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Review

The causes and implications of sex role diversity in shorebird breeding systems

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Males and females often exhibit different behaviours during mate acquisition, pair-bonding and parenting, and a convenient label to characterize these behaviours is sex role. The diverse roles that male and female shorebirds (plovers, sandpipers and allies) exhibit in mating and parenting have played a key role in advancing mainstream theories in avian ecology and behavioural biology including sexual selection, sexual conflict and parental cooperation. Recent advances in shorebird research have also highlighted the significance of the social environment in driving sex role behaviours by linking the adult sex ratio with breeding behaviour and population demography. Here we review the key advances in sex role research using shorebirds as an ecological model system. We identify knowledge gaps and argue that shorebirds have untapped potential to accelerate diverse research fields including evolutionary genomics, movement ecology, social networks and environmental changes. Future studies of sex roles will benefit from individual-based monitoring using advanced tracking technologies, and from multi-team collaborations that are facilitated by standardized data collection methodologies across different species in the field. These advances will not only contribute to our understanding of reproductive strategies, but they will also have knock-on effects on predicting population resilience to environmental changes and on prioritizing species for conservation.

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The polygamous ruff … is notorious for his extreme pugnacity; and in the spring, the males, which are considerably larger than the females, congregate day after day at a particular spot where the females propose to lay their eggs. Darwin (1871)

Animal breeding systems exhibit stunning diversity and birds provide some of the best examples of breeding system variation (Darwin 1871, Lack 1968, Ligon 1999, Bennett & Owens 2002, Kempenaers 2022). Species vary in the way the males and females acquire mates, the duration of their pair-bonds, and the intensity, type and mode of caring for their young (Székely *et al.* 2010, Royle *et al.* 2012, Mock 2022). The term breeding system encompasses all of these variations (Reynolds 1996), and so defines major aspects of an animal's social life that directly influence its fitness (Clutton-Brock & Sheldon 2010).

A powerful theoretical approach to understand the evolutionary interests of breeding males and females is sex role theory, which seeks to understand why males and females play certain roles in breeding (Schärer *et al.* 2012, Herridge *et al.* 2016). The term 'sex role' encapsulates male and female behaviour in mate searching, competitive traits that increase mating and fertilization opportunities, choosiness over mates, pair-bonding and parental care (Jennions & Fromhage 2017, Gonzalez-Voyer *et al.* 2022). By investigating the ecological, life history and demographic aspects of breeding for males and females, we can test why males (or females) compete more intensely for mating, why some males (or females) have multiple partners while others have few, and why some females (or males) provide more care than others (Queller 1997, Kempenaers 2022, Mock 2022). Given that successful sexual reproduction is essential for fitness in dioecious animals including birds, determining the causes and consequences of sex roles is essential to understanding avian evolutionary diversity. To place sex roles into an evolutionary context, researchers need to investigate life history evolution, population biology and behavioural ecology of the sexes (Short & Balaban 2004, Fairbairn *et al.* 2007). Understanding sex roles is also important for biodiversity conservation because breeding is an essential element of population maintenance and changes in breeding behaviour due to environmental changes can reduce the viability of wild populations (Lack 1968, Bennett & Owens 2002, Donald 2011).

There are three main theories explaining how divergent sex roles may emerge (Fig. 1). First, differences between male and female breeding behaviour may originate from sex differences in gamete size (anisogamy), because males produce smaller but vastly more gametes (sperm) than females, which produce nutrient-rich but highly limited numbers of gametes (eggs). The cascade initiated by anisogamy, including a bias in the number of males ready to mate compared with the number of females (biased operational sex ratio) is predicted to lead to sex differences in the strength of sexual selection and therefore sex differences in both mating competition and parenting tactics. This concept is summarized as the Darwin–Bateman paradigm (Dewsbury 2005, Parker 2014, Janicke *et al.* 2016, Mokos *et al.* 2021).

Second, sex differences in traits and behaviour may emerge as a result of selection driven by the ecological environment (Sandercock 2001). For example, frequency-dependent or density-dependent competition for shared ecological resources may each generate disruptive selection in resource acquisition traits between males and females. Such selection can lead to sexual dimorphism, which results in differences between males and females with regard to mating behaviour and parenting (Slatkin 1984, Bolnick & Doebeli 2003, Cooper *et al.* 2011, De Lisle 2019).

Third, both theoretical and empirical studies propose that the wider social environment may influence sex roles and breeding system variations (Székely *et al.* 2000b, 2014, Schacht *et al.* 2017, Liker *et al.* 2021). Because traits associated with sexual selection are expected to depend on the sex ratio in the population, the adult sex ratio (ASR) is emerging as a key predictor of pair-bonding and parenting (Donald 2007, Liker *et al.* 2013, Ancona *et al.* 2017, Schacht *et al.* 2017). The core idea is frequency dependence: when adult males are more abundant in a population than adult females, this provides the upper hand for females in choosing new mates or

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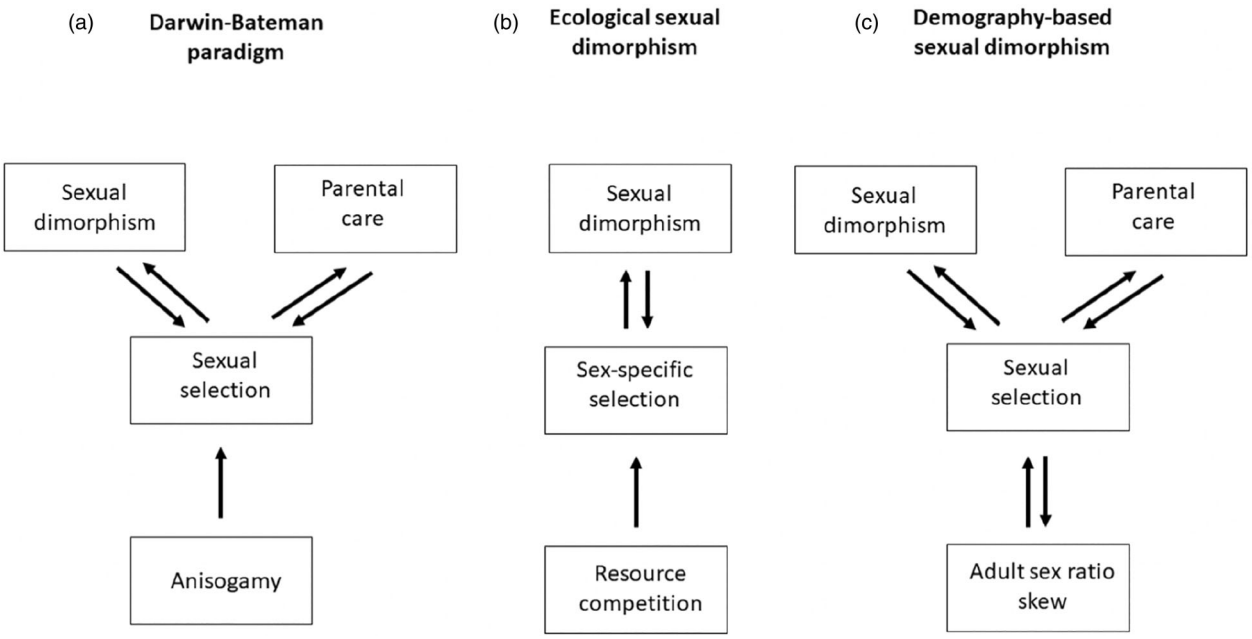

Figure 1. Schematic illustration of the emergence of sex roles. (a) Darwin–Bateman paradigm (Janicke *et al.* 2016), (b) ecological sexual dimorphism (De Lisle 2019) and (c) demographic origins of sex roles (Székely *et al.* 2006, Liker *et al.* 2021).

retaining their mate for future pair-bonds, and dividing how much care females provide for their young (McNamara *et al.* 2000, Székely & Cuthill 2000, Kokko & Jennions 2008). Competition for mates, pair-bonding and parenting have costs that may have mortality implications, so the breeding behaviour exhibited by males and females may feed back into ASR via the mortality implications of mating and/or parenting (Liker *et al.* 2013, Schacht *et al.* 2022).

Shorebirds (plovers, sandpipers and allies, 16 families and 255 species, Gill *et al.* 2022) are one of the most suitable avian groups for testing hypotheses about sex roles. First, shorebirds exhibit great diversity in traits involved in (or associated with) sex roles, by having diverse breeding systems, parenting, life histories and sexual size dimorphism (Billerman *et al.* 2022). For example, parental care in shorebirds includes nearly the full range observed in all birds including biparental care of the young, uniparental care by either sex and cooperative breeding (Thomas *et al.* 2007, Santos & Macedo 2019). These diverse parenting strategies are associated with variation in breeding systems (Fig. 2; van Kam *et al.* 2004, Thomas *et al.* 2007, Székely 2019, Kempenaers 2022), and they are the result of numerous independent evolutionary events (Reynolds & Székely 1997, Eberhart-Phillips 2019). Variations are also seen among closely related species; for instance, among *Calidris* sandpipers and *Charadrius* plovers polygyny, polyandry and social monogamy all occur within these genera, indicating that phylogenetic contingency cannot solely explain the observed variation (Fig. 2; Pitelka *et al.* 1974, Thomas *et al.* 2007, Eberhart-Phillips 2019). Here we review the advances in sex role research across shorebirds, highlight the potential drivers of sex role diversity across different facets of reproduction, and indicate key areas where shorebird breeding system research can be accelerated to further advance our wider understanding of sex roles and avian evolutionary diversity.

