborders Scolopaci and Charadrii.

Shorebirds breed and live on all continents. Although they frequently congregate in spectacular flocks over coasts, marshes and wetlands, shorebirds also inhabit grasslands, forests and even deserts. The bauplan of shorebirds is impressive: although their core structure is the typical shorebird shape, with long legs and a pointed straight beak, this has been moulded by natural selection into various shapes very much like those of the partridge (seedsnipes), quail (button-quails), heron (thick-knees) or pigeon (sheathbills). Tropical shorebirds tend to be year-round residents, exhibit short-term movements between breeding and non-breeding areas, or are nomadic and seek suitable breeding grounds over hundreds of kilometres depending on rainfall and/or breeding opportunities. In contrast, temperate and Arctic

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shorebirds are often long-distance migrants that cover over 10,000 km when flying between breeding and wintering sites (del Hoyo et al. 1996; Delany et al. 2009). In addition, shorebirds are ideal indicators of ecosystem health, e.g. of wetlands or tundra habitats, thus are not only indispensable for evolutionary studies but also for conservation biology (Colwell 2010).

Importantly, generations of shorebird biologists have trapped, ringed and observed shorebirds around the globe, and these dedicated scientists have developed powerful field techniques to gather data. Using these methods, a huge amount of information has been accumulated on shorebird biology. In addition, dedicated professionals and bird enthusiasts keep an eye on unusual species' occurrences, thus improving our knowledge about their movements and distribution. Luckily, most shorebird species are easy to identify, and often the males, females and juveniles can be distinguished based on their plumage. In addition, many shorebirds breed in open habitats on the ground, sometimes in a highly aggregated manner, so that the adults, the eggs and the chicks are easy to observe and are accessible for scientific investigations.

Thus we have an organismal group that can be conveniently investigated from several perspectives, the so-called Goldilocks organisms, a reference to the nineteenth century fairy tale *Goldilocks and the three bears*, since shorebirds, in accordance with the fairy tale, might well be 'just right'. Shorebirds are diverse enough to exhibit fascinating adaptations to their environment that can vary between species and populations; however, their diversity is not overwhelming but accessible to scientific research as they have a tractable ecology and life style that is amenable to investigation. Thus working on shorebirds is more like fun than a daunting and tedious task.

First results

Selecting a study organism is often thought to be a rational process whereby various options are evaluated and the right species chosen based on its suitability for the examination of a particular process or general problem. This approach is called 'Krogh's principle' "*For a large number of problems there will be some animal of choice or few such animals on which it can be most conveniently studied*" (Katz 2016). However, the way I have proceeded with my research objectives is anything like that: I found shorebirds admirable organisms (see ESM Box 1), and simply started to work out their basic natural history. My focal species of interest, the Kentish Plover *Charadrius alexandrinus*, a Goldilocks species that has just enough individuals in a population for collecting adequate data, but not so many that the marking

and recognition of most individuals in the population are hampered.

The first few years of my Kentish Plover fieldwork with co-workers produced two important insights (Székely and Lessells 1993). First, we confirmed previous findings in Kentish Plover that it breeds sequentially multiple times in a single breeding season (Lessells 1984; Warriner et al. 1986), and that some individuals divorce from their mate between subsequent serial nesting attempts. Unexpectedly, however, we found that plovers may fly to distant areas in search of new mates, with one memorable female showing sequential breeding attempts separated by 170 km within the same season. Second, whilst observing families, we noticed that, shortly after the hatching of the chicks, one parent went missing from the family, so that the chicks were reared by a single parent until they became independent. In principle, the missing parent could have been predated; however, we knew that this was not the case since we subsequently found several 'missing' parents that had re-mated and re-nested with a new mate. Curiously, the female parent left the brood more often than the male; this was unusual given that, across the animal kingdom, if any parent abandons the young, it is usually the male (Queller 1997). These two key observations on mating, parenting and breeding dispersal (Fig. 1) gave rise to four areas of research (see below).

Mating systems, parental care and sex roles

Understanding reproductive behaviour is one of the main goals of behavioural ecology and organismal biology (Davies et al. 2012; Alcock 2013). The distribution of matings (i.e. number of social and genetic mating partners, duration and strength of pair bonds, spatial and temporal distribution of mates) and of parenting (e.g. type of care, sex of care-giving parent if any, duration and kind of parenting) show immense diversity both among and within animal taxa, and much research has been invested into understanding the theoretical, experimental and phylogenetic aspects of these behaviours (Westneat and Fox 2010; McGraw et al. 2010; Royle et al. 2012). Research in this field is often characterised by the study of sex role evolution since one of the core patterns underpinning variation in mating and parenting is the different involvement of males and females in various stages of reproduction (Herridge et al. 2016; Janicke et al. 2016).

