
Sexual Conflict and the Evolution of Breeding Systems in Shorebirds

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I. SEXUAL CONFLICT AND SHOREBIRD BREEDING SYSTEMS

Sexual conflict emerges from the different evolutionary interests of males and females over reproduction (Arnqvist and Rowe, 2005; Chapman *et al.*, 2003). Males usually gain more from polygyny than do females from polyandry (Bateman, 1948; Queller, 1997). The interests of the sexes also differ over care provisioning since parental care is costly, so that each parent often does better by shunting care provisioning to its mate (Houston *et al.*, 2005; Lessells, 1999). Recent theoretical models (Gavrilets and Waxman, 2002; McNamara *et al.*, 2000; Parker and Partridge, 1998) and experimental studies (Arnqvist and Rowe, 2002; Holland and Rice, 1999; Royle *et al.*, 2002) suggest that sexual conflict has profound implications for the evolution of many morphological, behavioral, and life history traits. Our central thesis in this review is that sexual conflict is a powerful paradigm to understand breeding systems. We illustrate this thesis with shorebirds (Aves: Charadriiformes), which have played a central role in the development of breeding system theory.

Shorebirds have long been noted for their extreme diversity in breeding systems. We follow Reynolds (1996) and define breeding system as a description of both social mating system (the form and duration of

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pair-bonds) and parental care (the form and duration of care by each sex) of both sexes. Shorebird mating systems encompass social polygyny (polygyny hereafter; including lekking and territorial polygyny), social polyandry (polyandry hereafter; including classical polyandry and rapid multiclutching) and social monogamy (monogamy hereafter; including double-brooding and lifelong monogamy). This variation has attracted intensive research since the late 1960s (reviewed by [Erckmann, 1983](#); [Pitelka *et al.*, 1974](#); [Oring, 1986](#); [Székely *et al.*, 2006](#)). Initially, researchers focused on describing the mating patterns of individual populations or species, and putting this into an ecological context. Later research adopted experimental manipulations, genetic markers, and phylogenetic comparative methods.

There is still controversy over explanations for why some taxa are socially monogamous with biparental care, whereas others are polygynous or polyandrous with uniparental care ([Andersson, 1994, 2005](#); [Bennett and Owens, 2002](#); [Ligon, 1999](#)). While the concept of sexual conflict is not new ([Bateman, 1948](#); [Davies, 1992](#); [Lessells, 1999](#); [Parker, 1979](#); [Trivers, 1972](#)), the last decade has seen an upsurge of interest in sexual conflict as a driver of evolutionary change, including impacts on breeding systems ([Tregenza *et al.*, 2006](#)). This has led to a burst of theoretical, experimental, and phylogenetic studies (see references above). Although it is increasingly clear that some of the conflicts are played out at the genomic level (e.g., genomic imprinting, [Haig, 2004](#); selfish genetic elements, [Burt and Trivers, 2006](#)), these topics have not been investigated in birds. Thus, shorebirds (or in birds), thus as a necessity we are focusing on nongenomic issues.

Our main objectives are to review both how sexual conflict theory can be used to advance our understanding of the evolution of shorebird breeding systems, and how studies of shorebirds are advancing our understanding of sexual conflict theory. We begin by summarizing sexual conflict theory ([Section II](#)). We then review the diversity of shorebirds, focusing on the distribution of mating systems and parental care ([Section III](#)). In [Section IV](#), we discuss the evidence for conflicts over mating optima in shorebirds. In particular, we highlight field studies of behaviors in shorebirds that enable each sex to exploit, or coerce, the other and consider the evidence for conflict over reproductive rate and clutch size. We also discuss the links between sexual conflict and sexual size dimorphism (SSD). We then consider the role of sexual conflict over parental care in driving breeding system evolution ([Section V](#)). We argue that mating systems and parental care both influence, and are influenced by, mating opportunities and are involved in a coevolutionary feedback loop ([Section VI](#)). Finally, we highlight possible avenues for future research ([Section VII](#)), and provide the

shorebird data in the [Appendix A](#) that were used in our comparative analyses. We anticipate that access to these data will stimulate further research on evolutionary ecology of shorebirds.

II. SEXUAL CONFLICT THEORY

Males and females rarely have identical evolutionary interests over reproduction ([Arnqvist and Rowe, 2005](#); [Chapman *et al.*, 2003](#); [Wedell *et al.*, 2006](#)). Since reproduction is costly, conflict between the parents will arise because each parent will be selected to exploit the other ([Lessells, 1999](#)). Thus, except in species that breed once and then die (or have lifelong obligate monogamy), at least some form of conflict is inevitable ([Rice, 2000](#); [Wedell *et al.*, 2006](#)).

Precise definitions of sexual conflict are controversial and somewhat ambiguous ([Arnqvist and Rowe, 2005](#); [Tregenza *et al.*, 2006](#)). In the context of breeding system evolution, we use the division of pre- and postzygotic conflicts introduced by [Parker *et al.* \(2002\)](#). Prezygotic conflict arises from different mating and fertilization optima for males and females, whereas postzygotic conflict involves differences between the sexes in care provisioning. Many authors also distinguish between intra- and interlocus conflicts ([Arnqvist and Rowe, 2005](#); [Chapman *et al.*, 2003](#); [Wedell *et al.*, 2006](#)). Intralocus conflict arises where the same allele has different effects on the fitness of the two sexes, thus selection favors different values for a single phenotypic trait in males and females ([Arnqvist and Rowe, 2005](#); [Fisher, 1930](#); [Lande, 1980](#); [Wedell *et al.*, 2006](#)). In interlocus conflict the optimal outcome of a male–female interaction differs for the average male and the average female. For the vast majority of organisms we do not know whether mating and parental conflicts are driven by intra- or interlocus conflicts, therefore, these issues are not explored further here.

A. PREZYGOTIC CONFLICT

[Bateman's \(1948\)](#) classic experiments on *Drosophila* demonstrated that the benefits of multiple mating are not always equal for males and females: males increased their reproductive success by increasing the number of mates but females did not. In general, males stand to gain more by multiple mating than females ([Parker, 1979, 2006](#); [Queller, 1997](#)). Indeed, females may be harmed physically if they exceed their mating optima ([Arnqvist and Rowe, 2005](#)). For example, seminal fluid of male *Drosophila melanogaster* reduces both the competitive ability of sperm from other males and female survival due to toxic side effects ([Chapman *et al.*, 1995](#); [Rice, 1996](#)).

The conflict over mating optima can drive rapid evolutionary change. According to the “chase-away” model, preexisting sensory bias (Basolo, 1990, 1995; Ryan and Rand, 1998) in females selects for some form of display trait that enhances male attractiveness (Holland and Rice, 1998). The female response to the most attractive males is to mate in a suboptimal manner, for example by increasing their mating rate. Because of the deleterious effects of mating on female fitness, selection should favor resistance to male attractiveness by increasing the threshold for attractiveness. Selection then favors further exaggeration of the display trait above the new threshold. The cycle of male persistence and female resistance is known as sexually antagonistic coevolution (SAC). Although the chase-away hypothesis refers directly to female choice over a display trait, it has also been suggested that SAC can result in the evolution of male coercion and female avoidance through both behavioral and morphological adaptations in both sexes. Examples of coercion associated with SAC include the evolution of structures for grasping (in males) and avoiding grasping (in females) in water striders (Arnqvist and Rowe, 2002), diving to resist males in some diving beetles (Dytiscidae; Bergsten *et al.*, 2001), and traumatic insemination in bedbugs (Schuh and Stys, 1991). The burgeoning evidence for SAC suggests that it is widespread in nature (see Arnqvist and Rowe, 2005 for some fascinating cases of SAC).

B. POSTZYGOTIC CONFLICT

Postzygotic sexual conflict is an emergent property of the costs of providing parental care against the benefits of deserting. Parental care is beneficial for the survival and development of offspring, but it is costly for the parents because it demands time and energy, and it reduces the chances of exploiting additional mating opportunities (Balshine *et al.*, 2002; Clutton-Brock, 1991). Each sex is therefore selected to shift the burden of care to its mate (Houston *et al.*, 2005; Lessells, 1999). Sexual conflict over care can be resolved by one parent abandoning the brood to its mate, or by a truce whereby both parents remain with their brood and cooperate to raise the young (Chapman *et al.*, 2003; Houston and Davies, 1985; Parker *et al.*, 2002). A more extreme form of resolution may arise where one parent deserts and the other parent is at a disadvantage in rearing the young by itself, so ultimately, both parents abandon, and thus doom, the brood (e.g., Eurasian penduline tit *Remiz pendulinus*, Franz, 1991; Szentirmai *et al.*, 2005). Note, however, that resolution in this sense does not mean that there is no longer a conflict, rather that the phenotypic expression of conflict is in some way a compromise in the fitness optima of the two sexes.

The outcomes of sexual conflict over care have important implications for breeding system evolution. Recent studies suggest that parental care and social mating systems both influence, and are influenced by, mating opportunities such that mating systems and parental care are involved in a conflict driven by a negative feedback relationship (Section VI; Alonzo and Warner, 2000; Kokko and Jennions, 2003; Székely *et al.*, 2000a).

III. WHY STUDY SHOREBIRDS?

Shorebirds have a long history of interest among evolutionary biologists and ornithologists alike (Hockey *et al.*, 1995; Kam *et al.*, 2004; Pringle, 1987). Recent phylogenetic analyses (Fig. 1; Baker *et al.*, 2007; Fain and Houde, 2004; Paton and Baker, 2006; Paton *et al.*, 2003; Thomas *et al.*, 2004a,b) show that shorebirds have evolved along three main lineages consisting of approximately 350 species found on all continents: Scolopaci (sandpipers, jacanas, painted-snipes, seedsnipes, and plains-wanderer), Lari (coursers and pratincoles, gulls, alcids, terns, skimmers, and skuas), and Charadrii (plovers, oystercatchers, stilts and avocets, sheathbills, and magellanic plover). There is also compelling molecular evidence that buttonquails (Turnicidae), which have previously been included in either the Gruiformes, the Galliformes, or as their own order (Turniciformes; Monroe and Sibley, 1993), are most likely basal Lari (Baker *et al.*, 2007; Fain and Houde, 2004; Paton and Baker, 2006; Paton *et al.*, 2003). Across these three clades, shorebirds display exceptional diversity of life histories, ecology, and breeding systems (Erckmann, 1983; Oring, 1986; Pitelka *et al.*, 1974; Székely and Reynolds, 1995).

A. SHOREBIRD BREEDING SYSTEMS

The diversity of mating systems and parental care strategies in shorebirds has made these birds a popular group for studies of sexual selection. Indeed, Darwin (1871) illustrated his theory of sexual selection by reference to sex-role reversal in greater painted-snipe *Rostratula benghalensis* and to the lekking behavior of ruff *Philomachus pugnax*:

The polygamous ruff (*Machetes pugnax*) 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.