METHODS

For this review, we consulted past reviews, books and prominent historical literature, and supplemented this with recent literature via taxon- and topic-specific searches using online repositories in ecological, evolutionary and avian journals to synthesize the current state of the field. Although the review is focused on shorebirds, we aimed at

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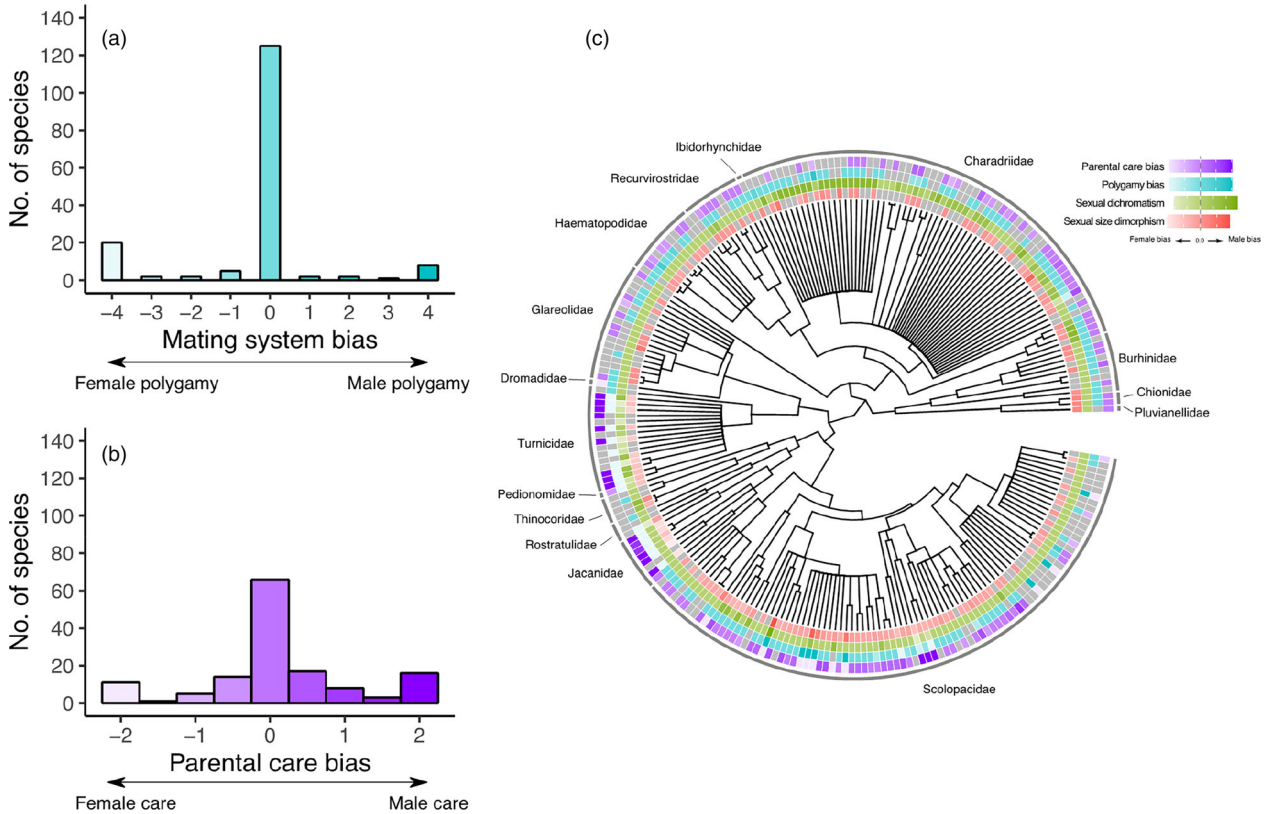

Figure 2. Interspecific variation in shorebird sex roles. (a) Frequency of female- versus male-biased social polygamy and (b) frequency of female- versus male-biased parental care. All metrics are standardized so that zero represents no sex bias. (c) The phylogenetic distribution of sex biases in parental care, polygamy, sexual dichromatism and sexual size dimorphism in shorebirds. The intensity of colour represents the intensity of sex bias from strongly female-biased (lighter) to strongly male-biased (darker) and grey indicates missing values (239 shorebird species); data are from Székely *et al.* (2022), and phylogeny from Jetz *et al.* (2012).

evaluating both the conceptual issues and the empirical evidence so that our review will be useful for researchers working on other avian and non-avian taxa as well.

TERMINOLOGY

Sex roles are complex traits and typically exhibit continuous variation (Herridge *et al.* 2016, Gonzalez-Voyer *et al.* 2022). To capture this complexity and continuity, we label sex differences in behaviour as 'sex-biased behaviour' and specify the type of behaviour in question. For instance, if males court or compete for mates more than females, we would label this as a 'male-biased courting/competing role'. Species where males and females have approximately similar reproductive behaviour we would label as 'unbiased sex role behaviour'.

COURTSHIP, MATE CHOICE AND TERRITORIALITY

Courtship displays are reproductive communication signals (Miller 1984, Mitoyen *et al.* 2019) that can assist mate attraction and mate choice by allowing evaluation of mate quality and condition before, during or after mating, and are therefore often crucial to reproductive success. Both males and females can engage in extravagant courtship displays (Box 1), but in some species, these are male-biased (e.g. lekking shorebirds: Ruff *Calidris pugnax*, Buff-breasted Sandpiper *Calidris subruficollis*) and in others female-biased (e.g. Bronze-winged Jacana *Metopidius indicus*, see Table S1).

Variation in courtship behaviour may be partly explained by differences in breeding system. For example, both males and females of a polygamous population of Snowy Plover *Charadrius nivosus*

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Box 1 Shorebird courtship.

During and after pair formation, males and females participate in stereotypical displays before copulating. The diversity of shorebird courtship can be condensed into three main types: (1) nuptial vocalizations, (2) aerial displays and (3) ground displays.

1 Nuptial vocalizations include high-pitched songs, drumming sounds or piping vocalizations (Lemnell 1978, Miller & Baker 2009) mainly used by males to attract females at long distances during aerial displays (Miller 1984, Miller & Baker 2009), but also used in ground displays and during copulations, where females may also express them (see Table S1).

2 Aerial displays are usually expressed by males and involve steep ascents and dives along with complex routines involving hovering, undulating movements or zig-zag flying, such as displayed by male Willets *Tringa semipalmata* and Northern Lapwings *Vanellus vanellus* (Sutton 1981, Miller 1983, Colwell 2010). However, in several species, males and females engage in joint aerial displays (e.g. Black-tailed Godwit *Limosa limosa*, Huxley & Montague 1926).

3 Ground displays may include a rapid sequence of postures, such as the wing-flashing displays of lekking male Buff-breasted Sandpipers (Colwell 2010) or the high jumps of lekking male Great Snipes *Gallinago media* (Lemnell 1978). Components of ground displays vary between species, although the nest-scraping ceremony is nearly ubiquitous (Huxley & Montague 1926, Pitelka *et al.* 1974). Scraping can be performed by both sexes, when males and females remove substrate with their feet and push their breast down creating a shallow depression where egg-laying will take place, although species vary in the number of scrapes initiated before egg-laying (Colwell 2006). Scraping occurs even in species that do not lay in scrapes (e.g. Solitary Sandpiper *Tringa solitaria* and Green Sandpiper *Tringa ochropus*; Colwell 2010, Moskoff 2020), but is absent in several polygamous lekking species (e.g. Buff-breasted Sandpiper, Ruff and Pectoral Sandpiper *Calidris melanotos*; Pitelka *et al.* 1974). Courtship feeding by males to females is almost absent in shorebirds, except in the Eurasian Stone-curlew *Burhinus oedicnemus* and the Subantarctic Snipe *Coenocorypha aucklandica* (Lack 1940, Miskelly 1990; Fig. B1).

Diversity of displays in shorebirds. (a) Eurasian Dotterel Charadrius morinellus wing display (credit: Vojtěch Kubelka). (b) Lekking Ruff males (credit: Jouni Männistö). (c) Great Snipe male vocalizing to attract

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females (credit: Pavel Lychkousky). (d) Aerial display of Northern Lapwing (credit: Neil Smith). (E) Little Ringed Plover *Charadrius dubius* pair courting (credit: Csaba Daróczi).

The types of courtship displayed by one sex can also vary within the same species. In the Ruff, males exhibit three genetically determined phenotypic morphs: independents, satellites and *faeders* (Jukema & Piersma 2004, Küpper *et al.* 2016, Lamichhaney *et al.* 2016). The males of these three morphs tend to differ in their sexual behaviours (van Rhijn 1991, Mustonen 2020). For example, independent males sport typically dark plumage, establish territories and display by themselves, whereas lightly coloured satellite males tend to form coalitions with other males and perform joint displays (van Rhijn 1991, Mustonen 2020). *Faeder* males are phenotypically female-looking and use a 'sneaker' strategy to access mating opportunities offered by females soliciting to dominant males.

spent more time courting than monogamous Kentish Plover *Charadrius alexandrinus* pairs (Fig. 3; Carmona-Isunza *et al.* 2015). Comparisons of these two populations also highlighted that sex biases in courtship behaviour can vary over a breeding season. Specifically, the sex bias in courting shifted from female-biased to male-biased in the polygamous population, but not in the monogamous population. This perhaps reflected an effect of changing mating opportunities in the polygamous population, as fewer females may have been available to mate as the breeding season progressed (Fig. 3; Carmona-Isunza *et al.* 2015).