Shorebirds exhibit immense variation in mating and parenting, which has been recognised by a string of eminent shorebird biologists (Pitelka et al. 1974; Oring 1986; Owens 2002). My research contributed to this field in two main ways. First, in order to maximise reproductive success, an individual makes a series of decisions: who to mate with and when; what resources to allocate to finding and securing a

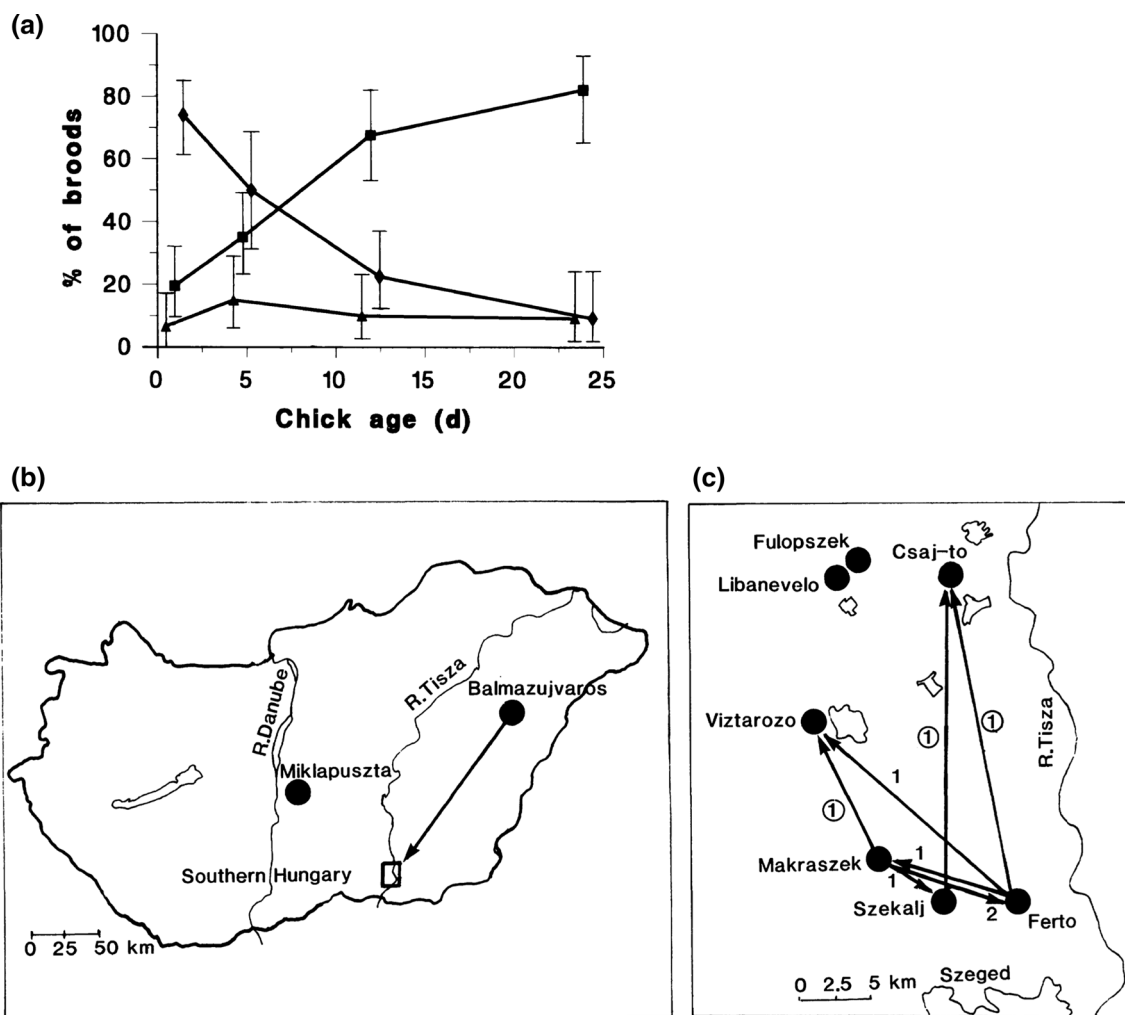


Fig. 1 Brood care and movements of Kentish Plover during the breeding season (Székely and Lessells 1993). **a** Percentage of broods cared for by both parents (diamonds), male only (squares) or female only (triangles) and their 95% confidence intervals in relation to brood age in days. **b** Movements of a colour-ringed female in Hun-