In shorebirds, as in most animals, mating systems tend to match closely with parental care. Polygynous species are defined as those in which males form multiple pair-bonds within a breeding season, or have sequential

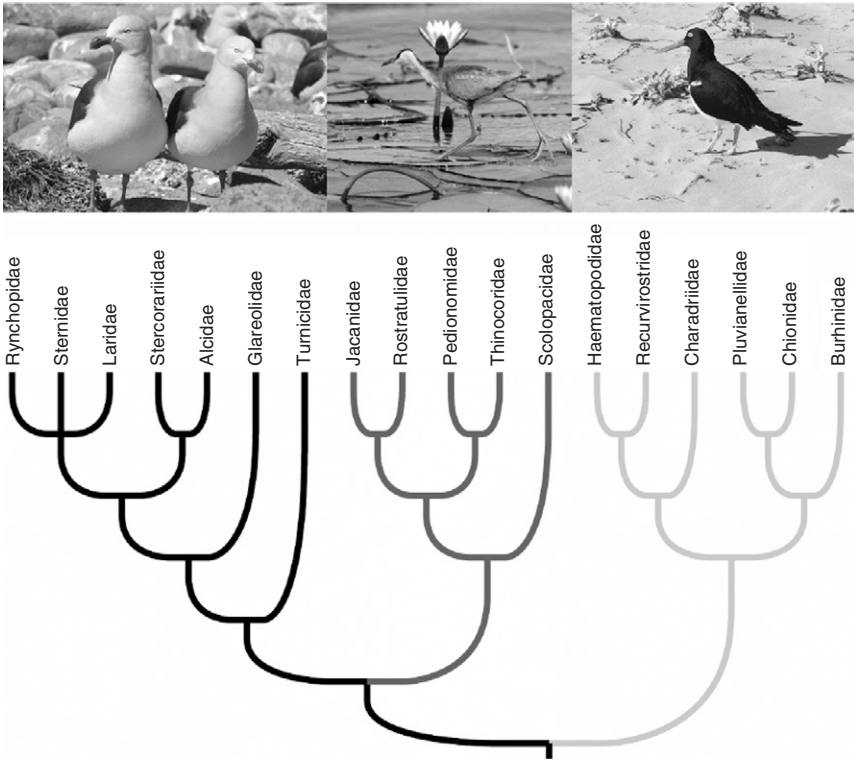


FIG. 1. A phylogenetic tree of shorebird families based on [Ericson *et al.* \(2003\)](#), [Paton *et al.* \(2003\)](#), and [Paton and Baker \(2006\)](#). Note that the monotypic family Dromadidae is missing because it has not been included in any molecular phylogenetic study to date. The differential shading illustrates the three major clades: light gray—Charadrii; dark gray—Scolopaci; and black—Lari. This is a hypothesis, undergoing perpetual improvement. Photographs (left to right): dolphin gull *Larus scoresbii* (Tamás Székely); African jacana (Aron Székely); and Magellanic oystercatcher *Haematopus leucopus* (Tamás Székely).

copulations while displaying on leks with multiple females. In monogamous species one male and one female form a pair-bond that lasts the duration of at least one breeding season. In polyandrous species, females form pair-bonds with more than one male in a breeding season. Shorebird mating systems range from full polygyny (e.g., territorial polygyny: pectoral sandpiper *Calidris melanotos*, northern lapwing *Vanellus vanellus*; lekking: ruff, buff-breasted sandpiper *Tryngites subruficollis*), through monogamy (oystercatchers, many plovers, gulls, alcids), to classical polyandry (e.g., phalaropes *Phalaropus* spp., African jacana *Actophilornis africanus*). Parental

care associated with these mating systems ranges from female-only care (e.g., jack snipe *Lymnocryptes minimus*, sharp-tailed sandpiper *Calidris acuminata*) to male-only care (e.g., plains-wanderer *Pedionomus torquatus*, Eurasian dotterel *Eudromias morinellus*). The diversity of mating systems in the three major clades of shorebirds is shown in Fig. 2. Note that in socially monogamous species, the duration of care provided by the sexes may be fully biparental, but is often biased toward predominantly male care (e.g., dunlin *Calidris alpina*, semipalmated plover *Charadrius semipalmatus*).

Shorebirds are frequently cited as the most appropriate group for studying polyandry and male-only care. Overall, the proportion of polyandrous shorebirds is marginally higher than that of birds as a whole (around 5% in shorebirds whereas probably less than 5% of all bird species; Bennett and Owens, 2002). Yet, among the clade that includes sandpipers and allies, 10–15% of known species are polyandrous (Fig. 2).

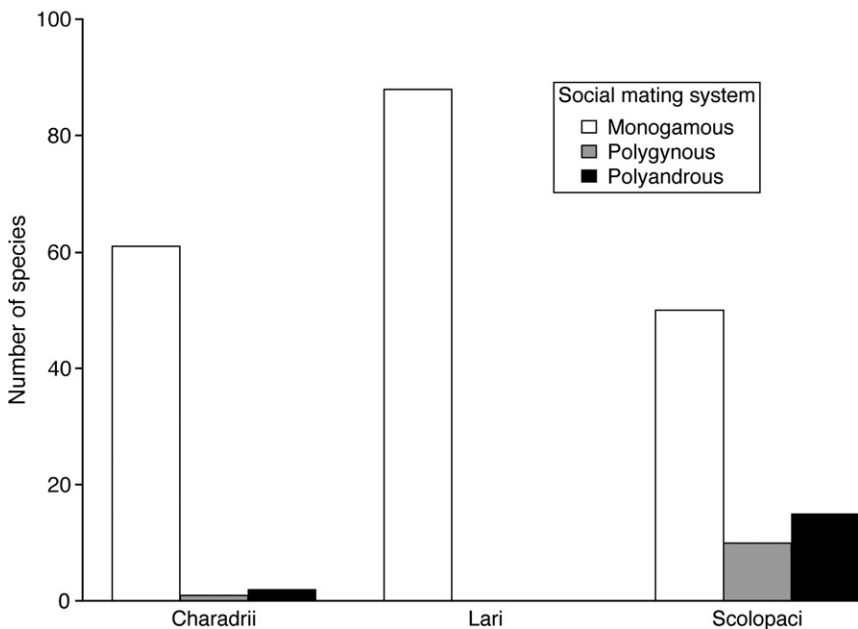


FIG. 2. The distribution of social mating system in major shorebird clades, including 11 polygynous species (female care), 199 monogamous species (biparental care), and 17 polyandrous species (male care). Note that data are not available for some species including the family Turnicidae which are not included.

The Lari clade, to which the Turnicidae evidently belong, is normally regarded as being conservative with regard to breeding system since most species are typically monogamous with biparental care. The addition of the Turnicidae to this clade is intriguing since at least one species of buttonquails (*Turnix sylvatica*) is likely polyandrous and the chicks are raised by the male only (Cramp and Simmons, 1980).

The distribution of polyandry in shorebirds is particularly striking when one considers that polyandrous species occupy a wide range of habitats around the world (Erckmann, 1983). There are polyandrous shorebirds from the tropics (e.g., pheasant-tailed jacana *Hydrophasianus chirurgus*, bronze-winged jacana *Metopidius indicus*) to northern temperate zones (spotted sandpiper *Tringa macularia*, Wilson's phalarope *Steganopus tricolor*) to the Arctic (e.g., red phalarope *Phalaropus fulicaria*, red-necked phalarope *Phalaropus lobatus*). Polyandrous species may breed in lowland grasslands (e.g., mountain plover *Charadrius montanus*), alpine heathland (e.g., Eurasian dotterel), or in tropical marshes (greater painted-snipe, African jacana). This raises the question, why do shorebirds, more than other birds, show such propensity for divergence in breeding systems? In Section IV, we argue that this divergence is driven by the high potential for conflict among species in which the need for biparental care is relaxed.

Rates of multiple paternity (MP) and extra-pair paternity (EPP) are also variable in shorebirds. Among socially monogamous species rates of MP are low: $2.9 \pm 2.8\%$ (SD) of chicks and $4.6 \pm 3.4\%$ of broods were extra pair [$n = 5$ and 11 species, using data from Griffith *et al.* (2002) and Küpper *et al.* (2004)]. These frequencies are lower than reported from socially monogamous birds other than shorebirds (chicks: $12.0 \pm 13.5\%$, $n = 89$ species, Mann-Whitney U test, $z = 2.296$, $p = 0.022$; broods: $20.4 \pm 21.8\%$, $n = 83$ species; $z = 2.272$, $p = 0.023$). In contrast, rates of MP are higher among polyandrous shorebirds (Table I; Emlen *et al.*, 1998; Oring *et al.*, 1992), and higher still among lekking species such as the ruff (Lank *et al.*, 2002) and buff-breasted sandpiper (Lanctot *et al.*, 1997).

The different duration of male and female care (Fig. 3) and the variety of mating systems suggest the costs and benefits to desertion are not identical for the sexes in different species. Thus, shorebirds are likely to express a wide continuum of sexual conflict over mating and care. Taken together, the immense natural variation in shorebirds with respect to mating and parental behavior makes them an ideal group to investigate the role of sexual conflict in breeding system evolution.