Rates of courtship are often but not always biased towards the more polygamous sex. For

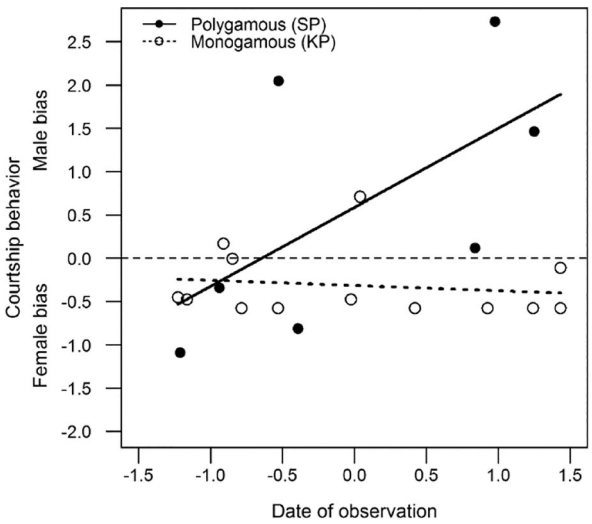

Figure 3. Sex bias in courtship behaviour (*z* score of the difference between males' and females' proportion of time courting) in relation to the date of observation in polygamous Snowy Plovers (SP, filled circles and continuous line) and in monogamous Kentish Plovers (KP, open circles and broken line; Carmona-Isunza *et al.* 2015).

example, many jacanas such as Northern Jacanas *Jacana spinosa* and Wattled Jacanas *Jacana jacana* show female-biased polygamy (Jenni & Mace 2020, Buck *et al.* 2021). However, in the Pheasant-tailed Jacana *Hydrophasianus chirurgus*, which also shows female-biased polygamy, males spend more time courting than females (Fresneau *et al.* 2021). This could be a consequence of intense male competition over a limited number of additional clutches laid by females following previously failed breeding attempts (Fresneau *et al.* 2021). In the case of the Northern Jacana, assessing the sex bias in courtship may be complicated by differences in the mechanisms of mate acquisition, for example because direct female aggression and territoriality are more important in mate acquisition compared with intersexual courtship (Jenni 1974, Jenni & Mace 2020). Together, these patterns indicate a complex relationship between courtship rates and polygamy and highlight where detailed studies of individual species may shed light on the mechanisms that generate variation in the relationship between sex biases in polygamy and courtship.

Sex biases and overall rates of courtship behaviour may also be associated with environmental conditions. For example, poor visibility may reduce display activity in shorebirds that rely on visual cues (Blomqvist *et al.* 1997) and strong winds may reduce aerial display activity (Miller 1979). Such patterns may reduce sex biases in courtship displays (De Jong *et al.* 2018), potentially increasing the reliance on other cues such as plumage ornamentation to assess mate quality (Møller & Pomiankowski 1993).

Shorebirds have played a key role in developing our understanding of mate choice for sex-biased exaggerated traits (e.g. whiter patches, enlarged badges; Höglund *et al.* 1990a, 1990b, but see:

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Sæther *et al.* 2000, Lendvai *et al.* 2004). In jacanas, phalaropes, Spotted Sandpipers *Actitis macularius* and Eurasian Dotterels *Charadrius morinellus*, females are larger and more ornamented than males, and they may have fleshy facial ornaments and wing spurs, large melanized spots or bright plumage (Owens *et al.* 1994, Emlen & Wrege 2004a, Lipshutz 2017). This ornamentation appears to indicate body condition in Spotted Sandpipers and Eurasian Dotterels (Owens *et al.* 1994, Blizard & Pruett-Jones 2017). Conversely, in populations where males are expected to compete more for female partners (e.g. sequentially polygamous populations with lek-breeding systems), male-biased expression in ornamentation seems common, including darker male breast bands and ear coverts (Kentish Plovers; Argüelles-Ticó *et al.* 2016), or whiter male tails (Great Snipe; Höglund *et al.* 1990b). However, for monogamous populations the evidence is mixed, suggesting unbiased or male-biased ornamentation (Schroeder *et al.* 2008, Argüelles-Ticó *et al.* 2016) that may reflect enhanced male immune capacity (Pardal *et al.* 2018).

Vocalizations are also a key part of mate attraction and intrasexual competition, and therefore an important component of sex roles in courtship (Butchart *et al.* 1999, Gil & Gahr 2002). Vocalizations can be male-biased (Box 1), such as the 'hooting' of polygynous male Pectoral Sandpipers (Riede *et al.* 2014) and the rattling of male White-rumped Sandpipers *Calidris fuscicollis* (Parmelee *et al.* 1968). However, bias in courtship vocalizations also varies widely, as demonstrated by female bias in courting vocalization in Wilson's Phalaropes *Phalaropus tricolor* (Howe 1975). Sex differences in vocalizations have also been identified in polyandrous jacanas, where larger females produce lower frequency vocalizations (Buck *et al.* 2021). However, it remains unclear to what extent these are a by-product of selection for large female body sizes or a direct target of sexual selection (Buck *et al.* 2021).

Importantly, variation in courtship displays between sexes may further contribute to broader patterns in sexual dimorphism. For example, Jehl and Murray (1986) suggested that reversed sexual size dimorphism (i.e. smaller males than females) may arise as a selective advantage of small body size for manoeuvrability in aerial displays. Follow-up studies supported this argument because agile displays facilitate mate acquisition in Northern Lapwings (Grønstøl 1996) and, across species, acrobatic displays are associated with reversed size dimorphism (Székely *et al.* 2000a). Importantly, the selective pressures that emerge from the contrast between ground and aerial displays have been thought to lead to a well-known macroecological pattern, Rensch's rule, since size dimorphism increases with size when the male is the larger sex, but decreases with size when the female is the larger sex (Székely *et al.* 2004).

The social environment may also influence display patterns (Pitelka *et al.* 1974). Territoriality and territorial displays often form a key component of bird reproduction before and after pair-formation as a result of their association with better access to food, nesting sites or mates (Brown 1969, Mentesana *et al.* 2020). As local competition for mates and resources may increase with the number of conspecifics, variation in local densities is likely to drive differences in territoriality between populations and species. In shorebirds, it is more common for males to establish a territory, and once mated, both sexes may participate in territorial defence (see Table S1). Yet, in some species, female-biased territorial defence is observed and increases in territory size are associated with the number of mates that females attain (e.g. Northern Jacana; Jenni & Mace 2020), suggesting that sex biases in territorial behaviour may be related to sex biases in mate competition. However, because territory size may be linked to territory quality and ecological factors other than mate competition, more detailed studies are required to unpack the mechanistic links between territoriality and reproductive success.

In summary, the direction and extent of sex biases in courtship and competition for mates or territories varies widely among shorebirds, and it remains unclear whether these patterns are consistent with key sex role hypotheses. First, we need quantitative descriptions of pre-mating behaviour from more species and to consider acoustic and olfactory as well as visual cues (Miller & Baker 2009, Grieves *et al.* 2022). Recent advances in quantifying complex aerial display patterns in three dimensions and high-tech sound recording will bring new insights into display behaviour that have so far evaded quantitative approaches (Matsubayashi *et al.* 2023). Second, courtship behaviours are often investigated from a sexual selection perspective (Andersson 1994, Rosenthal 2017) in isolation from other facets of sex role behaviour.

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However, courtship is a key constituent of the suite of sex role behaviours (Schärer *et al.* 2012, Gonzalez-Voyer *et al.* 2022, Kempenaers 2022) and needs to be investigated in conjunction with other reproductive behaviours such as pair-bonding and parenting. Third, more research, including comparative studies, is needed to integrate spatial, temporal and within-population variation in breeding systems and environmental conditions that may influence sex role variation in courtship and territoriality.

SPERM COMPETITION AND POST-COPULATORY FEMALE CHOICE

In truly monandrous breeding systems, only one male's ejaculate fertilizes a female's ova within a reproductive cycle, and sexual competition is therefore limited to before mating (i.e. pre-copulatory competition; Parker 2014, Taylor *et al.* 2014). However, in many birds, including shorebirds, females can copulate with multiple males in a given reproductive cycle (Parker & Birkhead 2013, Birkhead & Montgomerie 2020) and competition between males over the proportion of eggs that males fertilize can continue after copulation through sperm competition and cryptic female choice (Parker 1970, Thornhill 1983). As a result, post-copulatory sexual selection may favour traits that increase male paternity, such as larger testes, higher quality sperm or seminal fluid, and/or repeated copulations (Boschetto *et al.* 2011, Godwin *et al.* 2017, Alvarez-Fernandez *et al.* 2019, Carleial *et al.* 2020, Lüpold *et al.* 2020).

Evolutionary sex roles are expected to have tight links to patterns of sperm competition and post-copulatory competition, because (1) they describe the patterns of male and female mating behaviour including the rate at which females mate with multiple partners, and (2) multiple mating by females may feed back into sex roles in parental care (e.g. via reduced paternity assurance). Shorebirds provide scope for investigating the role of post-copulatory processes in shaping sex biases in reproductive behaviour, given that the frequency of multiple paternity across broods varies widely (0–51.5% among species; Thomas *et al.* 2007, Valcu *et al.* 2021). In comparison to socially monogamous passerines, in which extra-pair copulation and extra-pair paternity (i.e. multiple paternity) are common (Birkhead & Møller 1998, Griffith *et al.* 2002), multiple paternity tends to be low in socially monogamous shorebirds (e.g. Wallander *et al.* 2001, Maher *et al.* 2017) with some exceptions (Mee *et al.* 2004). For example, Casey *et al.* (2011) found that in the socially monogamous Upland Sandpiper *Bartramia longicauda*, 30% of broods contained extra-pair offspring, representing 15% of all chicks.

Despite the overall low occurrence of multiple paternity, some female shorebirds mate with multiple males as a behavioural strategy to avoid the negative effects of pairing with a genetically similar mate (Blomqvist *et al.* 2002). Similarly, in Red Phalaropes *Phalaropus fulicarius* multiple paternity appears to be largely driven by females seeking extra-pair copulations rather than being a by-product of stored sperm from previous mates after rapid mate change (Krietsch *et al.* 2022). However, in the sequentially polyandrous Spotted Sandpiper multiple paternity arises via sperm stored from previous mates after females change partners (Oring *et al.* 1992).