gary. **c** The study area in southern Hungary. Sites are indicated by filled circles, and arrows indicate the movements of birds between nesting attempts within a season. Numbers next to the arrows indicate the number of pairs (uncircled numbers) or divorced individuals (circled numbers) (copyright pending)

mate; and how much care to provide for the young. The concept that underpins many of these social decisions is based on the core idea of social behaviour, i.e. cooperation with a conspecific (e.g. mate with him/her, look after the young), or defection to seek a different mate or maintain resources for future breeding (Houston and McNamara 1999; McNamara and Weissing 2010). To understand how individuals balance the benefits of caring against the benefits of changing mates and family, we carried out a series of observational studies and experiments in Tuzla, Southern Turkey (ESM Box 2).

Why do parents cooperate with each other? Kentish Plovers have an unusually broad breeding range that spans multitude of biomes, including deserts. For example, in Abu Dhabi (United Arab Emirates) the daytime temperatures on the ground may reach above 50 °C, and parents incubating eggs struggle to cool themselves and their eggs to prevent

the death of the developing embryos. In the morning, when the ambient temperature is below 40 °C, the parents spend long periods of time away from their nests to feed and rest, although at midday when the ambient temperature soars above 50 °C they time their incubation shifts precisely so that one parent is always on the nest (AlRashidi et al. 2010). By experimentally cooling the eggs or manipulating shade for the incubating parent (and thus reducing the extent of direct solar radiation) we produced consistent results showing that cooperation was a fine-tuned behaviour driven by extreme heat in which the parents plastically adjusted their behaviour as a response to the ambient environment and/or to their mate's behaviour (Kosztolányi et al. 2009; AlRashidi et al. 2011).

Second, several lines of research suggest that mating opportunity is a major factor that links mating and parenting

decisions. Shorebirds are known to seek out breeding sites separated by hundreds of kilometres (Oring 1986; Stenzel et al. 1994; Székely and Lessells 1993), and recent studies using advanced telemetry have expanded on the findings of these seminal works by showing that, for example, male Pectoral Sandpipers fly thousands of kilometres within a breeding season, most likely to find a new mate (Kempnaers and Valcu 2017). Thus, mate search, mating decisions and parenting are all linked together via mating opportunities (Székely et al. 2000). I presented this idea at a conference in Erice (Italy) in 1998, at a time when mate choice, mating and parenting were all treated as unrelated aspects of reproduction (Fig. 2). The mathematical models that explained this conceptual framework were developed by McNamara et al. (2000) and reviewed by Houston et al. (2005, 2013). The main message of these theoretical investigations was that to understand breeding systems, researchers should be investigating entire adult populations, including those animals that are not breeding at any given time, since non-breeders exert pressure on breeding birds by altering mating opportunities.

Sex ratios

Mating opportunity seems like an intuitively obvious attribute of a population, although it is difficult to estimate in wild populations. First, one approach is to calculate the operational sex ratio in the population (i.e. the ratio of sexually active females to males), although this is fraught with difficulties as there are often no clear signs of sexual activity in many organisms, e.g. female ovulation may be concealed and/or males can maintain sexual activity even if they have

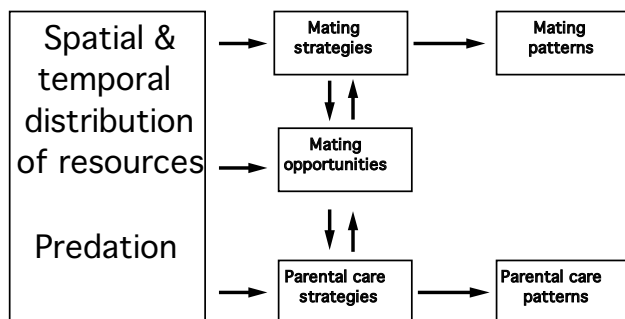


Fig. 2 The significance of mating opportunities linking mating strategies and parental care (Székely et al. 2000). Mating strategies refer to the behavioural decisions of unmated animals, e.g. to accept or reject a mate. Parental care strategies are the behavioural decisions of mated animals, e.g. to care for a brood or desert it. 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) (copyright pending)

already mated and are looking after offspring (Kokko and Jennions 2008). Second, mating opportunities can be estimated by observing the mating times and mating success of males and/or females in the population. This non-experimental approach, however, is also problematic given that a random sample representing the whole population needs to be observed to derive an estimate for the overall mating opportunity for males and females. Third, experimental removals of mates have been performed to quantify the time and effort it takes to secure a new mate (Balshine-Earn 1995; Székely et al. 1999); these estimates seem to provide the best approach to the quantification of mating opportunities for males and females in a given population.