TABLE I
MULTIPLE PATERNITY IN SHOREBIRDS^a

Species	Multiple paternity (broods, <i>n</i>) (%)	Multiple paternity (chicks, <i>n</i>) (%)	MF	CA	FC	ST	SS	References
Spotted sandpiper: <i>Tringa macularia</i>	11.1 (1/9)	2.9 (1/34)	N	N	–	Y	Y	Oring <i>et al.</i> , 1992
Wattled jacana: <i>Jacana jacana</i>	24.3 (18/74)	1.3 (24/235)	N	N	Y	–	N	Emlen <i>et al.</i> , 1998
Wilson's phalarope: <i>Steganopus tricolor</i>	0 (0/17)	0 (0/51)	N	N	N	–	Y	Delehanty <i>et al.</i> , 1998
Red phalarope: <i>Phalaropus fulicarius</i>	8.6 (6/70)	33.3 (6/18)	–	Y	–	–	Y	Dale <i>et al.</i> , 1999
Red-necked phalarope: <i>Phalaropus lobatus</i>	6 (4/63)	1.7 (4/226)	Y	Y	Y	Y	Y	Schamel <i>et al.</i> , 2004
Eurasian dotterel: <i>Charadrius morinellus</i>	9.1 (2/22)	4.6 (2/44)	Y	Y	N	Y	–	Owens <i>et al.</i> , 1995
Kentish plover: <i>Charadrius alexandrinus</i>	3.4 (3/89)	1.3 (3/229)	–	–	–	–	–	Küpper <i>et al.</i> , 2004
Ringed plover: <i>Charadrius hiaticula</i>	0 (0/21)	0 (0/57)	N	N	N	–	–	Wallander <i>et al.</i> , 2001
Semipalmated plover: <i>Charadrius semipalmatus</i>	4.2 (1/24)	4.7 (4/85)	Y	Y	Y	–	–	Zharikov and Nol 2000
Western sandpiper: <i>Calidris mauri</i>	8 (3/40)	5 (5/98)	Y	Y	–	–	–	Blomqvist <i>et al.</i> , 2002b
Purple sandpiper: <i>Calidris maritima</i>	3.7 (1/27)	1.2 (1/82)	N	Y	N	N	–	Pierce and Lifjeld 1998
Common sandpiper: <i>Tringa hypoleucos</i>	6.7 (1/15)	1.8 (1/53)	–	–	–	–	–	Blomqvist <i>et al.</i> , 2002a
Common sandpiper: <i>Tringa hypoleucos</i>	18.5 (5/27)	15.7 (13/83)	–	–	–	Y	–	Mee <i>et al.</i> , 2004
Eurasian Oystercatcher: <i>Haematopus ostralegus</i>	3.8 (1/26)	1.5 (1/65)	–	–	–	–	–	Heg <i>et al.</i> , 1993
Great snipe: <i>Gallinago media</i>	28.6 (2/7)	–	–	–	–	–	–	Cited in Lank <i>et al.</i> , 2002
Ruff: <i>Philomachus pugnax</i>	50 (17/34)	–	–	–	–	–	Y	Lank <i>et al.</i> , 2002
Ruff: <i>Philomachus pugnax</i>	51.5 (34/66)	–	–	–	–	–	–	Thuman, 2003
Buff-breasted sandpiper: <i>Tryngites subruficollis</i>	40.4 (19/47)	–	–	–	–	–	–	Lancot <i>et al.</i> , 1997
Brown skua: <i>Catharacta Antarctica</i>	0 (0/16)	0 (0/45)	–	–	–	–	–	Millar <i>et al.</i> , 1994
South Polar skua: <i>Catharacta maccormicki</i>	7.7 (2/13)	7 (2/14)	–	–	–	–	–	Millar <i>et al.</i> , 1997
Western gull: <i>Larus occidentalis</i>	0 (0/22)	0 (0/33)	–	–	–	–	–	Gilbert <i>et al.</i> , 1998
Common gull: <i>Larus canus</i>	8.3 (2/24)	3.6 (2/55)	–	–	–	–	–	Bukacinska <i>et al.</i> , 1998
Common murre: <i>Uria aalge</i>	7.8 (6/77)	7.8 (6/77)	–	–	–	–	–	Birkhead <i>et al.</i> , 2001
Common tern: <i>Sterna hirundo</i>	0 (0/10)	–	–	–	–	–	–	Griggio <i>et al.</i> , 2004
Little auk: <i>Alle alle</i>	0 (0/26)	0 (0/26)	–	–	–	–	–	Lifjeld <i>et al.</i> , 2005

^aPaternity assurance behaviors include: mate following (MF); close association with female (CA); frequent copulation (FC); strategic timing of copulation (ST); and sperm storage (SS). Studies in which observations of paternity assurance behaviors were recorded (Y); studies in which behaviors were not observed (N); and no information (–).

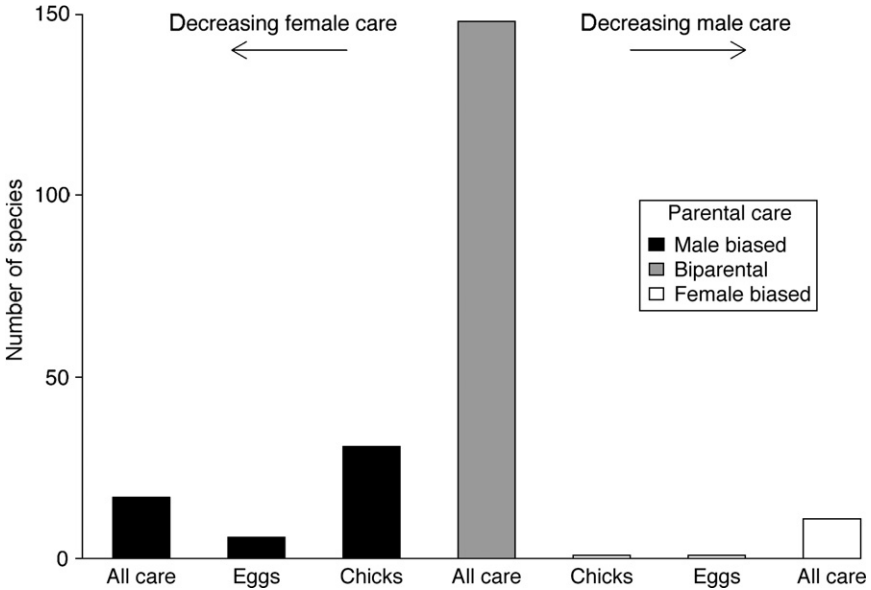


FIG. 3. Distribution of parental care in shorebirds (updated from Székely and Reynolds, 1995). “Male biased” means that the male contributes all care either until the chick fledge (“All care”), or the majority of care with females deserting before hatching (“Eggs”), or before fledging (“Chicks”). The same terminology applies to “Female-biased” care. In biparental taxa both parents provide care until the chicks fledge.

IV. CONFLICT OVER MATING

A. CONFLICT OVER MATING OPTIMA

1. Multiple Mating

Bateman’s classic experiments on *Drosophila* suggested that males should gain more by multiple mating than females (Bateman, 1948). However, this theory is no longer taken for granted; Sutherland (1985) showed that higher variance in mating success in males than females may occur as a result of random mating rather than any reflection of the relative investment of each sex. Furthermore, it now seems clear that both males and females can gain from multiple mating (e.g., the polyandrous pipefish *Syngnathus typhle*; Jones *et al.*, 2000) and promiscuity (Jennions, 1997; Tregenza and Hosken, 2005). In shorebirds, female gains from multiple mating are perhaps most obvious in polyandrous species, but there is also evidence of females holding the upper hand in conflict over mating in lekking species. The highest rates of multiple paternity among shorebirds are found in

lekking species: ruff, buff-breasted sandpiper, and great snipe. Gowaty (1996) proposed that where females are largely independent of males, rates of MP are expected to be high (the “constrained female” hypothesis). Lekking shorebirds fit well into Gowaty’s hypothesis since males do not contribute to parental care and consequently have little leverage over female choice. In these lekking shorebirds, males do attempt to disrupt copulations, although rates vary across species. The ruff has very low rates of copulation disruption by males (2.7%; Widemo, 1997) despite showing the highest recorded degree of multiple mating (Table I). Rates of copulation disruption are highest in the buff-breasted sandpiper (43.2%; Lanctot *et al.*, 1998) and intermediate in the great snipe (28.6%; Saether *et al.*, 1999). Disruption attempts by males may simply be due to male–male competition, but it is also likely that some are by males trying to prevent females with whom they have already mated copulating with other males.

Among sex-role reversed shorebirds, it is the female that gains most from nesting with multiple partners. For instance, in the polyandrous spotted sandpiper female reproductive success increased with the number of mates, although polyandrous females also tended to be older and more experienced than monogamous ones. Males were limited to only one clutch per year, regardless of age or experience although some males increased reproductive success through sperm storage and subsequent fertilization of eggs in later clutches (Oring and Lank, 1986). Similarly, red-necked phalarope females may have successful clutches with two consecutive males per year whereas males never raise young from more than one clutch (Reynolds, 1987). This dichotomy sets the stage for strong sexual conflict over mating opportunities. For example, female red-necked phalaropes often approach incubating males, and are driven off with conspicuous squeaking and fluttering displays called “driving flights” (Reynolds, 1987). These displays (also observed in red phalaropes; Kistchinski, 1975) could not be explained by an alternative explanation of prevention of infanticide by females, which is considered in the context of sexual conflict in Section IV.A.3.

In both spotted sandpipers and red-necked phalaropes, the operational sex ratio (OSR; ratio of sexually active females to males; Emlen and Oring, 1977) becomes more female biased in the population as males take up incubation and thereby drop out of the mating pool (Lank *et al.*, 1985; Reynolds, 1987). Lank *et al.* (1985) showed that within a breeding season the reproductive rate of females declined as the sex ratio became more female biased, and suggested that this was due to the increase competition between females for males. It has been noted that the frequency of polyandry in small populations may be highest in locations and years when there are male-biased sex ratios (e.g., northern jacanas *Jacana spinosa*,

Jenni and Collier, 1972; red phalaropes, Schamel and Tracy, 1977; red-necked phalaropes, Reynolds, 1987). We can therefore expect the extent of sexual conflict over multiple pair-bonds to show similar variation within species, although we acknowledge that the evidence linking OSRs to mating systems comes primarily from polyandrous species.

The availability of mates appears to be important in determining the direction and strength of sexual conflict over mating, as the examples discussed above illustrate, and it is therefore particularly relevant to our understanding the evolution of polyandry. This goes against a previous hypothesis proposed for shorebirds that in species with fixed clutch sizes, the only way for females to increase their reproductive output is to seek multiple mates (Alcock, 2005; Davies, 1991; Erckmann, 1983; Oring, 1986). The latter hypothesis also ignores an obvious conflict between the sexes over which parent should desert the brood—which is the central focus of this review. The key assumption of the clutch-size hypothesis is that shorebirds have a fixed upper limit on the number of eggs that can be laid and incubated. This upper limit is generally considered to be four eggs (Maclean, 1972), although across species clutch size ranges from one to four (Appendix A), and they even vary within species.

In our opinion, the clutch-size constraint hypothesis lacks generality. First, several bird taxa with “fixed” (i.e., less variable) clutch sizes do not exhibit sex-role reversal (e.g., bustards, albatrosses, and many seabirds). Furthermore, polyandry is absent (or rare) among Lari and Charadrii, even though these taxa lay clutches that are as “fixed” as those of sandpipers Scolopaci. Second, the argument focuses on females only, assuming that males are widely available and they will “automatically” assume the full care of eggs. Given that the males in general can gain more by being polygamous than females (Queller, 1997), it is not trivial to explain why the males “sacrifice” themselves for the sake of their mate. Third, polyandry with multiple mates occur in birds that have variable clutch sizes, such as tinamous, coucals, the penduline tit, and several passerines (Andersson, 2005; Owens, 2002; Szentirmai *et al.*, 2005). Taken together, the fixed clutch size may contribute to the evolution of mate change and polyandry, because females in species with fixed clutch size may gain more from multiple mates than females in species with variable clutch sizes, but it cannot fully explain polyandry.

2. *Multiple and Extra-Pair Paternity*

Westneat and Stewart (2003) proposed that extra-pair copulations (EPCs) result from sexual conflict in a three-way interaction between the female, pair male, and extra-pair male. It is in the best interests of both sexes to produce offspring with a high chance of survival and future reproductive success, but males gain an additional benefit from fertilizing as

many eggs as possible. Conflict arises if the females' criteria are not fully met by mating with a particular male (Schamel *et al.*, 2004; Westneat and Stewart, 2003). Thus, females may often benefit from mating with an extra-pair male, for example through guarding against infertility of the social mate (Wetton and Parkin, 1991), increased genetic diversity of the offspring (Blomqvist *et al.*, 2002a; Westneat *et al.*, 1990; Williams, 1975), enhanced genetic compatibility between the parents (Kempnaers *et al.*, 1999; Tregenza and Wedell, 2000), obtaining good genes (Birkhead and Møller, 1992; Hamilton, 1990; Westneat *et al.*, 1990), or direct benefits to the offspring (Burke *et al.*, 1989; Colwell and Oring, 1989). However, extra-pair mating itself results in conflict between the pair due to selection on pair males to reduce the risk of cuckoldry. Indeed, we suggest that sexual conflict over extra-pair mates is consistent with a form of chase-away selection: first male paternity assurance behaviors evolve (e.g., high rates of within-pair copulations), then females counteract with sperm storage or cryptic mate choice, males escalate the conflict by further paternity assurance behaviors (e.g., delayed copulation) and the cycle continues.