Rates of multiple paternity are higher among shorebirds in which females form simultaneous pair-bonds with multiple males (e.g. Wattled Jacana; Oring 1982, Emlen *et al.* 1998), and it seems even higher among lekking species such as Ruff and Buff-breasted Sandpiper (Lanctot *et al.* 1997, Lank *et al.* 2002). Across species, Johnson and Briskie (1999) found that social breeding system variation was related to sperm size, as non-monogamous shorebirds had longer spermatozoa than monogamous shorebirds. Similarly, relative testis size was greater in non-monogamous than monogamous sandpipers (Carter 1985), including the Ruff, which has the largest testes and longest sperm among shorebirds (Johnson & Briskie 1999) and has among the highest rates of multiple paternity (50% of broods; Lank *et al.* 2002).

Together, these results suggest a link between sex role variation and sperm traits, and future work is needed to ascertain the associations among post-copulatory competition, trait elaboration and sex role variation in shorebirds. In a step towards this goal, a comparative study of over 400 bird populations (including shorebirds) revealed that rates of extra-pair paternity are related to latitude, generation length and the duration of pair-bonds (Valcu *et al.* 2021). However, the extent to which these patterns relate to the greater suite of sex role

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diversity, including patterns of parental care, remains unclear (Kokko & Jennions 2008, Brouwer & Griffith 2019). Moreover, the current lack of detailed sperm data across shorebirds, in comparison to information on egg measurements, hampers the testing of predictions emerging from the Darwin–Bateman paradigm, for example that the extent of anisogamy should be linked to role biases in mating competition (see Fig. 1). Future detailed single-species studies of post-copulatory competition in shorebirds will facilitate comparative examinations.

We suggest that such studies should take into consideration that breeding systems, and the potential for post-copulatory competition, can vary over time and space (e.g. via changes in demography and breeding densities). For example, Eurasian Curlews *Numenius arquata* show higher extra-pair paternity in high-density populations compared with low-density populations (Currie & Valkama 2008). Moreover, even within one population the risk and intensity of sperm competition may be spatially variable. For example, in Sanderlings *Calidris alba* and Kentish Plovers, monogamy, polyandry and polygyny can occur within the same population (Székely & Lessells 1993, Reneerkens *et al.* 2014). These intraspecific variations offer additional avenues for untangling the putative associations among paternity, breeding ecology and sex role variations. In summary, shorebirds hold great potential to investigate links between sex roles, breeding system variation and post-copulatory sexual selection, and this potential has only been partly explored to date.

PAIR-BONDS

A pair-bond is a selective affiliation between two individual mating partners, which occurs before mating and often continues into parental care (Black 1996, McGraw *et al.* 2010). It is highly variable across animal taxa and is associated with breeding behaviours, reproduction and survival (Reichard & Boesch 2003, McGraw *et al.* 2010, Lukas & Clutton-Brock 2013). Understanding the ecological and life history predictors of the formation of different pair-bonds is therefore a crucial component of sex role studies.

Shorebirds display wide variation in the duration, nature and contribution of the sexes to pair-bonds. The formation or dissolution of a pair-bond often results from an individual's decision to mate with or divorce a partner (i.e. mating decision; Culina *et al.* 2015), thus resulting in different breeding systems. Socially monogamous shorebirds typically form an exclusive pair-bond between a single male and a single female within a reproductive event or for consecutive breeding attempts (e.g. Gates *et al.* 2013), or even a lifetime (Thomas *et al.* 2007). In contrast, in several species that are polygamous, males (and/or females) form simultaneous (or serial) pair-bonds with multiple individuals within a reproductive event (i.e. simultaneous or serial polygamy, respectively; Thomas *et al.* 2007). Pair-bonds can be quantified for a given population and a given sex as the frequency distributions of having zero, one, two, three or more mates within a reproductive period (e.g. breeding season). Although researchers also use the term 'promiscuity' to refer to the lack of social affiliation between males and females, this label is undesirable as it can refer to either short pair-bonds or incongruence between social and genetic breeding systems (Black 2001, Reichard & Boesch 2003).

The most common breeding system in shorebirds is social monogamy with a stable pair-bond across breeding attempts, common among many plovers (Fig. 2; Eberhart-Phillips 2019, Halimubieke *et al.* 2020), larger shorebirds (such as curlews and godwits), and also among semi-precocial species that feed their young (e.g. oystercatchers; Ens *et al.* 1993, Heg *et al.* 1993). Simultaneous polygamy, where one sex pairs with several mates at the same time, is mostly found in sandpipers, woodcocks and Northern Lapwings (Pitelka *et al.* 1974, Cartar & Lyon 1988, Parish *et al.* 1997, del Hoyo *et al.* 2018). Ruff and Buff-breasted Sandpipers exhibit lekking polygyny (see Box 1). Importantly, shorebirds also exhibit some of the best examples of simultaneous (and sequential) polyandry, such as most jacanas, painted-snipes, phalaropes and buttonquails (del Hoyo *et al.* 2018, Fresneau *et al.* 2021, Safari & Goymann 2021).

An array of factors drive variation both in breeding systems and in pair-bonds, so that closely related species may exhibit different extents of mate fidelity (Fig. 4). Theoretically, pair-bonds can be influenced by ecological and life history factors. Ecological constraints determine the availability of resources, such as food and territories, that an individual can acquire to improve their reproductive success. Variations and stochasticity in such

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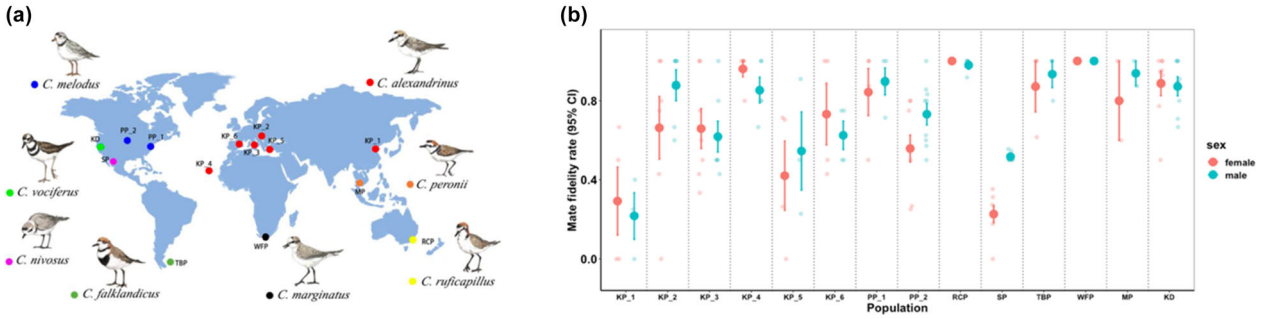

Figure 4. Mate fidelity in plovers. (a) Plover populations that exhibit different extent of mate fidelity (n = 14 populations, eight species). (b) Within-season mate fidelity rates may differ for males and females (means, lower and upper 95% confidence intervals). Adapted and modified from Halimubieke *et al.* (2020).

resources may affect the reproductive benefits of different mating decisions (Gilburn & Day 1994, Welch 2003, Candolin *et al.* 2007, Eberhart-Phillips 2019). For example, food availability altered the timing of brood desertion in Kentish Plovers such that pairs – counterinuitively – had longer pair-bonds at sites with higher food availability (Kosztolányi *et al.* 2006).

Abiotic factors such as temperature and precipitation may also play important roles in altering the duration of suitable breeding periods, thereby limiting (or promoting) pair-bond maintenance. A prolonged breeding period normally allows individuals to have multiple breeding events with the same or different mates (Botero & Rubenstein 2012, Eberhart-Phillips 2019, Halimubieke *et al.* 2020). For example, shorebirds breeding at high latitudes or altitudes may have a relatively short window for breeding when temperatures are most suitable (Meltofte *et al.* 2007), so breeding pairs are more likely to stay together to rapidly capitalize on suitable conditions (van Leeuwen & Jamieson 2018). However, in temperate and tropical latitudes, some species (e.g. Kentish Plovers and White-faced Plovers *Charadrius dealbatus*) have prolonged breeding seasons so these individuals may initiate a second or even third clutch, often with different mates (Huang & Que 2019). The latter observation is consistent with the finding that across 14 plover populations, those in warmer climates show lower mate fidelity than those that breed in colder climates (Fig. 4; Halimubieke *et al.* 2020). In spite of intense research on food availability, spacing patterns and social systems of shorebirds (Holmes & Pitelka 1964, Pitelka *et al.* 1974, Erckmann 1981, Currie *et al.* 2001, Saalfeld & Lanctot 2015), no clear pattern has emerged: this area of research is ripe for formal meta-analyses.

Past breeding success may be an important factor influencing mating decisions in birds (Choudhury 1995). In some species of shorebirds such as Eurasian Oystercatchers *Haematopus ostralegus*, the breeding pair retains their pair-bond to improve offspring survival (Van De Pol *et al.* 2006), whereas in other species divorce may follow breeding failure (Choudhury 1995). Counterintuitively, a study of plover species showed that successful nesting leads to divorce, whereas nest failure leads to mate retention within the same breeding season because individuals that divorce their partners and desert their broods are able to remate and produce more offspring with a new partner, but individuals in pairs that failed in their breeding attempts may retain their mate to facilitate rapid re-nesting (Halimubieke *et al.* 2020). Such a pattern has also been demonstrated in Dunlins *Calidris alpina*, where re-nesting after previous nest failure was faster for reuniting pairs than newly formed pairs (van Leeuwen & Jamieson 2018). These patterns further suggest that variation in nest failure between populations (e.g. via predation risk) may drive inter-population variation in pair-bond maintenance.

The developmental mode of offspring may also impact pair-bonds. In species with semi-precocial chicks that need to be fed by their parents, parents have longer and more stable pair-bonds in order to improve offspring survival (Thomas & Székely 2005). However, in most other shorebird species, chicks are precocial and only require modest care, providing the opportunity for one parent to terminate care and initiate a new clutch with another mate (Székely *et al.* 1996, Houston *et al.* 2005, McDonald *et al.* 2023).