Experimental estimation of mating opportunities in three plover species produced tantalising results (Parra et al. 2014). In the Kentish Plover, male and female mating times were substantially different whereby most females mated with a new partner in less than 1 day whereas males typically took over 10 days to find a partner. However, mating times were not different between males and females in White-fronted Plovers, whereas they were female-biased in Kittlitz's Plovers (Parra et al. 2014). Since we used identical experimental methodology for all three species, these experiments suggest that the sex ratio of adult males and females differ remarkably between plover populations.

Sex allocation is one of the most important subjects of evolutionary biology, since the theory is well developed and large amount of qualitative (and sometimes quantitative) empirical data show patterns that are consistent with theoretical expectations (Hardy 2002; West 2009). Most of these works, however, focus on offspring sex ratios and/or sex-related parental investment prior to offspring independence, although in many organisms this stage only represent a small portion of the full life cycle of an individual (Ancona et al. 2017). To understand why mating opportunities may differ between males and females, our team carried out three lines of investigation that focused on the adult sex ratio (ASR; the proportion of males in the adult population).

First, we used a cohort-based demographic model to estimate the proportion of males at birth, at independence, and at various adult ages in a well-studied Kentish Plover population in Turkey (Kosztolányi et al. 2011). Using sensitivity analyses, we showed that ASR is male biased, and that this bias is consistent with the mating opportunity experiment that was carried out in the same population (Székely et al. 1999).

More recently, Eberhart-Phillips et al. (2017) used a two-sex demographic model to estimate ASR. Demographers are usually interested only in females since they are the sex that produce offspring, and thus population trajectories crucially depend on what age females start breeding, how many offspring they produce, and how long they continue to reproduce for. To model ASR, however, we had to use an explicit

model that quantifies both male and female reproductive patterns. By using a two-sex demographic model, we showed that population changes are better predicted by the two-sex model than the conventional one-sex demographic model (Eberhart-Phillips et al. 2017). This finding has implications for biodiversity conservation as it shows that a demographic approach that is based on both males and females more accurately predicts population trends than a conventional single-sex model. Using the two-sex model, Eberhart-Phillips et al. (2018) projected ASR for six different plover populations and showed that some of them exhibit male-biased ASRs whereas others show female-biased ASRs (Fig. 3), which is consistent with previous analyses of ASR (Kosztolányi et al. 2011) and mating opportunities (Parra et al. 2014).

Second, the existence of courting and polygamous females, and caring males [termed classic polyandry and/or sex-role reversal (Oring 1986; Clutton-Brock 1991)] has

puzzled evolutionary biologists, since in these species the ‘conventional’ roles of the sexes appear to be swapped: “... *Classical polyandry is probably the most interesting and certainly is the least well understood, of the recognized avian mating systems*” (Ligon 1999). Substantial effort, often by shorebird biologists, has gone into identifying the circumstances that led to sex-role reversal, since shorebirds provide some of the best-known examples (Darwin 1871; Erckmann 1981; Andersson 1995; Owens 2002), although no causal factor was identified. As data on adult sex ratios became available over the years, we were able to test whether ASR variation across shorebirds predicts sex role variation.

According to the mating market theory (Schacht et al. 2017), individuals of the rarer sex have greater bargaining power in the marketplace and can leverage their scarcity to realise their preferred type of relationship, while the more common sex must cater for the preferences of the rarer sex