There is ample scope for conflict over multiple and extra-pair mating in shorebirds, judging from the numerous reports of MP (Table I). The highest levels of MP occur in lekking species such as the ruff (50% of broods with at least one extra-pair chick) and the buff-breasted sandpiper (40% of broods). In general, MP appears to incur greater costs for pair males in species with polygamous mating systems. For example, in the wattled jacana *Jacana jacana*, MP was 0% in monandrous pairs, whereas in polyandrous groups extra-pair males sired 41% of broods and 17% of chicks (Emlen *et al.*, 1998). In bronze-winged jacobins, females copulated with all males in their harem before laying their first clutch, leading to a high risk of cuckoldry for all males within the group (Butchart, 1999). In the wattled jacana, the main source of MP was from co-mates with whom females copulated at exceptionally high rates (1.3 per hour; Emlen *et al.*, 1998). High copulation rates have also been recorded in the polyandrous red phalarope (Schamel *et al.*, 2004), and in the socially monogamous semipalmated plover (Zharikov and Nol, 2000). In some species, notably the red-necked phalarope, high copulation rates occur within pairs rather than with extra-pair mates: this is presumably a form of paternity assurance (Reynolds, 1987).

The risk of being cuckolded is particularly high for males breeding late in the season if females store sperm from earlier copulations. For example, male spotted sandpipers that pair early in the breeding season cuckolded their mate's subsequent mates via stored sperm (Oring *et al.*, 1992). Females of all three species of phalarope are thought to use sperm stored from earlier mates to fertilize eggs late in the breeding season (Dale *et al.*, 1999;

Delehanty *et al.*, 1998; Schamel *et al.*, 2004; see Table I). This sets up a strong sexual conflict between females and mates late in the breeding season and favors male choice against females that have already mated. This behavior was noted in the red-necked phalarope by Whitfield (1990) but was not detected in the same species by Schamel *et al.* (2004). It is not yet known how males may distinguish between already mated and unmated females. Nonetheless, if males can detect females that have already mated, then females should be selected to conceal their mating status. This response by males to sexual conflict could place a strong cap on the frequency of polyandry in this species.

Males can minimize sexual conflict over paternity by strategically timing their copulation attempts. Owens *et al.* (1995) suggested that in the Eurasian dotterel, males only attempt to copulate with females after having been paired for several days. By strategically delaying copulation, males can gauge whether the clutch is likely to have been sired by a previous mate. If the clutch is laid too early then the male may desert because the clutch is unlikely to be his. The costs of desertion may be lower for males than females, as female-biased OSRs in this species imply that males will be able to find new mates more readily than can females. Such tactics suggest that the benefits of EPCs for females may be offset by the possible loss of male care (Delehanty *et al.*, 1998). Females, however, may be able to reduce the risk of male desertion by maintaining a short distance from their mate, thereby providing greater paternity assurance (Dale *et al.*, 1999; Owens *et al.*, 1995; Schamel *et al.*, 2004). Strategic timing of copulations has also been reported in the spotted sandpiper, where male copulation attempts coincide with the female fertile period (Oring *et al.*, 1994). Similarly, the copulation rate of paired males in the common sandpiper increases just before and during egg laying (Mee *et al.*, 2004).

Individual-based focus on sexual conflict over EPP can be scaled up to species-specific differences in morphology. Both sperm length (Johnson and Briskie, 1999) and testis size (Cartar, 1985) are greater in nonmonogamous species than in monogamous ones, even after controlling for allometry with body size. This is consistent with the observation that rates of MP tend to be highest in polygamous species (Table I), implying intense sperm competition. Indeed, the largest testes (Cartar, 1985; Johnson and Briskie, 1999) and longest sperm (Johnson and Briskie, 1999) are found in the ruff, a species that breeds on leks, and is also notable for high rates of EPP (50% of broods, Lank *et al.*, 2002; 51.5% of broods, Thuman, 2003) and for sperm storage by females. It is interesting to compare how the interpretations of these results differed over the 14 years that spanned the 2 studies. Cartar (1985) suggested that larger testes had evolved in response to selection on males in polygynous species to be able to avoid running out of sperm. In the 1980s,

few people were thinking about sperm competition in birds, and Cartar's pioneering comparative study was therefore not framed in terms of sexual conflict. With the advent of DNA paternity analyses through the 1990s, it became clear that extra-pair fertilizations could be common, leading to the emphasis on sperm competition that was evident in Johnson and Briskie's study (Johnson and Briskie, 1999).

While shorebirds have been supportive models for advancing general theories of conflicts over EPP, several issues remain unresolved. While it seems possible that sperm storage could be widespread in shorebirds, there is little hard evidence about this, and we do not know the extent to which stored sperm may be swamped by subsequent mates or used preferentially by females. Sperm storage is clearly an important part of the three-player interaction identified by Westneat and Stewart (2003). Furthermore, data are needed on the costs and benefits of EPCs for females. Do females use extra-pair mating as a means for assessing and acquiring future mates, as has been suggested in the spotted sandpiper (Colwell and Oring, 1989)? Alternatively, if females form pair-bonds with relatives they may avoid the cost of inbreeding by copulating with unrelated males (Blomqvist *et al.*, 2002a). Why pair-bonds between close relatives should occur in the first place is contentious, although it may simply reflect a lack of alternatives (Blomqvist *et al.*, 2002a). Intensive field studies including paternity analysis and behavioral observations of the kind carried out by Schamel *et al.* (2004) would help resolve these issues.

3. *Infanticide*

Infanticide is an extreme form of sexual conflict that was first highlighted among polygynous mammals in which males are behaviorally dominant over females (e.g., rodents, primates, and carnivores; Hrdy, 1979; Packer and Pusey, 1984). Males in these species kill unrelated offspring, leading to faster reproduction by their new mates. Emlen *et al.* (1989) hypothesized that in sex-role reversed jacanas the females, which are larger and behaviorally dominant over males, may commit infanticide for similar reasons (Stephens, 1982). To test this hypothesis, Emlen *et al.* experimentally removed harem-holding female wattled jacanas, and followed the consequences. As predicted, new females quickly overtook the vacant territories, they killed or evicted the broods of usurped males, and solicited copulations within two days of driving off or killing the males' offspring. In three of four broods, the males intervened by attacking the female or through distraction behavior. In one brood the male did nothing and allowed the female to drive the brood away. This brood was the oldest of those in the study (35–40 days old compared to a maximum of 30 days in the other 3 broods), suggesting that those chicks may have had some chance of survival. This study convincingly showed female-driven infanticide in an experimental

situation. The frequency of infanticide in natural populations and its implications for reproductive success of males and females, however, remain to be quantified. It would be interesting to perform tests analogous to those of Emlen *et al.* (1989) but with a male-territorial polygynous species such as the pectoral sandpiper, to see whether males are infanticidal in species with this breeding system.

B. MATE CHOICE AND SEXUAL SIZE DIMORPHISM

Shorebird species span nearly the entire range of sexual size dimorphism (SSD) shown by the world's birds (Székely *et al.*, 2004). This includes extremes in both male- and female-biased dimorphism. Sexual dimorphism can lead to intralocus sexual conflict since one or the other sex may not be at its optimum body size (Arnqvist and Rowe, 2005; Fairbairn, 1997; Wedell *et al.*, 2006). Thus, the extreme range of SSD in shorebirds implies a variety of conflicts over body size optima. These are difficult to discern, because body size is a complex trait controlled by multiple loci and linked to fitness in many ways. Here, we focus on the best-understood links between SSD and sexual selection in each sex.

Recent evidence, notably from a series of comparative studies, suggests that sexual selection is the main driver of SSD in shorebirds, including species in which males are the most competitive sex but are smaller than females (Figuerola, 1999; Lindenfors *et al.*, 2003; Székely *et al.*, 2000b, 2004). The hypothesis that SSD results from sexual selection was proposed by Payne (1984) and Jehl and Murray (1986). They suggested female-biased SSD evolves as a response to selection for male display agility. The size-agility-sexual dimorphism hypothesis requires first that sexual selection favors more acrobatic flight displays, second that small male size enhances flight agility, and third that this results in the evolution of males that are smaller than females in species with acrobatic displays. Grønstøl (1996) confirmed the first assumption that display agility is important for mating success. He analyzed video recordings of song-flights in male northern lapwings and found that an energetically demanding component of the flight display, the roll angle in the alternating flight, significantly predicted both the number of mates attained by the male and the clutch laying date of his mate. Lanctot *et al.* (2000) suggested that song-flights in the western sandpiper *Calidris mauri* are more likely used to attract mates than to defend territories (i.e., they are effectively display flights) since the frequency of song-flights by males peaked during the pair formation period, rather than earlier when territories were established. The next step to confirming the size-agility-sexual dimorphism hypothesis was provided by Blomqvist *et al.* (1997), who showed that both display rate and the time spent displaying decreased with male size in the dunlin.