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Finally, the social environment is likely to have a principal influence on pair-bonds. Mating opportunities often differ between sexes, leading to different mating decisions by males and females (Székely *et al.* 2000b, Parra *et al.* 2014). Differences in population demographics, such as birth rates and survival, can lead to biased ASRs and affect the availability of breeding partners (Liker *et al.* 2013, Eberhart-Phillips *et al.* 2018). A biased ASR may then increase competition for mates between members of the over-represented sex and reduce it in the under-represented sex (Schacht *et al.* 2022). Consequently, one sex may benefit more by searching for additional mating partners rather than remaining as part of a monogamous pair, potentially leading to increased rates of divorce. For example, field experiments have shown that artificially widowed male Kentish Plovers take significantly longer than females to find a replacement partner in a male-biased population (Székely *et al.* 1999, Kosztolányi *et al.* 2011).

Moreover, the latter experimental result is consistent with observations under natural conditions that female Kentish Plovers often desert their brood and divorce their mate to pair with a new male, whereas the males provide care to the offspring alone (Székely & Lessells 1993, Amat *et al.* 1999, McDonald *et al.* 2023). A follow-up experimental study found that remating times were similar for males and females in White-fronted Plovers *Charadrius marginatus*, whereas in Kittlitz's Plovers *Charadrius pecuarius*, contrary to expectation, female remating times were longer than those of the males (Parra *et al.* 2014), suggesting that mating opportunities are substantially different between these closely related species. Importantly, the strength of pair-bonds appears to be different between the latter two species, because White-fronted Plovers, but not Kittlitz's Plovers, re-established the pair-bond with their previous mate after their experimentally removed partner was released from captivity (Parra *et al.* 2014). Site fidelity probably plays a role in such patterns (Eberhart-Phillips 2019, Kwon *et al.* 2022) given that in species with territoriality and high site fidelity such as Lesser Sheathbill *Chionis minor*, Black Turnstone *Arenaria melanocephala* and Eurasian Oystercatcher, breeding pairs are likely to maintain a long-term pair-bond (Ens *et al.* 1992, Bried & Jouventin 1998, Handel & Gill Jr 2000), whereas in nomadic or migratory bird populations, the pair-bond appears to be more flexible (Cézilly *et al.* 2000, Naves *et al.* 2006, Friedrich *et al.* 2014).

In summary, shorebirds differ greatly in how pair-bonds form and dissolve, and in the duration and intensity of reproductive associations between males and females. Variation in both the ecological and social environment, alongside life history and demographic traits, probably together predict an individual's mating decisions. However, it has yet to be determined whether these factors may have a causal influence on mating decisions, and we recommend experimental manipulations to further study the mechanisms underlying the variation in pair-bonds because these findings will be crucial to understanding the evolution of sex roles.

PARENTAL CARE

Once a clutch of eggs has been laid, shorebird parental care spans two key components: incubation and brood care after hatching (Fig. 5). Care during incubation is key to ground-nesting shorebirds to warm eggs in cold climates and avoid heat stress in hotter climates (Amat & Masero 2004, AlRashidi *et al.* 2011, Bulla *et al.* 2014, 2016). During incubation, parents may also conceal their eggs from predators and actively defend their nests by, for example, luring predators away or attacking intruders (Humphreys & Ruxton 2020, Brynychová *et al.* 2022, de Framond *et al.* 2022). After hatching, parents care for their chicks which are typically precocial (self-feeding chicks, e.g. plovers, sandpipers and jacanas) or semi-precocial (parents feed the chicks, e.g. oystercatchers and stone curlews; Thomas *et al.* 2006, Colwell 2010). Aside from differences in offspring feeding, brood care comprises broadly similar tasks across species; parents brood their young chicks, which cannot fully independently thermoregulate, and lead their chicks to suitable habitats to feed and defend them from threats (Visser & Ricklefs 1993, Kosztolányi *et al.* 2007, Humphreys & Ruxton 2020, de Framond *et al.* 2022). However, despite these broad similarities, patterns of shorebird parental care across species are diverse in the roles that males and females play, making them an ideal group to study evolutionary and ecological mechanisms that shape sex differences in parental care (Székely 2019, McDonald *et al.* 2023).

A key component of sex role differences in parenting is the duration of care across offspring

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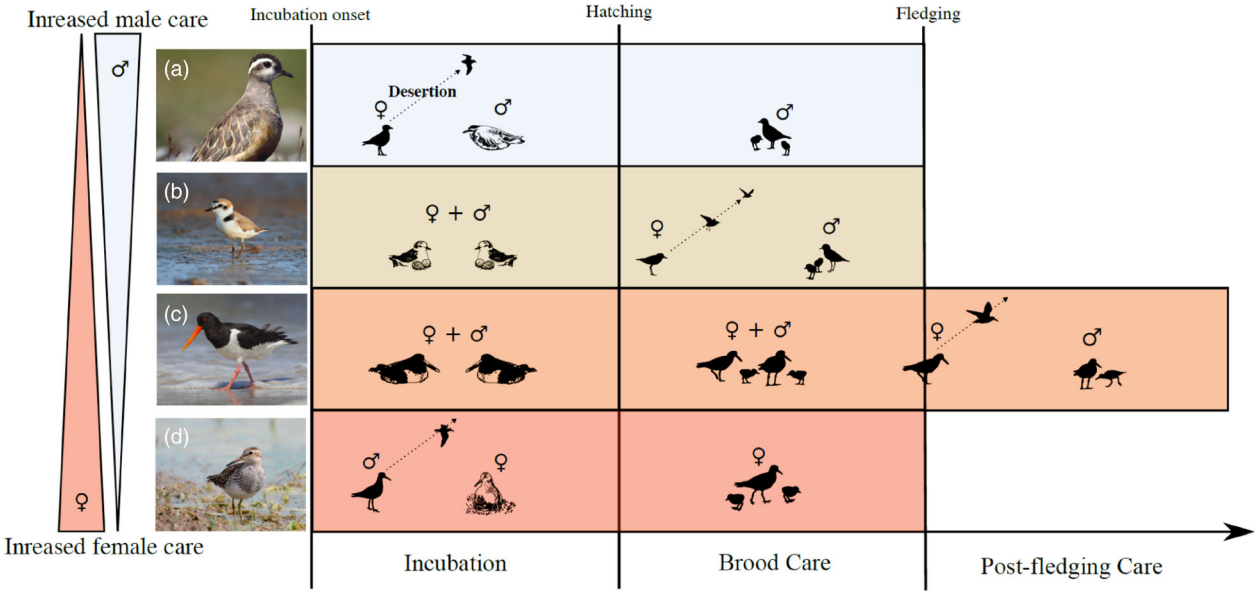

Figure 5. Dynamic sex roles in shorebird parental care. Diagram highlights differences in the duration of male and female parental care across the typical stages of offspring development from incubation, brood care to extended care after fledging for four example species of shorebirds: (a) Eurasian Dotterel, (b) Kentish Plover, (c) Eurasian Oystercatcher and (d) Pectoral Sandpiper. Image credit: (a) and (b) Andreas Trepte (creativecommons.org/licenses/by-sa/2.5/); (c) David Raju (creativecommons.org/licenses/by-sa/4.0/) and (d) Helwig Brunner (creativecommons.org/licenses/by-sa/2.5/deed.en).

development, where either both parents care for their young until independence or one parent, male or female, leaves their partner to care alone (i.e. offspring desertion, Fig. 5; Székely *et al.* 2007, Vincze *et al.* 2013, Bulla *et al.* 2014). Even in species that typically incubate biparentally, there is potential for flexible uniparental incubation (Bulla *et al.* 2017). Brood care is similarly diverse and can be male-biased, female-biased or biparental (Fig. 5; Erckmann 1981, Reynolds & Székely 1997, Colwell 2010).

Within species, care patterns may also be variable. For example, in the Semipalmated Sandpiper *Calidris pusilla*, most females desert their broods just days after hatching, but a minority remain to care for their broods until fledging, alongside males (Gratto-Trevor 1991). Similarly, in Kentish Plovers, Snowy Plovers and Killdeer *Charadrius vociferus* both parents incubate their clutches. However, after hatching, all three parental care patterns (male-only, female-only and biparental care) may be observed within a single population (Warriner *et al.* 1986, Brunton 1988, Johnson *et al.* 2006, McDonald *et al.* 2023). In addition, temporal variation in the overall duration of care ranges from care until fledging over several weeks (Colwell 2010) to the extended post-fledging care of several months in Eurasian Oystercatchers, Crab Plovers *Dromas ardeola* (De Sanctis *et al.* 2005, Méndez *et al.* 2021), and also in three plover species in Madagascar (Kittlitz's Plover, White-fronted Plover and Madagascar Plover *Charadrius thoracicus*; Tanner 2022).

At the level of the individual parent, the decision of whether or not to provide care is shaped by the balance of the benefits of care (e.g. increased offspring survival) and its costs (e.g. missed mating opportunities; Székely *et al.* 1996, Alonso-Alvarez & Velando 2012, Mock 2022, McDonald *et al.* 2023). Attempts to explain care diversity ultimately rely on understanding these costs and benefits for both males and females, how they change over offspring development and how sex differences in cost–benefit ratios vary between species and populations (Erckmann 1981, Gratto-Trevor 1991, Houston *et al.* 2005, Székely 2014).

The social environment, and in particular the ASR, has emerged as a primary driver of sex roles during care because it shapes the potential benefits of deserting offspring (Székely 2014, Schacht *et al.* 2022). Biased ASRs may increase the mating benefits of deserting for the under-represented sex,

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creating a bias towards care by the over-represented sex (Liker *et al.* 2013). For example, in male-biased populations of Kentish Plover, there is male-biased brood care and female-biased brood desertion (Amat *et al.* 1999, McDonald *et al.* 2023). Moreover, female Kentish Plovers that desert their broods may benefit by initiating subsequent breeding attempts within the same season compared with females that continue to care with their male partner (McDonald *et al.* 2023). Although desertion for mating benefits may occur at any time during offspring development, the precocial nature of shorebird chicks, such that the demands of offspring care are relatively low compared with altricial species, may underlie the particularly variable sex roles in shorebirds, as brood care may be conducted successfully by one parent (Temrin & Tullberg 1995, Thomas & Székely 2005, Thomas *et al.* 2006, Long *et al.* 2022).