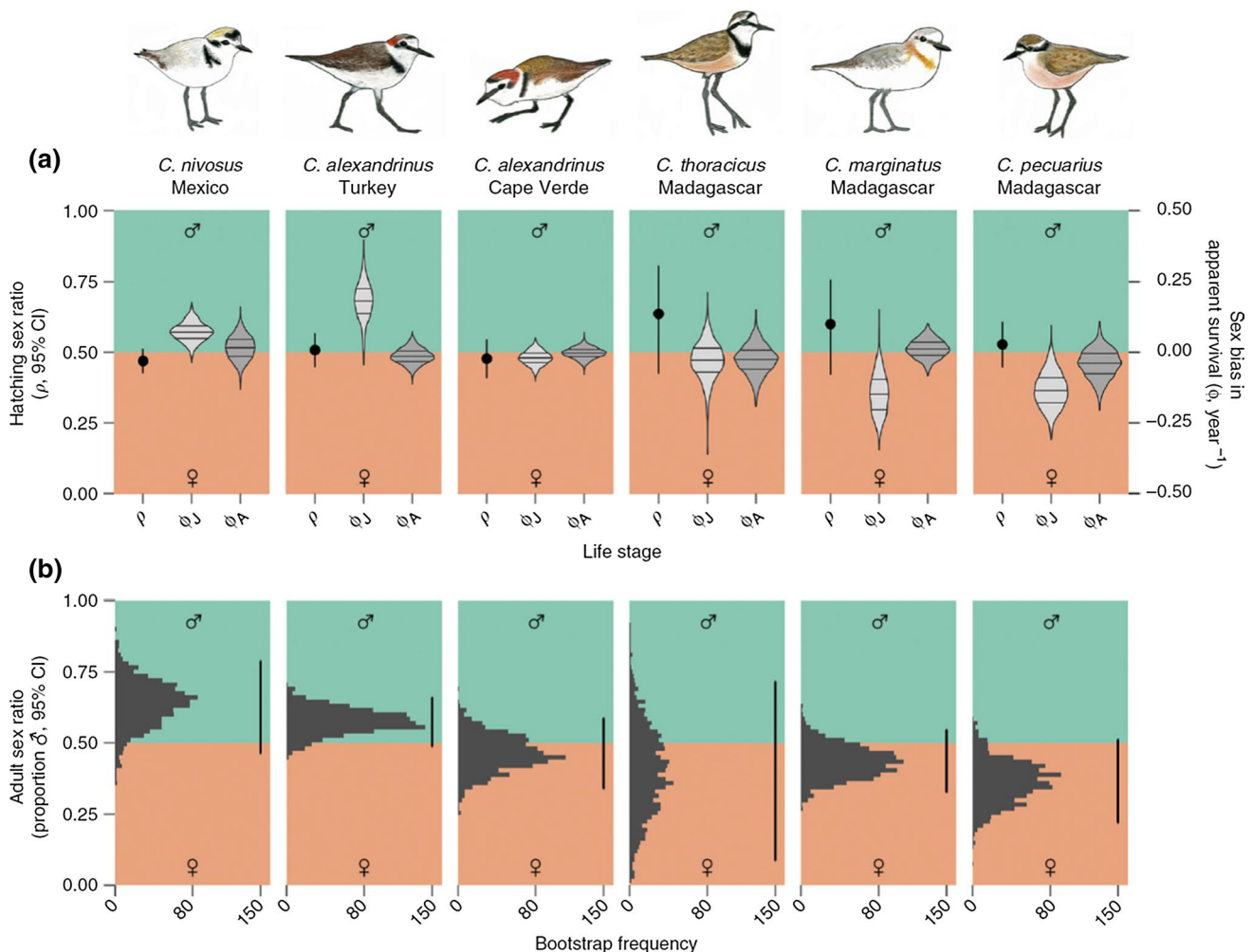


Fig. 3 Plover populations exhibit different adult sex ratios (Eberhart-Phillips et al. 2018). **a** Sex ratios of successfully hatched clutches (proportion of chicks that are male $\rho \pm 95\%$ confidence intervals; left-hand y-axis), and sex bias (i.e. difference between males and females)

in annual apparent survival rates of juveniles (ϕ_j) and adults (ϕ_A ; right-hand y-axis). **b** Distributions of adult sex ratios based on the sex- and stage-specific apparent survival rates shown in **a** (copyright pending)

in order to acquire a partner. Based on this theory, we conjectured that populations with female-biased ASRs should have higher mating opportunity for males so that males may exploit the female-skew and mate polygamously, whereas the females are left with the care of the young. In contrast, populations with male-biased ASR would benefit the females so that they should exhibit female polygamy, with male-only care. Using phylogenetic analyses of 18 shorebird species these predictions were born out (Fig. 4; Liker et al. 2013) and supported Darwin's (1871) arguments that sex ratio bias may lead to sex role reversal. Whilst phylogenetic comparative analyses often have low explanatory power—perhaps unsurprisingly given that most traits are variable within a population rather than a single datum, and these analysis are carried out over a long periods and have low accuracy—in our models ASR alone explained an impressive 50–60% of interspecific variation in mating and parenting (Liker et al. 2013). Remarkably, the patterns exhibited by shorebirds are consistent with those of birds as a whole (Liker et al. 2014).