The final step to confirmation of the hypothesis has been provided by comparative studies among species. For example, in a study of socially monogamous shorebirds, [Figuerola \(1999\)](#) found that female-biased SSD was associated with more acrobatic displays by males. [Székely *et al.* \(2000b\)](#) showed that males were larger (relative to females) in polygynous taxa, compared with monogamous or polyandrous taxa, whereas male size was smaller (relative to female size) in polyandrous taxa. However, in taxa in which males perform acrobatic flight displays, males are smaller relative to females than in taxa with nonacrobatic or ground displays ([Fig. 4](#)). The interaction between social mating system, a proxy for mating competition, and selection for display agility has been argued to drive a pattern between body size and SSD, termed Rensch's rule ([Székely *et al.*, 2004](#)). Rensch's rule is an allometric trend in body

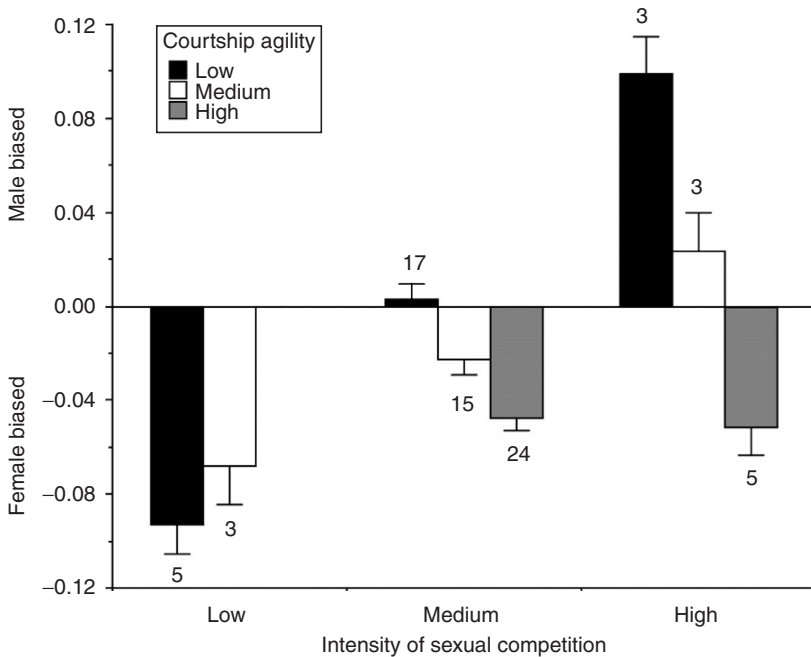


FIG. 4. Sexual dimorphism in body mass [mean \pm SE $\log_{10}(\text{male mass}) - \log_{10}(\text{female mass})$] in relation to the intensity of sexual competition and male agility. Intensity of sexual competition refers to competition between males and is based on the social mating system of each species (low = polyandrous; medium = monogamous; high = polygynous). The numbers of species are given below (or above) each bar. From [Székely *et al.* \(2004\)](#); copyright © 1993–2005 by The National Academy of Sciences of the United States of America, all rights reserved).

size in which the degree of SSD increases with body size when males are the larger sex but decreases with body size when females are the larger sex.

Taken together, the evidence is consistent with the hypothesis that mate choice is an important factor in determining the direction and extent of SSD in shorebirds. However, one important caveat is that many shorebirds spend long periods away from the breeding grounds and we know little about how body size is affected by selection outside the breeding season (Székely *et al.*, 2000b). Future analyses would benefit from taking into account data on, for example, sex differences in resource use on the nonbreeding grounds and differential migration (Nebel, 2007).

There is some evidence that the extent of SSD is mediated by both natural selection and sexual selection. In a comparative study of 71 shorebird species in which the males incubate the eggs, Lislevand and Thomas (2006) demonstrated that egg size increases as the degree of female-biased size dimorphism decreases. Lislevand and Thomas (2006) imply that this pattern is driven primarily by increases in male size, since female size also increases with egg size in the same model. Large males could be more efficient incubators, resulting in selection for increased male size. This implies that selection on incubation efficiency operates in opposition to selection for display agility. An alternative explanation is that male body size is being dragged along by sexual selection that favors larger females. In polyandrous species, males may be close to their natural selection optima, and pull females toward a smaller size than they would achieve if sexual selection for large female size were unconstrained by genetic correlations. Lindenfors *et al.* (2003) refer to this as the chauvinistic rubber band hypothesis since it focuses on selection acting on males with the females dragged along through a genetic correlation. The authors expressed a degree of skepticism about their own hypothesis, since it is not clear why only females would be subject to this effect.

Sexual selection and mate choice over traits other than display agility may also mediate the extent to which conflict of body size occurs. In particular, sexual conflict over body size may be minimized where sexual selection favors contrasting pigmentation in males with acrobatic flights. Graul (1973a) argued that male displays could be amplified by dark, or contrasting pigmentation. Bókony *et al.* (2003) found strong support for Graul's hypothesis using 101 species of Charadrii. After controlling for phylogenetic nonindependence, they found that aerial flight displays were associated with both more extensive plumage melanization and increased melanin dichromatism. Similar relationships occur among bustards (Dale, 2006). These comparative studies suggest that plumage characteristics play an important role in mate choice or territorial displays and may consequently

influence body size evolution. Sexual selection on agility may be less intense in species with contrasting pigmentation because of the amplification effect of pigmentation contrast on display flights (Bókony *et al.*, 2003; Graul, 1973a). Thus, based on Graul's logic, we predict that in species where males perform acrobatic displays, the degree of female-biased SSD will decrease with increases in the degree of contrast in pigmentation. This hypothesis might also be extended to traits other than pigmentation that could exaggerate the complexity of flight displays.

To date only a few studies have sought to test explicitly the role of other traits such as color patterns and plumes in mate choice in shorebirds. For example, female golden plovers *Pluvialis apricaria* and Eurasian dotterels prefer males with brighter or more extensively melanized plumage (Edwards, 1982; Owens *et al.*, 1994). Reynolds (1987) measured seven characteristics of plumage of male and female red-necked phalaropes, and found evidence of assortative mating where large females mated with dull males. The interactions between different putative sexually selected traits warrant further investigation, particularly with respect to the mediating effects they may have on sexual conflict over body size.

V. PARENTAL CARE

A. TUG-OF-WAR OVER CARE

Since it is in the best interests of each parent to have its partner pay the costs of raising the young (Houston *et al.*, 2005; Lessells, 1999), the patterns of parental care at the population level might be considered as the resolution of a 'tug-of-war'. In general, we would expect that offspring benefit most from biparental care. Erckmann (1981) used removal experiments to show that neither males nor females could (or would) raise a clutch alone in western sandpiper *C. mauri*, although males attended the clutch for longer than males. Lessells (1983) found consistent results in Kentish plover *Charadrius alexandrinus* by removing either the male or the female during incubation: single parents struggled to continue incubating the clutch, and males persisted incubation longer than females. More recent studies have shown that survival of Kentish plover chicks is higher in biparental families than uniparental families (Székely and Cuthill, 1999; Székely and Williams, 1995). The tug-of-war leaves its imprint in two ways. First, either parent can try to stop its partner from deserting by interfering with mate attraction or using direct aggression (Chapman *et al.*, 2003). Second, a parent may increase its parental effort following desertion by its partner. Houston and Davies (1985) showed that parental cooperation in rearing young is

only stable if, when one parent reduces its parental effort, the other parent increases its effort to compensate. However, compensation is predicted to be incomplete (Houston *et al.*, 2005).

Behaviors used by parents to manipulate one another may involve sophisticated signals, or sheer force. Males of the polyandrous bronze-winged jacana use a call, termed a “yell,” to attract females to mate (Butchart *et al.*, 1999). Yelling for sex may signal male quality since the males that yell at the highest rate receive most copulations. Males with the highest yell rates were also subject to intrusions by other females. The territorial female’s response can be interpreted as an attempt to prevent other females from copulating with males in their territory. By preventing harem males from copulating with other females, the males are coerced into remaining with the territory holder and raising her young. In northern lapwings, which commonly are polygynous, females were aggressive toward males when presented with a female dummy near to their nest (Liker and Székely, 1997). Liker and Székely suggested that this female aggressive behavior is an attempt to monopolize paternal care by actively preventing the males from exploiting potential mating opportunities.

Field studies and phylogenetic comparative analyses suggest that compensation for the loss of the partner occurs in shorebirds. Kosztolányi *et al.* (2003) experimentally removed one parent (the male or the female) from their nests in the Kentish plover, a species with natural variation in care, ranging from fully biparental to either sex deserting soon after hatching. When the female was removed, her mate increased its time spent incubating, but not sufficiently to compensate for the loss of the female. Females did not compensate for the loss of their mate. One interpretation is that males may normally withhold care whereas females operate at their investment maxima.

Such behavior may coerce females into remaining with the brood, and also afford males the opportunity to desert more readily than their partner. However, the balance of power over coercion may vary between species since female magnificent frigatebirds *Fregata magnificens* nearly doubled their feeding rate after male desertion, presumably to compensate for the loss of care (Osorno and Székely, 2004).

The tug-of-war over care also manifests itself at the phylogenetic level. Using phylogenetically independent differences between related taxa, Reynolds and Székely (1997) demonstrated that evolutionary increases in the duration of care in one sex were associated with evolutionary decreases in the duration of care by the other sex (Fig. 5).

Further studies are required to understand how conflicts over care are resolved, at both the phylogenetic and individual level. First, most comparative studies have used fairly crude scored variables based on the duration of

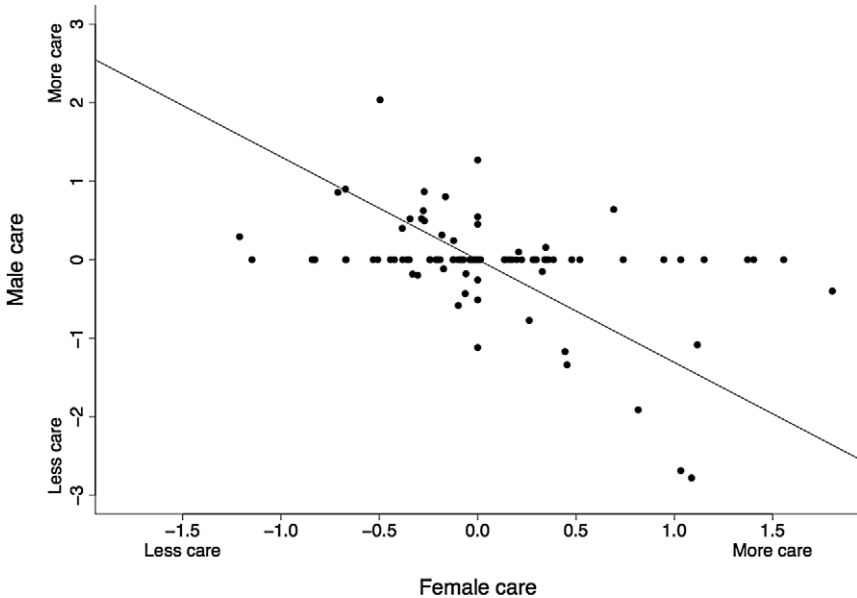


FIG. 5. The relationship between the duration of female care and the duration of male care in shorebirds. The independent axis shows phylogenetically independent contrasts in the duration of female care. The dependent axis shows phylogenetically independent contrasts in the duration of male care (as in Reynolds and Székely, 1997 but updated with recent information; see Appendix for details parental care scores). Fitted line is the major axis regression through the origin (slope -1.309, lower confidence interval -2.246, upper confidence interval -0.570).”

care relative to the total fledging period, as an index of parental effort (Reynolds and Székely, 1997; Székely and Reynolds, 1995; Thomas and Székely, 2005). Ideally, quantitative data on a range of parental care activities including incubation, brooding, antipredator behavior and (in some taxa) feeding would be incorporated into cross-species studies. Second, at the individual and population level, it would be informative to quantify how the contributions of each sex to these different aspects of care influence both offspring survival and mortality of the parents. Third, experimental tests, including removal experiments in several shorebird species, are required to examine the response of parents to the removal of their mates. It is likely that these responses will not be linear, thus designing and executing experiments at sufficient resolution of parental manipulation (or handicapping, see Houston *et al.*, 2005) will be challenging.