The social environment may also affect care via breeding densities and intensity of intraspecific competition, for example if high densities increase conflict between families and increase the need for biparental defence of offspring from neighbouring conspecifics (Kosztolányi *et al.* 2006, Yasué & Dearden 2008). Variation in the social environment to which young chicks are exposed may also impact directly on their development. In Eurasian Oystercatchers, offspring migration strategy typically follows that of the male parent, suggesting that offspring adopt migration strategies through social learning from fathers or differences in the wider social environment that they experience when following resident versus migratory fathers post-fledging (Méndez *et al.* 2021). Social learning can be an important aspect of avian offspring development (Slagsvold & Wiebe 2011, Farine *et al.* 2015), yet the extent to which male and female shorebird parents differentially contribute to offspring social learning is not known. However, if sexes differ in anti-predator responses, or habitat preferences, this could lead to differences in learned responses in chicks raised by males only, females only or biparentally. The diversity and flexibility of care patterns within shorebird species provide scope to investigate such potential sex roles in avian social learning, for example by manipulations of the family unit via parent removal experiments or cross-fostering chicks between families (Székely *et al.* 1999, Székely & Cuthill 1999, 2000), or by monitoring the lifetime behaviour of chicks that were raised by the male or the female.

The social environment is emerging as a major predictor of diverse breeding systems across birds (Liker *et al.* 2014, Safari & Goymann 2021, Kempenaers 2022), although other factors are likely to further shape patterns of parental cooperation within and between shorebird populations. For example, life history traits such as the need of parents to prepare for migration may influence care patterns (Harrod & Mumme 2021). Also, hostile environments are typically expected to generate more similar sex roles in care, as the greater challenge of raising young in difficult situations requires greater parental cooperation (Owens & Bennett 1997). For example, using the global distribution of plover species, Vincze *et al.* (2017) showed that higher ambient temperatures are associated with a greater and more equal share of diurnal male incubation, probably driven by the greater need of both parents to protect embryos from potentially fatal heat stress. Extreme weather and low food availability are also likely to negatively impact chick survival during brood care. However, if such conditions cannot be better mitigated by biparental care, it may instead pay for one parent to desert broods that suffer higher mortality (Kupán *et al.* 2021), driving variation between populations in care patterns. Further research is needed to develop our appreciation for how rapid climatic change may shape the trajectories of male and female cooperation dynamically across different stages of care in the face of increasing threats to shorebird populations (Colwell 2010, Sutherland *et al.* 2012).

The decision to care or desert is not the only axis over which male and female care roles can vary. Even within families where both parents care, there may be sex differences in parental division of labour (Bulla *et al.* 2017, Vincze *et al.* 2017). For example, Red-capped Plover *Charadrius ruficapillus* incubation schedules suggest that sexual dichromatism may give rise to a temporal division of incubation duties, where the brighter and more conspicuous males incubate at night to avoid detection by visual predators, while the less conspicuous females incubate during daylight (Ekanayake *et al.* 2015). However, such patterns are not universal. For example, incubation by brighter male Rufous-chested Dotterels *Charadrius modestus* is biased towards the day, whereas the duller females incubate at night (St Clair

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et al. 2010). Similarly, male and female Hooded Dotterels *Thinornis cucullatus* are monomorphic, but males still incubate more at night (Ryeland *et al.* 2022). Such differences indicate that other sex differences in the costs and benefits of care may shape diel sex roles in incubation, such as sex differences in the need to forage at the most efficient time of day (St Clair *et al.* 2010, Bulla *et al.* 2014). Differences in the incubation efficiency of males and females could also drive these patterns (Cresswell *et al.* 2003, 2004), although the lack of daily routines in Arctic-breeding Common Ringed Plover *Charadrius hiaticula* populations suggests that light, rather than temperature, drives the male-bias in night-time incubation for temperate populations of this species (Wanders *et al.* 2023a).

Generally, sex differences in the costs and benefits of care are predicted to drive diversity in the division of labour between male and female parents. For example, if females pay a higher cost when defending offspring compared with males, then males may become specialized to defend, whereas females may become specialized to perform other care tasks (Barta *et al.* 2014, Henshaw *et al.* 2019). In other avian groups, task division can be extreme. For example, in many raptor species, females exclusively incubate and males exclusively provision the young (Barta *et al.* 2014). Because many shorebirds do not feed their young, such specialization may be less clear, although in Wattled Jacanas, both females and males contribute to offspring defence but only males brood the chicks (Emlen & Wrege 2004b). Although, in practice, measuring the costs and benefits of care is challenging, future research is needed to understand how sex-specific costs and benefits may shape patterns of parental cooperation. Moreover, given that shorebird parenting has played a key role in the development of game theoretic models that underpin our understanding of parental negotiation and cooperation (McNamara *et al.* 2000, Houston *et al.* 2013), further investigations of the physiological mechanisms, costs, benefits and phylogenetic constraints that underlie shorebird care will be likely to enhance the development of future modelling approaches that account for such complexity (Klug *et al.* 2012, McNamara 2022).

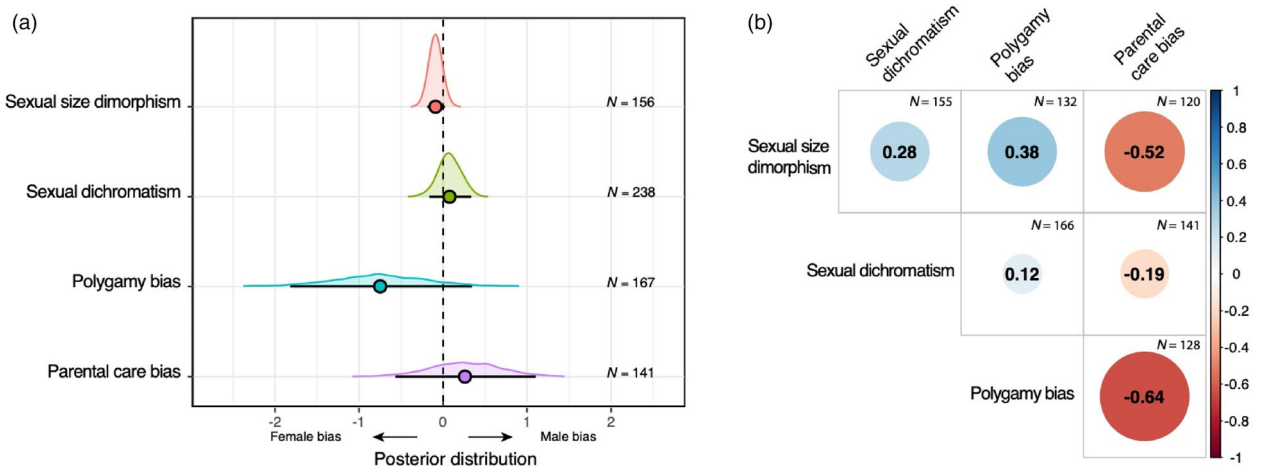

Figure 6. Sex role (co-)variation in shorebirds. (a) Sex biases in traits related to sex roles. Each variable was computed as the relative value of males to females, where a value of zero means no difference between the sexes, positive values represent a sex bias towards males and negative towards females. Coloured points indicate mean estimates with their respective upper and lower 95% credible intervals. Each sex role component was defined according to Gonzalez-Voyer *et al.* (2022). Data were extracted from Székely *et al.* (2022), where we filtered out alcids, gulls and skuas, resulting in a total of 239 species. We used the methodology presented in Valdebenito *et al.* (2023), where density distributions were obtained by constructing intercept-only generalized mixed models using Markov Chain Monte Carlo models in the R package MCMCglmm (Hadfield 2010). All models were corrected by phylogenetic relatedness using a consensus tree from 1000 available from the avian phylogeny proposed by Jetz *et al.* (2012). (b) Bivariate phylogenetically corrected correlations among sex role components in shorebirds. These correspond to marginal correlation accounting for phylogenetic relatedness using the 'mvBM' function in the R package mvMORPH (Clavel *et al.* 2015). Numbers inside circles indicate the value of the phylogenetically controlled correlation, also depicted by the size and colour of circles. *N* = number of species.

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WHY DO SHOREBIRDS EXHIBIT VARIABLE BREEDING SYSTEMS?

We have shown that sex roles across different aspects of shorebird reproduction vary widely, and the associations among these traits (Fig. 6, r_{min} = 0.12 and r_{max} = 0.64) suggest that there is a 'sex role syndrome' (Székely *et al.* 2014), so that traits associated with sex roles tend to co-evolve with each other. Understanding the selective forces that shape complex traits such as mating strategies and parenting is not simple, and involves testing both historical (i.e. evolutionary) and contemporary (i.e. ecological) predictors. Here we propose three ecological and evolutionary processes that could contribute to the exceptional variation in breeding systems and associated traits in shorebirds: diverse breeding environments, developmental modes and social contexts.

First, shorebirds have an unusually wide geographical distribution that spans all continents, and although they predominantly breed on shorelines and in wetlands, they also breed in other habitats, including tundra, boreal, temperate or tropical forests, grasslands, deserts and high mountains (Colwell 2010, del Hoyo *et al.* 2018). Many species also breed in human environments, including intensively cultivated agricultural landscapes, industrial mining sites or building roofs (Hayman *et al.* 1986, Billerman *et al.* 2022). As we argue above, these ecologically diverse breeding habitats probably select for different male and female strategies that together produce both intra- and inter-specific variations in sex role behaviour. However, even within a breeding habitat, sex roles and breeding strategies can vary. For example, calidrine sandpipers in the Arctic exhibit a wide array of breeding systems while breeding sympatrically, indicating a role for other factors (Pitelka *et al.* 1974, Erckmann 1981, Thomas *et al.* 2007, Kempenaers 2022).