Third, variations in ASR may have ramifications for species beyond shorebirds. Ornithologists have long been aware that bird populations tend to have more males than females (Mayr 1939); this pattern is usually explained by sex-biased predation of incubating females (Lack 1968). Conversely, mammalian populations tend to harbour more females than males—a pattern credited to sexual selection since competition among males is assumed to directly lead to higher male than female mortality or to suppression of the immune system which makes males more vulnerable to disease and parasites (Moore and Wilson 2002). Using these arguments as working hypotheses, Pipoly et al. (2015) compared ASRs between mammalian-type sex determination systems (XY/XX) to those with bird-type sex determination (ZW/ZZ) by exploiting the natural variation in sex determination systems exhibited by amphibians and reptiles. Intriguingly, the patterns exhibited by amphibians and reptiles were consistent with those observed in birds and mammals, suggesting that

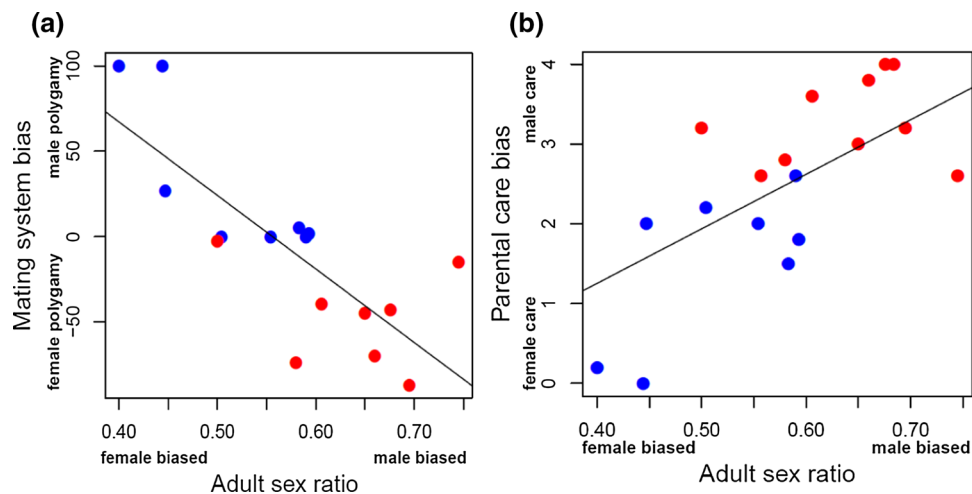
sex determination systems are associated with ASRs in tetrapods. The latter result opens up new lines of research by suggesting that sex determination systems, sex ratios and sex roles may have evolved in concert. This relationship—if supported by follow-up work—would indicate a novel aspect of social evolution by emphasising the roles of adult sex ratios and mating opportunities.

Speciation

The birth and death of species are central to biology, as indicated by the landmark works of Darwin (1859) and the modern synthesis (Huxley 1942). Research on birds is at the cutting edge of speciation research, and excellent reviews have brought together huge amount of theoretical, empirical and comparative evidence (Price 2008; Newton 2003). Can studies of shorebirds contribute to this core, and rapidly advancing, field of evolutionary science?

The movements of plovers during the breeding season (Fig. 1) indicate that mating behaviour could have knock-on effects on population structure and geographic differentiation. For example, White-fronted Plover and Kittlitz's Plover are both common breeding birds in Madagascar, although their social structures are substantially different. The socially [and genetically (Maher et al. 2017)] monogamous White-fronted Plovers interact with a small number of conspecifics, whereas the polygamous Kittlitz's Plover has far more social interactions with conspecifics (Cunningham et al. 2018). The social interactions, when considered spatially, imply more movements between distant geographic locations and over time, which is expected to blend the gene pool. This inference is consistent with findings in wild populations, since the monogamous White-fronted Plovers shows more geographic differentiation, and thus genetically structured breeding populations, than the polygamous Kittlitz's Plover in Madagascar (Eberhart-Phillips et al. 2015). Whilst the

Fig. 4 Adult sex ratio predicts both mating system (a) and parental care (b) in 18 species of shorebirds. Blue dots indicate species with conventional sex roles, red dots indicate species showing sex role reversal (Liker et al. 2013) (copyright pending)



behavioural and genetic data are suggestive of these inferences, future studies should investigate alternative explanations; for example, Kittlitz's Plover may be a more recent arrival to Madagascar than the White-fronted Plover, which could mean that it has not had the time to differentiate geographically (dos Remedios et al. 2015; Eberhart-Phillips et al. 2015).