B. CONSTRAINTS ON THE DURATION OF CARE

Parents may benefit from avoiding (or at least minimizing) their contribution to care, if their partner is willing, or can be coerced into, taking on the workload. Yet biparental care is still the most common resolution to sexual

conflict over care in shorebirds (Fig. 3). Why do parents rarely succeed in fully exploiting their partners in most species? The most likely explanation is that the requirements of the progeny are high so that both parents are required to successfully raise the brood (Erckmann, 1981; Lack, 1968). This is particularly important if parents provision food to their young, and food availability is poor (Ens *et al.* 1992). In precocial species both parents may lose weight during brood rearing such as in the hooded plover *Charadrius rubricollis*, implying that the burden of care is high and must be shared (Weston and Elgar, 2005). The requirements of the offspring may include incubation, brooding, defense against predation and feeding. We envisage two main ways in which the demands of the young vary among species. First, demand may vary according to the developmental mode of the young, specifically their feeding ability. Second, there may be variation due to environmental and ecological conditions including temperature and predation risk.

Some shorebird species have chicks that feed themselves within hours of hatching but are dependent on the parents for brooding and defense against predation (precocial young; Scolopaci, Charadrii except oystercatchers, thick-knees, and sheathbills), whereas in other species the young additionally depend on the parents for feeding until they fledge (semiprecocial young; Lari, oystercatchers, thick-knees, and sheathbills). In precocial species the parents are relieved from feeding the young. Consequently, uniparental care and social polygamy are expected to occur more frequently in precocial than semiprecocial species (Lack, 1968; Orians, 1969). An alternative view is that the evolution of uniparental care results in selection on chicks to be more independent and thus lead to precocial offspring, thus implying a reversal in the direction in cause and effect. However, developmental mode has changed only a handful of times across the shorebird phylogeny (i.e., it is not a labile trait). Thomas and Székely (2005) found that evolutionary changes across the shorebird phylogenetic tree toward precocial young preceded evolutionary changes toward reduced parental care. This result is important for two reasons. First, it suggests that developmental mode is more likely to be the causative factor in the relationship with parental care. Second, it implies that the resolution of sexual conflict toward desertion is facilitated by the evolution of precocial young (i.e., that uniparental care is more likely to occur in precocial species). The latter result was corroborated by a subsequent analysis comparing rates of trait evolution in precocial and semiprecocial species, because among precocial species both parental care and mating systems diverged more rapidly relative to semiprecocial taxa (Thomas *et al.*, 2006). Taken together, these phylogenetic analyses suggest that the feeding capability of the offspring has a major influence on whether one parent has the opportunity to desert. We note, however, that species that share the same developmental mode

could also be similar with respect to other ecological and life history traits, so that we cannot be certain of a cause and effect relationship between developmental mode and desertion.

The main alternative hypothesis based on environmental harshness predicts that in extreme environments (e.g., very low or very high temperature regimes, high risk of predation), the need for parental care is high and sexual conflict can only be resolved through biparental care. However, despite the fact that many shorebirds inhabit extreme locations and that they do incur costs as a result, there is little evidence to corroborate the environmental harshness hypothesis. For example, the daily energy expenditure (DEE) of incubating shorebirds in the Canadian and Eurasian Arctic (little stint *Calidris minuta*, white-rumped sandpiper *Calidris fuscicollis*, dunlin, ringed plover *Charadrius hiaticula*, sanderling *Calidris alba*, purple sandpiper *Calidris maritima*, ruddy turnstone *Arenaria interpres*, red knot) is about 50% higher than in temperate breeding birds when measured using doubly labeled water techniques (Piersma and Morrison, 1994; Piersma *et al.*, 2003). One might expect uniparental care to be constrained by such high metabolic requirements of adults. Yet there is nothing to suggest that these costs constrain desertion as a resolution to sexual conflict, since in several Arctic-breeding species care is uniparental (e.g., buff-breasted sandpiper, red and red-necked phalaropes, and pectoral sandpiper). The Kentish plover nests in areas where ground temperatures are high enough to cook the eggs (50 °C in the shade, Amat and Masero, 2004, or beyond 60 °C in exposed sites Kosztolányi, A., personal communication) if left unattended for only a few minutes. Here we might expect both parents to be required for incubation and brood care although no such constraint is obvious, because either the male or the female may desert shortly after the eggs hatch (Székely *et al.*, 1999). Studies of predation by gull-billed terns *Gelochelidon nilotica* on Kentish plover chicks showed that the duration of care increased in years when predator numbers were high (Amat *et al.*, 1999). While this implies that the resolution of sexual conflict could potentially be restricted in favor of biparental care as a result of predation risk, it also indicates that the environmental harshness hypothesis is rather idiosyncratic and does not generalize across species.

An additional alternative is that low food availability may limit the potential for the evolution of uniparental care. For example, biparental (monogamous) shorebirds lay their eggs earlier than uniparental (polyandrous) species in the Arctic (Whitfield and Tomkovich, 1996). Whitfield and Tomkovich suggested that the availability of food early in the breeding season constrains the outcome of conflict over care: only biparental species are evidently able to exploit the relatively low abundance of food early in

the breeding season. If variation in food abundance is unrelated to latitude or climate, then this may partially explain the apparent lack of widespread support for general environmental constraints on incubation and care.

C. DESERTION AND MATING OPPORTUNITIES

Identifying whether desertion of the brood and subsequent remating is possible is only part of the story of sexual conflict over care. The second major challenge is in predicting which sex should desert. Two major hypotheses have been proposed. The differential cost of parental care hypothesis argues that the deserting parent should be the sex that incurs the largest direct costs of care (e.g., high energy expenditure or high mortality costs). In contrast, the differential mating opportunities hypothesis posits that the sex that has more opportunities to remate following desertion should desert (e.g., if there are many adults of the opposite sex in breeding condition available in the population). Below, we discuss the weight of evidence for these two hypotheses and argue that there is little supporting evidence for the differential cost of parental care hypothesis, and that differential mating opportunities are a more viable predictor for the resolution of sexual conflict in breeding systems.

1. *Differential Costs of Parental Care*

Do males and females differ in the costs that they pay for parental care? Such differences could determine which sex likely to desert. However, current evidence is inconclusive. In a comparative analysis across all birds (including several shorebird species), [Liker and Székely \(2005\)](#) showed that male mortality increased with the duration of male care only after controlling for the degree of mating competition (i.e., mating system). In contrast, female mortality was unrelated to the duration of female care. This implies that males incur greater costs of care and should be more likely to desert than females. Nonetheless, the differential mortality costs of care cannot fully explain the outcome of sexual conflict over parental care since either the male or the female may desert. Furthermore, the relationship between male care and male mortality was significant only after controlling for mating competition and the full model explained only 18% of the variation in male mortality.

Few studies to date have considered how the division of parental care might affect the outcome of sexual conflict. For example, in both black-tailed godwits *Limosa limosa* and northern lapwings, males are more involved in nest defense, whereas females spend more time on incubation ([Hegyí and Sasvári, 1998](#); [Liker and Székely, 1999](#)). Consequently, the opportunity for either parent to desert may depend on the type of external

threats, for instance, high predation risk or climate, that most influences offspring survival. There are two general outcomes of sexual conflict for each parent if males and females perform different tasks in parental care. First, if the need for the main male component of care (e.g., nest defense) is low then the male parent has the opportunity to desert. Second, if the need for the male component of care is high then that sex may not have the opportunity to desert and is constrained on care. The latter explanation is equivalent to a relaxation of the constraints on care discussed above, except that in this case the constraints apply only to one parent. We do not envisage this explanation alone could generally determine which sex deserts for two reasons. First, the division of sex roles in components of parental care may be liable in many species. Second, where there are low constraints on parental care in both sexes, the division of labour hypothesis makes no prediction on which sex is more likely to desert. To determine whether the division of labour hypothesis is plausible, new experimental manipulations on the division of parental duties between the sexes are needed.

2. *Differential Mating Opportunities*

Mating opportunities of individuals within a population may vary for two main reasons. First, sex ratios could be biased, influencing mating opportunities of all individuals within a population. Second, mating could be state dependent (i.e., mating opportunities vary from individual to individual). Mating opportunities appear to be male biased in several shorebirds, which should favor female “emancipation” from care. Male-biased sex ratios, and presumably female-biased mating opportunities, are well known from some polyandrous species, with examples in the wattled jacana (Emlen and Wrege, 2004), red phalarope (Whitfield, 1995), and bronze-winged jacana (Butchart, 2000). Adult sex ratio appears to be male biased in Kentish plover populations too. Over a 10-year period adult sex ratios were male biased in breeding populations in Sweden (Jönsson, P. E., personal communication; Székely and Williams, 1995) and California (Warriner *et al.*, 1986). This male bias favors female desertion and the evolution of polyandry, and suggests a causative explanation for the rapid remating of female Kentish plovers. The mating opportunities for male and female plovers were experimentally compared by Székely *et al.* (1999) by removing either males or females from breeding pairs, and recording the time taken for the abandoned parent to remate. Males took on average 25.4 days to find a new mate whereas females took only 5.3 days. Furthermore, the time taken to reneest increased for both sexes as the breeding season progressed. However, biased sex ratio per se is not necessarily a prerequisite for the evolution of polyandry. Erckmann (1981) found that the male to female ratio in the polyandrous Wilson’s phalarope was 0.61. Nonetheless, and consistent with

the sexual conflict framework that we describe in [Section VI](#), he pointed out that local sex ratios can change rapidly in phalaropes and polyandry in these species is facultative.

Exploitation of mating opportunities may also be state dependent. In spotted sandpipers, older (and presumably more experienced) females are able to outcompete younger individuals in the search for mates ([Oring and Lank, 1986](#)). Young females that attain a mate are typically monogamous and provide parental care. In contrast, older females often abandon the clutch. This behavior is probably most frequent in high-density populations, implying that abandonment by older females is contingent on there being males available for mating. In some species, males adjust their behavior in order to seek out meeting opportunities. The buff-breasted sandpiper, an Arctic-breeding sandpiper, displays lekking behavior and [Lanctot and Weatherhead \(1997\)](#) observed that while the sex ratio of an Alaskan population was almost constant throughout a breeding season, the absolute number of males at a lek increased with the number of fertile females. They suggested that the Arctic breeding season, where snow accumulation and melt is highly changeable between sites and years, is notable for the variability of mating opportunities. Consequently, males moved opportunistically between sites in search of females (although it is also possible that females moved to leks with more males), a behavior also noted in the ruff ([Lank and Smith, 1987](#)). We speculate that the ability to move between sites is state dependent and may be largely restricted to the best quality individuals.

Mathematical models ([Houston *et al.*, 2005](#)) and evidence from field studies suggest that mating opportunities, rather than differential costs of care, are the likely determinant of desertion. This has been corroborated by a phylogenetic comparative analysis of birds. Female-only care occurs in taxa where remating opportunities are abundant for both sexes, whereas male-only care occurs in taxa where remating opportunities are rare, particularly for males ([Owens, 2002](#)). The implication is that to predict the mating system of a species we need some measure of mating opportunities, such as the time to remating for males and females in a population ([Székely *et al.*, 1999](#)), or the OSR ([Emlen and Oring, 1977](#)). However, OSR and the time to remate are tied to one another, and may be as much an outcome of the breeding system as they are an explanation for it (see below). It will be valuable to test differential mating opportunities in more shorebird species to complement work on the Kentish plover. We predict that in monogamous biparental species there will be less bias in mating opportunities between males and females than in the Kentish plover, in which females desert more often than do males.