Second, the modest levels of care that precocial and semi-precocial shorebird chicks require in comparison to altricial nestlings means that both parents might not be essential for parental care in many shorebirds (Starck & Ricklefs 1998, Colwell 2010). Such scenarios, possibly coupled with high insect food abundance during the peak hatching season, may facilitate partner desertions and promote uniparental care (Erckmann 1981).

Third, shorebirds often do not breed as individual pairs but form more or less connected breeding associations, ranging from coloniality to sparse breeding populations where individuals travel large distances within breeding seasons (e.g. Hötker 2000, Owens 2002, Colwell 2010, McDonald *et al.* 2020, Šálek *et al.* 2022). Moreover, evidence suggests wide-ranging ASRs among populations (Liker *et al.* 2013, Eberhart-Phillips *et al.* 2018). Given the key role of variation in the social environment, including breeding density and ASR, in shaping variation in mating patterns and parental care, this wide variety in social structure probably plays a key role in shaping the exceptional diversity in shorebird breeding systems (Székely *et al.* 2006, Thomas *et al.* 2007, Colwell 2010, Liker *et al.* 2013).

It is possible that we are missing the true level of sex role variation in shorebirds because of taxonomic and geographical biases in research effort. Northern temperate and Arctic species such as Northern Lapwing, Common Redshank *Tringa totanus*, Eurasian Oystercatcher, *Charadrius* plovers and *Calidris* sandpipers dominate the shorebird literature, with tropical and southern hemisphere species and families having relatively little research investment, a pattern seen across birds generally (Fig. 7; Xiao *et al.* 2017). Factors that predispose species to be more amenable to research, such as high breeding densities or proximity to habitats dominated by humans, may further bias research focus (Székely 2019). In contrast, families such as buttonquails (Turnicidae), that display sex role reversal and large interspecific variation in sexual dimorphism (Madge & McGowan 2002), may have received less attention because of their cryptic behaviour and their predominantly southern hemisphere distribution. Filling such gaps will be particularly important to identify threats to under-studied, rare and endemic species.

SEX ROLES, POPULATION RESILIENCE AND CONSERVATION

Shorebirds face threats across their geographical range, often associated with climatic and other anthropogenic changes, including loss of breeding habitats, threats on migratory stopover sites and increased predation rates (Kubelka *et al.* 2018, 2022, Von Holle *et al.* 2019, Jackson *et al.* 2021, Flemming *et al.* 2022, Wang *et al.* 2022). The capacity of shorebird populations to tolerate and

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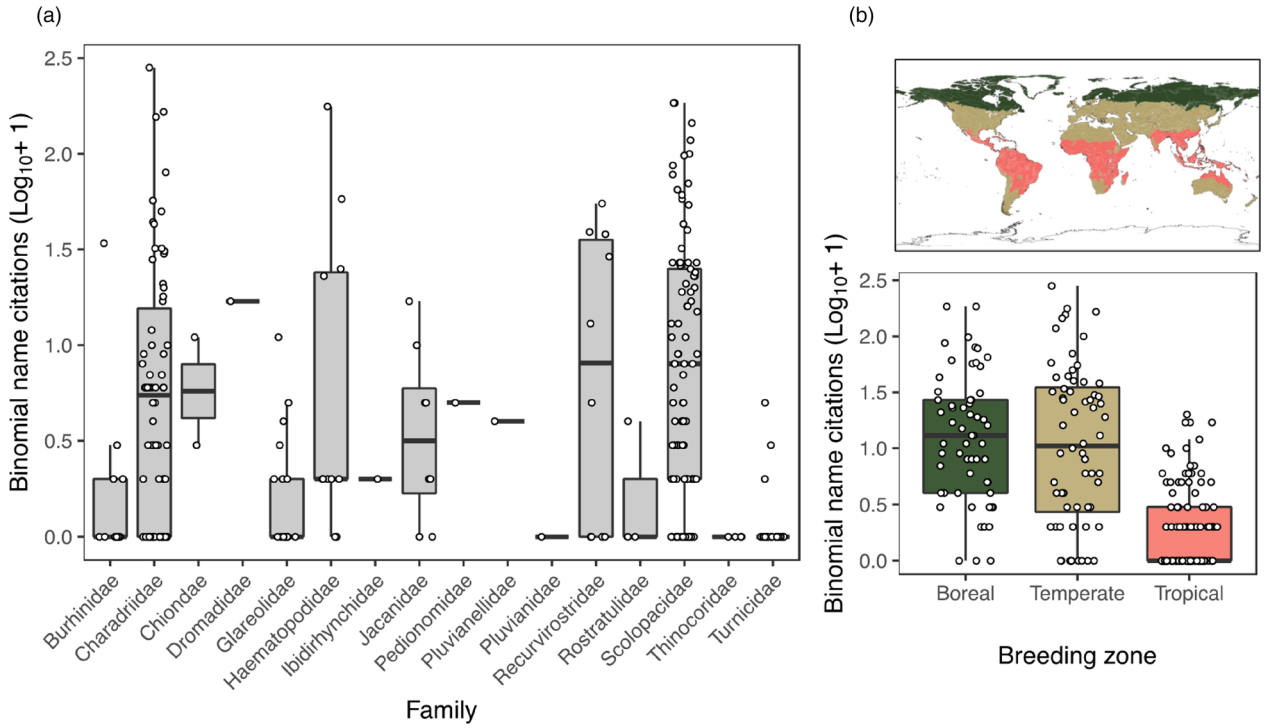

Figure 7. Occurrences of the binomial names in the scientific literature for 242 shorebird species. The number of citations for each species is $\log_{10}$ transformed. Species are (a) grouped into 16 families and (b) grouped by main breeding zone (green: Boreal, tan: Temperate and pink: Tropical). Inset map shows approximate geographical extent of each zone (Dinerstein *et al.* 2017). Searches were conducted in ISI Web of Science on 6 May 2023. Search terms included the species and multiple terms aimed at limiting studies to those relevant to breeding and sexual behaviour including ('lek*' OR 'breed*' OR 'parental care' OR 'court*' OR 'pair-bond*' OR 'pair bond*' OR 'incubat*' OR 'mating'). The number of studies per species varies widely between families and between breeding zones with a maximum of up to 281 citations for one species in Charadriidae but zero citations for nearly all species of Thinocoridae and Turnicidae.

adapt to these challenges is likely to be modulated by sex role variation, although there is no consensus as to the direction of such an effect (Legendre *et al.* 1999, Doherty *et al.* 2003, Morrow & Pitcher 2003). On the one hand, skewed mating success of polygynous shorebird populations with female-only care reduces the effective size of the male population (Corl & Ellegren 2012, Verkuil *et al.* 2014), with similar predictions for female effective population sizes in polyandrous populations (Nunney 1993). Smaller effective population sizes result in greater mutation loads and reduced adaptability, which may indicate greater population vulnerability (Willi *et al.* 2006). On the other hand, if only the highest quality males and females mate successfully, then strong sexual selection may reinforce natural selection (Whitlock & Agrawal 2009), lowering mutation load and increasing adaptability for polygamous species. Although there is evidence for such effects across birds in general (Wanders *et al.* 2023b), this has not been tested in shorebirds.

Polygynous and polyandrous populations may exhibit greater dispersal rates than monogamous populations (Stenzel *et al.* 1994, Küpper *et al.* 2012, D'Urban Jackson *et al.* 2017, Kempenaers & Valcu 2017, Kwon *et al.* 2022), which increases the effective size of a population by connecting otherwise isolated groups of individuals. Such connections can reduce the mutation load and increase the effectiveness of selection across the metapopulation, but also slow down local adaptation (Slatkin 1987). Further research into these questions using shorebirds as model organisms has the potential to improve our understanding of population vulnerability, and a short-term goal should be to clarify the relationship between sex roles and genomic signatures of effective population size, gene flow and purifying selection.

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In addition to moderating a population's vulnerability to current threats, sex roles may themselves be altered by changing selection pressures. If individuals engage in extra-pair mating to avoid inbreeding, as has been described for some shorebirds (Blomqvist *et al.* 2002; see also sperm competition and post-copulatory female choice), then declining populations may drive individuals towards greater levels of extra-pair mating. In addition, if males and females use different habitats or have different resource needs, such as Bar-tailed Godwits *Limosa lapponica* and Black-tailed Godwits that sexually segregate to use different resources in non-breeding periods (Alves *et al.* 2013, Duijns *et al.* 2014), then anthropogenic effects that differentially impact male and female habitats could lead to sex-specific mortality. For example, if pollution changes the structure and abundance of invertebrate communities, this may differentially impact males and females within a species because of sex differences in foraging strategies (Alves *et al.* 2013). In turn, such effects may impact on ASRs and consequently influence sex roles (Grüebler *et al.* 2008).

Further research should address whether greater divergence in sex roles between males and females increases population vulnerability, by increasing the number of potentially threatened ecological niches that the population requires or reduces vulnerability by increasing the breadth of ecological niches that the population can exploit (Bonduriansky 2011). This depends on how quickly the sex-biased gene expression patterns that underlie divergent sex roles can be generalized to both sexes, and requires long-term monitoring of threatened populations (e.g. Spottiswoode *et al.* 2006).

CONCLUSIONS

Over the past decades, shorebird studies have made fundamental contributions to behavioural ecology, evolutionary biology and population biology by uncovering novel patterns in breeding systems and parenting, sexual dimorphism and speciation (Jehl & Murray 1986, Tomkovich 1989, Ens *et al.* 1993, Székely & Reynolds 1995, Blomqvist *et al.* 2002, D'Urban Jackson *et al.* 2017, Kempenaers 2022). Sex roles offer a conceptually attractive approach to understand breeding system diversity by comparing the proximate processes and ultimate outcomes between males and females. As we argue above, the diverse breeding systems of shorebird species, populations and individuals offer great opportunities to test evolutionary and ecological hypotheses for these variations. Currently, we feel it would be premature to conclude which of the three hypotheses (see Fig. 1) explains this diversity, but we suggest three points.