Sexual selection is often viewed as an engine of speciation since sexually selected traits emerging in a population are expected to lead to rapid diversification and mating isolation (Ritchie 2007; Gavrilets 2014). Alternatively, sexual selection can counter local adaptation and lead to a deceleration of speciation (Servedio and Bürger 2014). Data on plovers support the latter argument since rates of differentiation over geographic distances were lower for polygynous species (i.e. those subject to intense sexual selection) than for monogamous ones (D'Urban Jackson et al. 2017). This suggests that dispersal by male and female shorebirds, which is presumably driven by seeking out of new mates, can lead to a blending of the gene pool over evolutionary time. Although the latter results are consistent with speciation across shorebirds as a whole, there is a need for further studies since other, as yet uninvestigated, factors may confound the relationships between geographic differentiation, sexual selection and dispersal behaviour.

Biodiversity conservation

We live in the Anthropocene, and shorebirds encounter more than their fair share of the consequences of human's ecological footprint. Whilst carrying out field studies of breeding shorebirds in over 20 countries, we began to realise how fragile most shorebird populations are. Wetlands, which account for some of the main breeding and non-breeding habitats of shorebirds, are disappearing at an alarming rate globally, and by working in the field on a day-to-day basis, we saw numerous examples of nest predation by feral cats and dogs, illegal hunting and rapid habitat loss. True, many shorebirds have flexible breeding strategies—indeed, the fluctuating nature of suitable habitats is one of the theories put forward to explain diverse breeding strategies (Oring 1986; Erckmann 1981)—nonetheless, if suitable habitats decline, this can only mean declining overall population sizes, reduced productivity and/or increased mortality (Méndez et al. 2018). Shorebird species have indeed gone extinct since records began (e.g. the Canary Islands Oystercatcher, Javan Lapwing, Eskimo Curlew), and one estimate puts the number of landbird species (including shorebirds) that has gone extinct in the Pacific Islands alone at close to 1000 (Duncan et al. 2013).

I have also been motivated to care about conservation by my academic colleagues. I spent a year at Harvard University as Hrdy Visiting Fellow in Conservation Biology, where I taught a course on conservation and interacted daily with scientists who were not only experts in their research field, but also passionate about conservation, namely E. O. Wilson, David Haig, Scott Edwards, Naomi Pierce and Jonathan Losos. Personal interaction with these and other conservation biologists working at other universities and conservation agencies made me decide that I must not only observe and report how biodiversity is eroding in front of our very eyes, but also act to reduce anthropogenic impacts on wildlife.

I act on two different fronts to combat biodiversity loss: research and active conservation. Macroevolutionary and phylogenetic analyses of conservation-related issues are flourishing, and their results are used in various policy-level decisions such as identifying animal taxa that need better conservation measures or estimating the conservation status of species that have never been previously studied in detail (Fisher and Owens 2004; González-del-Piiego et al. 2019). Using phylogenetic comparative analyses to understand population changes in waterbirds (Amano et al. 2018), we have quantified population trends in their populations worldwide. Amano et al. (2018) showed that waterbirds are declining in many parts of the world, and that the best predictor of population changes is governance, i.e. the efficacy of the conservation measures one country may adopt.

More recently, Kubelka et al. (2018) has shown that rates of nest predation of many shorebirds have increased substantially in recent years, and that the largest increase was in the Arctic. The effects on Arctic shorebirds, many of which are long-distance migrants, are twofold: nest mortality is increasing, and adult survival is decreasing (Méndez et al. 2018). These pressures are, unfortunately, likely to feed into declining shorebird populations worldwide, and especially in the Arctic (Kubelka et al. 2018). The international media coverage of Kubelka et al.'s study (2018) was impressive in that it not only promoted scientific research in general but also brought shorebird conservation to the public's attention.

Second, I assist conservation actions on the ground. My colleagues and I work with conservationists at several shorebird sites, and also train locals in field biology and carry out capacity building. In one of our current study sites, Maio (Cape Verde), we established a conservation non-governmental organisation, the Maio Biodiversity Foundation. This shorebird project is run as a genuine collaboration between local conservationists and shorebird biologists. A direct outcome of this collaboration is the recent designation of one of the prime shorebird breeding sites in Cape Verde, the Salina Porto Ingles, as a Ramsar Site. Joint efforts by conservation biologists and evolutionary biologists, together with the involvement of local communities, looks like one of the most promising avenues of wildlife protection.

Conclusions and outlook

Scientific progress is often depicted as a top-down and theory-driven process. This rigid and somehow idealised viewpoint may be more applicable to some projects than others. In my research, the pattern was very different: observations were made on the natural history of plovers, and to understand their behaviours, works were produced that are relevant to several areas of evolutionary biology, population demography and biodiversity conservation. En route to pursuing seemingly insignificant aspects of natural history, we have advanced evolutionary theory and mathematical biology (van Dijk et al. 2012; Houston et al. 2013; Barta et al. 2014), comparative phylogenetics (Liker et al. 2013; Pipoly et al. 2015; Kubelka et al. 2018), experimental behavioural analyses (Kosztolányi et al. 2009; Cunningham et al. 2018) and neuro-genomic analyses of behaviour (Young et al. 2019; Maher et al., submitted).