3. *Feedback Between Parental Care and Social Mating System*

To assess the gains (i.e., payoffs in game-theoretic parlance) from caring and deserting, one needs models in which the behavior and the number of mated and unmated individuals in the population are consistently followed throughout the breeding season (McNamara *et al.*, 2002; Webb *et al.*, 1999). The emphasis is placed on a feedback loop between mating strategies (to mate or not), mating opportunities, and parental care strategies (desert or care, Székely *et al.*, 2000a).

The essence of the aforementioned game-theoretic models can be summarized as follows. The quality and availability of mates in a population depends on the mating decision of all other members of the population, and the best strategy may differ for each individual. Once mated, the parent is then faced with the dilemma: “should I stay or should I go?.” To stay could enhance the chances of offspring survival, but to go could afford new mating opportunities and more offspring. The payoff from caring is likely to be high if the brood is of high quality or if staying results in mate-retention. But desertion also has high payoffs if mating opportunities are abundant. If a parent deserts, it is returned to the pool of unmated individuals, and the mating optimum is shifted across the population. Mating opportunities are determined by the mating and parental care strategies of each individual in the population. At the same time, the decision of each individual determines the mating opportunities, and consequently the optimal mating and parental care strategy for the rest of the population.

Does this scenario have any relevance for natural populations? We argue that it may. For instance, in Temminck’s stint *Calidris temminckii* many females lay two clutches, each for a different male. After the female has laid a clutch, the pair splits and both the male and the female attempt to attract a new mate and produce a new clutch. If both of them are successful in finding a new mate, then the male starts incubating the first clutch, whereas the female incubates the second one (Hildén, 1975). There are, however, deviations from this pattern: some females lay three successive clutches leaving successive partners to deal with the first two clutches; some males mate with two females, for whom this is their first clutch. We argue that these deviations are produced by the race for new mates. The race for mates can be wasteful. Hildén (1975) noted that both the male and female abandoned some clutches. These wasted clutches may be the outcome of intense sexual conflict: both parents are seeking new mates while assuming (wrongly) that their former mate will take up parental duties.

Parental care patterns and social mating system are emergent outcomes of the mating opportunity-mediated feedback loop. We argue that these emergent traits are observable and leave their imprint at the phylogenetic level. The correlation between parental care and social mating system is

well known: male-only care is often associated with social polygyny, biparental care with social monogamy and female-only care with social polyandry (Bennett and Owens, 2002; Lack, 1968; Ligon, 1999). The relationship is strong across species in shorebirds, after accounting for phylogenetic relationships (Fig. 6). However, it is usually assumed that the direction of causation runs from parental care to social mating system. That is, the sex that invests less in offspring care competes more intensely for mates. But the feedback model above suggests that this need not be the case, since mating and parental behaviors may mutually influence one another (Alonzo and Warner, 2000; Reynolds, 1996; Székely *et al.*, 2000a).

At the phylogenetic level, the feedback model predicts that changes in the mating system of a species are just as likely to precede changes in parental care as the reverse. According to parental investment theory (Trivers, 1972) evolutionary transitions toward social polygamy should arise only after transitions toward uniparental care and the reverse transitions should be absent, or very rare. In contrast, sexual conflict theory predicts that changes back to biparental care from uniparental care in

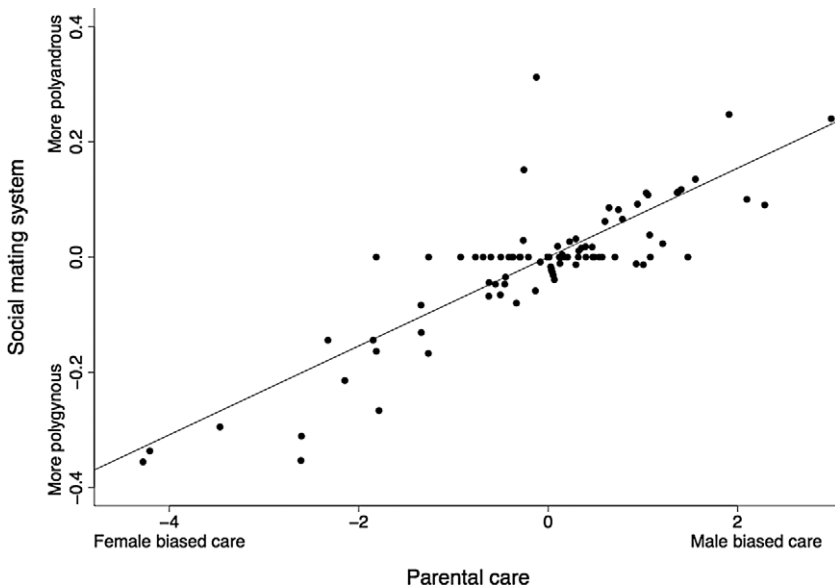


FIG. 6. The relationship between parental care and social mating systems in shorebirds. The independent axis shows phylogenetically independent contrasts in parental care bias between the sexes (duration of male care—duration of female care). The dependent axis shows phylogenetically independent contrasts in social mating system (polygyny → monogamy → polyandry). Note that social mating system refers to the type of pair-bond, whereas parental care refers to the duration of care. Fitted line is the major axis regression through the origin (slope 0.077, lower 95% confidence interval 0.067, upper 95% confidence 0.091). Adapted from Thomas (2004).

socially polyandrous species are likely, as are changes to social monogamy from social polygamy in uniparental species. Recent phylogenetic methods using continuous-time Markov models allow the most likely order and direction of trait evolution to be evaluated (Pagel, 1994). Using this approach, implemented in the computer program DISCRETE (Pagel, 1994), Thomas and Székely (2005) showed that the phylogenetic patterns of transition of parental care and social mating system in shorebirds are consistent with the predictions of the feedback model. Thus Trivers's dictum that "*what governs the operation of sexual selection is the relative parental investment of the sexes in their offspring*" appears to be incorrect, at least in shorebirds (Trivers, 1972).

VI. A SEXUAL CONFLICT FRAMEWORK FOR BREEDING SYSTEMS

The classical views of shorebird breeding system evolution focused on ecological hypotheses (Erckmann, 1983, Oring, 1986; Pitelka *et al.*, 1974). Yet only two ecological traits have been shown to correlate with breeding systems in comparative studies that include shorebirds, and both have relatively low explanatory power. Owens (2002) showed that nesting density was associated with desertion in polyandrous versus nonpolyandrous birds, a result consistent with the predictions made by Emlen and Oring 25 years earlier. Reynolds and Székely (1997) found that the duration of care declined with increasing migration distance in shorebirds, although the latter result only applied to males. Reynolds and Székely (1997) suggested that it is likely that migration distance evolved in response to parental care, since migratory patterns must have evolved since the last glacial retreat 12,000 years ago (Alerstam, 1990). This need not necessarily be true though, because while the absolute migration distance will have undoubtedly changed for many species, the relative migration distance across species, along with its correlation with parental care, may have its roots much deeper in evolutionary time.

The dynamic nature of the feedback between parental care and mating strategies may explain why general correlates of social mating system and parental care have been difficult to identify (Ligon, 1999; Owens, 2002). We suggest that it is time to move on, and explicitly consider interactions between individuals in addition to the more general factors that make desertion possible. In outlining their hierarchical view of avian mating systems, Bennett and Owens (2002) recognized three levels of mating system determinants: phylogenetic constraint, ecological facilitation, and social interactions. We concur with this broad concept. However, the forms of social interactions were not detailed by Bennett and Owens (2002). We emphasize the significance of sexual conflict, particularly with respect to its influence on mating opportunities for each sex.

The general framework for breeding system evolution we proposed above is based on sexual conflict, starting from the viewpoint of a mated pair. Whether one parent has the *potential* to desert depends on the survival prospects of the young. The evidence reviewed above suggests that the most important constraint on the potential to desert is the developmental mode of the offspring (e.g., precocial or semiprecocial), rather than a specific aspect of the environment. Phylogenetic comparative approaches are likely to provide further insight into these constraints. Similarly, long-term data on changes in parental care in relation to seasonal variation in predation risk, food availability, and climate variables would be helpful. However, we stress that relaxation of these constraints does not determine whether desertion actually occurs, nor which sex is more likely to desert. We believe that relative mating opportunities for each sex, and thus population sex ratio, are key factors in determining which sex deserts.

Emlen and Oring (1977) also stressed the importance of mating opportunities in relation to the spatial distribution of mates and the OSR. The fundamental difference between Emlen and Oring's view and the sexual conflict one that we are presenting here is that we consider mating opportunities and parental behaviors as being in a dynamic state. In particular, the decisions of mated and unmated individuals of each sex are both a cause and a consequence of mating opportunities and parental behaviors. In this view, the parental care and mating patterns of a species are ultimately the result of conflicts between the sexes over mating and parental investment in the offspring.

Testing the links between mating opportunities, parental care, and mating system will be challenging. In particular, data on mating opportunities are lacking for most shorebirds. Further experimental manipulations, particularly removal studies, are needed. We believe that the sexual conflict model of breeding system evolution has the potential to explain the patterns of parental care and social mating system observed across species in shorebirds, and can be readily adapted to other groups. Furthermore, by explicitly accounting for variation in mating opportunities for each sex, it also indicates which sex should pursue mating more vigorously and thus informs on the potential for extra-pair fertilizations.

VII. FUTURE DIRECTIONS

Throughout this chapter we have argued that sexual conflict is an important concept for understanding breeding systems of shorebirds. However, we acknowledge that much of the current evidence is qualitative, observational, and indirect. To corroborate (or falsify) the influence of sexual conflict, a new generation of experiments, advanced comparative analyses, and theoretical

models are needed. Given that several extensive field projects have been carried out with shorebirds, it is somehow surprising that only a few of them have carried out experiments. In addition, sexual conflict theory potentially has impacts beyond reproductive behaviors, particularly with respect to large-scale evolutionary processes including speciation and extinction. Below we briefly outline areas of research that are ripe for future development.

A. DISPLAY TRAITS

In [Section IV](#), we highlighted the link between male display behavior and sexual conflict over body size evolution. As [Graul \(1973a\)](#) noted, male displays could be amplified by contrasting pigmentation. To fully understand how mate choice might influence conflict in body size, future research should expand the analyses of sexually dimorphic traits, specifically plumage and display behavior, in three major ways. First, display agility has been quantified in only a few shorebirds, and plumage colors and ornaments in fewer still. Methods for measuring these traits are well established (e.g., plumage color reflectance, [Bennett and Cuthill, 1994](#); [Olson and Owens, 2005](#); and agility of display behavior: [Blomqvist *et al.*, 1997](#); [Grønstøl, 1996](#)). Quantitative descriptions would be particularly valuable in those taxa that exhibit large intraspecies and/or interspecific variation in these traits ([Reynolds, 1987](#)). Second, experimental alteration of these traits would be very illuminating. For instance, no study has yet manipulated flight maneuverability in shorebirds to test the effect of agility on mate attractiveness and male–male competition. Finally, it is important to assess effects of these studies beyond behavioral response (e.g., mating time, number of mates). Measuring reproductive success over the full breeding season, and possibly the reproductive success of the offspring produced by manipulated and control individuals would be very valuable. Given the highly mobile nature of many shorebirds, these will be challenging tasks.