First, if contemporary levels of anisogamy underlie sex roles, we would expect – as one side of the anisogamy coin – sperm in monogamous shorebirds to be typically larger than those in polygamous species. However, data from a small number of species suggest the contrary, i.e. polygamous shorebirds tend to have larger sperm (Johnson & Briskie 1999). Long sperm tails can facilitate fertilization success (e.g. Bennison *et al.* 2015), and hence intense sperm competition among males may not lead to reduced sperm size. A further difficulty of the anisogamy argument is that gamete production alone is unlikely to translate directly into fertilization success or reproductive success (Liker *et al.* 2015, Mokos *et al.* 2021). The path from fertilization to successful recruitment of offspring into the breeding population is complex and may include male–female involvement in nest-site selection, incubation and rearing of the young, and post-care survival of the young. Therefore, while anisogamy remains a key step in the sexual cascade that predisposes males to more intense mating competition (Parker 2014, Lehtonen 2022), it seems insufficient alone to explain the diversity of shorebird sex roles.

Secondly, sex differences in foraging strategies and feeding habitats are well studied among shorebirds (Goss-Custard 1996, Sandercock 2001, Nebel *et al.* 2002, van Kam *et al.* 2004, Alves *et al.* 2013), although the evidence that such differences should lead to sex role variation is currently weak. If ecological competition between the sexes favours sexual dimorphism, then the strongest dimorphism, especially in foraging-related traits such as bill shape and size, would be expected among shorebirds in which males and females share the same territory. Across bird species including shorebirds, however, there is no support for the latter prediction (Székely *et al.* 2007). Many shorebirds spend up to 10 months away from their breeding grounds and competition for resources can be intense. However, different shorebird species often feed together so interspecific competition may be more important than competition between males and females of a given species (Székely *et al.* 2000a).

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Thirdly, although ASRs have been associated with pair-bonding systems and parenting in shorebirds (Székely *et al.* 2006, Liker *et al.* 2013, Eberhart-Phillips *et al.* 2018), we need better ASR estimates to verify associations between sex roles and ASR (Kempenaers 2022, Schacht *et al.* 2022). ASRs tend to fluctuate over time and vary spatially (Székely *et al.* 2014, Grant & Grant 2019), and currently it is not known how robust the results of comparative studies are to temporal fluctuations and spatial variations in ASR.

FUTURE DIRECTIONS

The diverse breeding systems, extreme range of sexual dimorphism and unusual variation in sex roles among shorebirds have attracted much attention ever since the seminal studies by Darwin (1871), Huxley and Montague (1926) and Tinbergen (1935). These works produced important advances in behavioural ecology, evolutionary biology and conservation. However, much of our current knowledge is based on a small number of relatively well-studied shorebirds and often relies on modest sample sizes. In future, it is essential to investigate more species and gain larger sample sizes to achieve statistically robust results. Shorebird biologists should also embrace new technical advances and continue building cross-team collaborations. Specifically, we identify six key areas where further research in shorebird breeding systems is urgently required:

1 *Individual differences in sex roles*. While some species show little variation in the sex roles of different individuals, in many others there is substantial individual variation within sexes, and the latter aspect of sex role biology is poorly studied (Hogan-Warburg 1966, Reneerkens *et al.* 2014, Bulla *et al.* 2016, Herridge *et al.* 2016, Gonzalez-Voyer *et al.* 2022, McDonald *et al.* 2023). The extent to which such individual differences are genetically determined (e.g. Küpper *et al.* 2016, Lamichhaney *et al.* 2016) or plastic changes within individuals (e.g. Reneerkens *et al.* 2014) remains unknown. Between the extremes of fixed and plastic sex roles, there undoubtedly lies a spectrum of sex role determination systems with complex gene–environment interactions. To advance this field, we need long-term studies of sex role behaviour using individually marked shorebirds, particularly in longer-lived species that may show greater individual, lifetime sex role variation (Sheldon *et al.* 2022).

2 *Consistent data collection methods to facilitate cross-population analyses*. Unlike many morphological or life history traits, quantifying sex role behaviours is not trivial: researchers tend to adopt different fieldwork protocols to collect data and record behaviours. Such inconsistencies hamper large-scale comparisons between geographically and/or phylogenetically distant taxa. Several initiatives have emerged aiming to facilitate comparability across species, study sites and research groups. For example, protocols have been developed for carrying out field investigations and monitoring (Székely *et al.* 2008, Bart & Johnston 2012), and collecting and coding sex role variables that are adaptable to a variety of species and study sites (Székely & Kubelka 2019, Appendix S1). Consistent data collection protocols will facilitate future analyses using more species and multiple populations in diverse locations. Furthermore, considering the substantial intraspecific variation in shorebird ecology and sex role behaviour, it is essential to replicate studies across multiple populations as this will help to overcome the challenge of generalizing findings from one population to an entire species.

3 *Sex roles and spatial movements*. We need to combine more breeding system studies with detailed analyses of movements and social connectivity between individuals (Kempenaers & Valcu 2017, Cunningham *et al.* 2018, McDonald *et al.* 2020, Méndez *et al.* 2022). Shorebird scientists are at the forefront of migratory animal tracking (Jetz *et al.* 2022, Piersma *et al.* 2022), but compared with other avian groups shorebirds have lagged behind in terms of the new generation of detailed automated tracking of social structure and social networks (Rutz *et al.* 2012, Firth *et al.* 2018, Shizuka *et al.* 2022). Given the key role shorebirds have played in our understanding of the social environment, including ASRs, on breeding biology, future automated tracking studies of shorebird populations provide exceptional potential to further advance our understanding of the feedback between the social environment and reproductive strategies.

4 *Physiological predictors of sex roles and demography*. Recent studies have revealed that avian

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sex determination involves chromosomal, epigenetic and hormonal mediators (Ioannidis *et al.* 2021), but growth in this area is needed to develop our understanding of the ontogeny of sex-biased behaviours and traits (e.g. plumage coloration and mating behaviour). Preliminary research has linked endocrinology with breeding behaviour (Kosztolányi *et al.* 2012, Wang *et al.* 2020), but there are substantial unexplored areas. Likewise, research has begun to unveil the proximate drivers of sex biases in mortality from comparative studies that suggest sex differences in immunocompetence may favour the survival of males over females (Valdebenito *et al.* 2022), although further research on the physiological and immunological predictors of behaviour and demography seem essential.

5 *Better use of genetic/genomic advances*. DNA and RNA sequences are increasingly available for many shorebird species (Moghadam *et al.* 2013, Feng *et al.* 2020) and shorebird biologists should embrace more vigorously the recent advances in sequencing and 'omics' analysis. The use of genetics has largely been restricted to studies of paternity, sexing, phylogeny and population structure in shorebirds. Looking forward, increasing genome data availability offers opportunities to understand the effect of sex roles on molecular evolution and genetic diversity, with implications for population vulnerability and conservation strategies. Given that sequencing techniques are becoming cheaper, and shorebird blood sampling is already widespread for sexing and paternity applications, we expect a rapid growth in shorebird population genomics. Compared with genomics, transcriptome sequencing requires more complex sampling and storing techniques. In addition, the use of less invasive tissue sampling techniques (e.g. blood) must be traded off against the destructive sampling of tissues that may be more informative about sex role variation (e.g. gonads; Harrison *et al.* 2015). Nevertheless, studies of gene expression differences between male and female shorebirds represent an exciting avenue for further research.

6 *Climate change impacts on sex roles*. The global environment is changing rapidly, and monitoring shorebirds in multiple locations across the planet offers great opportunities to follow the impact of global changes on sex roles, including climatic variations, extreme weather, wildlife health and disease. For example, in future, climate change and increasing temperatures may drive changes in patterns of sex biases in incubation and brood care, or make it impossible for some shorebirds to adapt and prevent egg mortality in hot environments (Carroll *et al.* 2018, McCowan & Griffith 2021). Shorebirds inhabit some of the coldest and hottest habitats on the planet (i.e. polar regions and deserts, respectively), so they will be excellent study systems to track the responses of individuals, populations and entire species to climatic variations.

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AUTHOR CONTRIBUTIONS

Tamás Székely: Conceptualization; writing – review and editing; writing – original draft; funding acquisition. **Maria C. Carmona-Isunza:** Writing – original draft; writing – review and editing; visualization. **Noémie Engel:** Writing – original draft; writing – review and editing. **Naerhulan Halimubieke:** Writing – original draft; writing – review and editing; visualization. **William Jones:** Writing – original draft; writing – review and editing; visualization. **Vojtěch Kubelka:** Writing – original draft; writing – review and editing. **Romy Rice:** Writing – original draft; writing – review and editing. **Claire E. Tanner:** Writing – original draft; writing – review and editing. **Zsófia Tóth:** Data curation; writing – original draft; writing – review and editing. **José O.**

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Valdebenito: Writing – original draft; writing – review and editing; visualization; data curation. **Kees Wanders:** Writing – original draft; writing – review and editing. **Grant C. McDonald:** Conceptualization; writing – original draft; writing – review and editing; visualization.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

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ETHICAL NOTE

None.

Data Availability Statement

The data used in this study are available from Székely *et al.* (2022) (data used in Figs 2 and 6), the phylogeny of Jetz *et al.* (2012), Carmona-Isunza *et al.* (2015) (Fig. 3) and Halimubieke *et al.* (2020). Data used in Figure 7 were archived at doi: 10.6084/m9.figshare.24132066 and the map came from Dinerstein *et al.* (2017).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Protocol for collecting behavioural data for the ÉLVONAL shorebird project.

Table S1. Summary of courtship behaviours present in shorebird species by sex.

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