Also, by pursuing the questions that have emerged from study of the natural history of plovers, we have made methodological advances in evolutionary game theory (McNamara et al. 1997), phylogenetics (Thomas et al. 2006), field biology (Székely et al. 2003) and population dynamics (Eberhart-Phillips et al. 2017). To gain an overview of the progress of specific areas of research, we have written reviews (Székely et al. 1996, 2014; Houston et al. 2005; Thomas et al. 2007; Székely 2014), and books (Fairbairn et al. 2007; Székely et al. 2010). This was, and still is, teamwork at its best, as it combines several key skills for the completion of a specific piece of scholarship: there were no fixed roles, and each team member contributed what was necessary.

There are four essential conclusions from this work:

1. The Goldilocks principle in the choice of study organisms. Pursuing research on a charismatic organism can provide novel insights into general processes in ecology and evolution. Science is often portrayed as a rational process in which investigators seek to work with model organisms, i.e. species that are best suited to the study of a problem. Indeed, model organisms are immensely useful for testing ideas in the biomedical sciences, neurobiology and genetics. Nonetheless, we should treat the model-species approach with care, since the success of many model organisms relies on the fact that they are fast breeders that proliferate in a laboratory environment. By only focusing on these few dozen species, it is not possible to understand the full scale of adaptation and selection.

One downside of the model system approach is that by trying to answer questions using conventional model species we may constrain our research to that fits some organisms better than others, and thus we may miss eco-

logically interesting and important discoveries. So, the danger is to try to find a key not where it lies, but rather in a place where there is light [as in the Sufi story about the lost key (Shah 1973)].

There is a need for the Goldilocks principle in selecting study organisms: the most convenient species may not be the best nor the one that has the most complex behavioural adaptation. Indeed, the best choice may be a species that exhibits aspects of the trait of interest, although it is observable, approachable and amenable to investigation. With new technological advances in field biology, genetics and phylogenetics, an increasing number of species will become suitable for research.

2. Different research tools and multi-level research. Science is increasingly specialised but now there is a more urgent need than ever to use multi-pronged approaches: *If your only tool is a hammer then every problem looks like a nail* (Abraham H. Maslow). To avoid falling into this trap, it is important to widen the research palette and work with colleagues who are specialised in different fields. Using multiple levels of research (from populations to species and to higher taxa) allows us to test the generality of an idea in multiple ways, and perhaps help solve questions that have been posed in another research field. Moving into a new research field with fresh eyes can be tough but rewarding given the insights an outsider can bring. The success of plover research may attest to the fact that a multi-pronged and multi-level approach can work.
3. The Goldilocks principle in research. Unexpected difficulties and forced detours in scientific research can lead to novel insights. One of the major hurdles in contemporary science is funding: I believe that research funding should be not too little, but not too much either (ESM Box 3). If one constantly pursues the ever-changing priorities of funding agencies, the overall goals of a research programme can be easily lost from sight.

Importantly, as the above quote from Albert Szent-Györgyi shows, one needs to be aware of the unexpected. Much of my interest in sex ratios originated from quantifying the offspring sex ratios in the Kentish Plover. It took me about 4 years to realise that the strong male-bias in chick sex ratios that we reported in Székely et al. (2004) can have exciting implications for mating system evolution.
4. Science and advocacy. I strongly believe that, in addition to producing exciting research and making discoveries, as scientists we also have responsibilities. We need to support and nurture the next generation of scientists and conservationists. For this, I have ten pieces of advice

for young shorebird biologists based on my forays into shorebird biology (ESM Box 4).

We especially need to look after those who live in less favourable circumstances than those of us in the developed world. Financial inequalities are, unfortunately, ever increasing between countries and peoples. Scientists will never have the power to reverse these trends but, at least as individuals, we can make a contribution by helping colleagues, students and young enthusiasts who happen to be born in a less fortunate part of the planet.

Biologists also have a responsibility to preserve as much biodiversity as they can. This job is not only for ecologists and conservation biologists, but for all biologists, given that we all study living organisms that are the products of evolution by natural selection. An ever-increasing number of species and populations are now at risk, so we should all make an effort to help reducing biodiversity loss (Kelsh et al. 2011).

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