B. DIVERSIFICATION

Sexual selection by mate choice may result in the coevolution of attractive traits and choice for those traits ([Fisher, 1930](#)). Thus, secondary sexual characters can evolve rapidly in a positive feedback runaway process. According to the sexual selection hypothesis, rapid divergence in female mate choice is likely to result in the formation of reproductive barriers in isolated populations and thus promote speciation ([Barraclough *et al.*, 1998](#); [Lande, 1981](#); [Panhuis *et al.*, 2001](#); [West-Eberhard, 1983](#)). Sexual conflict has been identified as an alternative driver for speciation as a result of chase-away selection on male and female reproductive traits ([Arnqvist *et al.*, 2000](#); [Gavrilets, 2000](#); [Gavrilets and Waxman, 2002](#); [Martin and Hosken, 2003](#); [Parker and Partridge, 1998](#)). Testing these hypotheses in

any group will be challenging, in particular quantifying sexual conflict and sexual selection. Previous studies on species richness and speciation used variables such as mating system and SSD as proxies for sexual conflict (Arnqvist *et al.*, 2000; Gage *et al.*, 2002). More direct measures of both sexual selection and sexual conflict are required (Mills *et al.*, 2007).

C. EXTINCTION RISK AND POPULATION DECLINES

While interlocus conflicts are likely to be the primary source of sexual conflict-driven speciation, heightened extinction risk could arise through either inter- or intralocus conflicts. Theory developed for sexually selected traits suggests that the accumulation of exaggerated male traits through female choice may be energetically costly (Tanaka, 1996). Energetic costs from traits subject to sexually antagonistic coevolution (SAC) may also occur, and indeed be exacerbated by direct harm from the traits themselves. The effect of selection load may directly influence survival and therefore drive population declines. Alternatively, it may make some species more susceptible to external threats. As we discuss in Section IV, intralocus conflicts may prevent one (or both) sexes from reaching their fitness optima. Comparative analyses of population trends or threat status will be fruitful.

VIII. SUMMARY

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

APPENDIX. TABLE 1.
SHOREBIRD DATA SET^a

	Male mass (g)	Female mass (g)	Male wing length (mm)	Female wing length (mm)	Male bill length (mm)	Female bill length (mm)	Social mating system	Male display type	Male care	Female care	Egg mass (g)	Clutch size	Chick feeding	Breeding habitat	Male polygamy	Female polygamy	References
<i>Actophilornis africanus</i>	143.2	260.7	145.8	167.5	–	–	3	GD	7	0	8.6	4	0	–	0	4	1;1;1;1;1;1;1;1;1;1;2;2;3;4;1; _1;1
<i>Aethia cristatella</i>	267.7	251.4	143	140.3	12.6	11.8	1	GD	7	7	54.2	–	2	–	0	0	5;5;5;5;5;5;5;6;5;5;5;_5; _6;6
<i>Aethia pusilla</i>	–	–	89.9	90.8	9.3	9.3	1	GD	7	7	17.4	–	2	2	0	0	_5;5;5;5;5;5;5;5;6;_5; 7;5;5
<i>Aethia pygmaea</i>	–	–	107.8	109.2	–	–	1	–	–	–	–	–	2	–	–	–	_3;8;8;_6;_1;_1;_1;_6; _1;_1
<i>Alca torda</i>	734	700	209.7	207.6	35.7	34.5	1	–	7	7	–	–	2	–	0	0	9
<i>Alle alle</i>	154	151	123.3	120.7	16.1	15.5	1	GD	7	7	28	1	2	1.5	0	0	9;9;9;9;9;9;9;9;9;9;9;9;9;9; 9;9;9
<i>Anarhynchus frontalis</i>	58.6	56.7	119.3	119	29.9	28.8	1	GD	7	7	12.4	2	0	–	1	0	3;3;10;10;10;10;11;7;11; 11;3;11;11;_10;10
<i>Anous minutus</i>	–	97.5	226.5	221.2	44.1	41.3	1	–	7	7	25.1	1	2	–	0	0	_1;2;12;12;12;12;12;_1; 12;12;6;6;12;_1;12;12
<i>Anous stolidus</i>	196.4	172.3	283	273	40.8	38.1	1	AA	7	7	–	1	2	2	0	0	12;12;12;12;12;12;6;12; 12;12;_1;1;12;9;1;1
<i>Anous tenuirostris</i>	92	114	210	213.3	41.9	39.2	–	–	7	7	17.4	1	2	–	–	–	12
<i>Aphriza virgata</i>	186.3	216.3	171.8	178.8	24.1	26.5	1	AA	7	7	22.4	4	–	1	–	–	6;6;6;6;6;6;6;6;6;6;_6; _3;_1
<i>Arenaria interpres</i>	108	113	155	157	22.4	22.8	1	AA	7	4	17.9	3.5	0	2	0	0	13;13;13;13;13;13;14;15; 14;14;3;13;13;13; 13;13
<i>Arenaria melanocephala</i>	113.6	124.2	147	151.9	22.5	23	1	ANA	7	7	17.3	4	0	–	0	0	16;16;6;6;6;6;17;6; 17;17;18;3;19;_6;6

(Continued)

<i>Calidris canutus</i>	126	148	169	173	32.6	34.4	1	AA	7	6	19.3	3.7	0	2	0	0	13;13;13;13;15;15;13;13; 29;29;18;13; 13;13;13;13
<i>Calidris ferruginea</i>	63.2	63.3	132	133	36.2	40.1	2	AA	0	7	12	4	-	2	-	-	13;13;13;13;15;15;3;15; 30;30;3;3;13;13
<i>Calidris fuscicollis</i>	39.7	45.8	122	125	23.2	24.4	2	AA	0	7	10.8	4	0	1.5	3	0	13;13;13;13;15;15;31;6; 31;31;3;3;7;6;6
<i>Calidris maritima</i>	67.6	76.3	127	132	27.5	32	1	AA	7	3	13.3	3.9	0	2	0	0	13;13;13;13;13;13;13;15; 13;13;3;13; 13;13;13;13
<i>Calidris mauri</i>	28	31	97.1	101	23.1	26.7	1	AA	7	4	7.5	3.9	0	1	0	0	12;12;13;13;15;15;32;15; 32;32;3;33;32;3;6;6
<i>Calidris melanotos</i>	97.8	65.1	144	131	29.6	27.7	2	ANA	0	7	13.1	4	0	1	-	-	13;13;13;13;15;15;34;15; 34;34;3;3;6;13;13
<i>Calidris minuta</i>	24	27.1	96.4	99.5	18.1	18.5	4	AA	7	0	6.3	3.8	-	-	1	2	13
<i>Calidris minutilla</i>	20.3	22.2	89.8	91.6	18.2	19.5	1	AA	7	5	6.4	3.9	0	2	0	0	13;13;13;13;13;13;35;6; 35;35;3;3;6;13;6;6
<i>Calidris pilocnemis</i>	76.3	83	121.3	125.5	26.8	29.8	1	AA	7	4	14.2	4	0	1.5	0	0	16;16;37;37;37;37;26;26; 26;26;3;3;13;7;6;6
<i>Calidris pusilla</i>	25	27	95.9	100.1	18.6	20.2	1	AA	6	5	6.9	4	0	2	0	0	13;13;13;13;15;15;38;15; 38;38;3;3;6;13;6;6
<i>Calidris ruficollis</i>	25.7	26.6	103.5	106.2	17.5	18.7	1	AA	7	4	8.3	4	-	2	0	0	13;13;13;13;15;15;26;15; 26;26;3;3;13; 13;26;26
<i>Calidris subminuta</i>	29	32	93.1	95	17.8	18.8	1	AA	7	4	7.5	4	-	1.5	-	-	13;13;13;13;13;13;26;26; 39;39;3;3;7;13
<i>Calidris temminckii</i>	24.3	27.8	98.2	99.3	16.9	17.2	4	AA	7	0	5.8	4	0	-	3	3	13;13;13;13;13;13;40;13; 40;40;3;13;13; 13;13
<i>Calidris tenuirostris</i>	156	174	185	192	42.1	43.8	1	AA	7	3	22	4	-	1	0	0	13;13;13;13;13;13;26;26; 26;26;3;3;13;26;26
<i>Catharacta maccormickii</i>	1277	1421	410	415	49.4	50.9	1	AA	7	7	-	1.8	2		0	0	12
<i>Catharacta skua</i>	1735	1935	411.9	420.6	54.7	55.3	1	AA	7	7	111.7	2	2	2	0	0	12

(Continued)

APPENDIX. TABLE 1. (Continued)

	Male mass (g)	Female mass (g)	Male wing length (mm)	Female wing length (mm)	Male bill length (mm)	Female bill length (mm)	Social mating system	Male display type	Male care	Female care	Egg mass (g)	Clutch size	Chick feeding	Breeding habitat	Male polygamy	Female polygamy	References
<i>Catoptrophorus semipalmatus</i>	273	301.4	205.2	213.5	59.4	64.1	1	AA	7	5	39.5	4	0	-	0	0	3;3;3;3;3;41;41; 41;41;3;3;41;_6;6
<i>Cephus carbo</i>	510	480	195	189.5	-	-	-	-	-	-	-	1	-	-	-	-	8
<i>Cephus columba</i>	487	483	187.5	187.5	-	-	1	-	7	7	-	-	2	-	0	0	6;6;6;_6;_7;_7;_7;_7; _6;6
<i>Cephus grylle</i>	376	386	164	165	33.3	33.2	1	GD	7	7	50	1.43	2	2	1	0	5;5;5;5;5;9; 5;5;9;5;9;9
<i>Cerorhinca monocerata</i>	510	456	182.9	177.7	18.3	18.5	1	GD	7	7	77.7	1	2	-	-	-	6
<i>Charadrius alexandrinus</i>	48.2	47.1	111	112	15.4	15.2	1	ANA	7	4	9	3	0	2	2	1	13;13;13;13;13;13;42;13; 42;42;43;13; 13;13;13;13
<i>Charadrius asiaticus</i>	75.6	76.2	150	150	19.8	20.1	1	ANA	7	7	-	-	0	-	-	-	13
<i>Charadrius bicinctus</i>	58.8	58.4	130.2	127.2	17.2	17	1	ANA	7	7	11.5	2.93	0	-	0	0	10
<i>Charadrius dubius</i>	38.3	39.2	117	116	12.7	12.9	1	ANA	7	4	7.7	3.9	0	2	0	0	13;13;13;13;15;15;13;13; 44;44;13;13; 13;13;13;13
<i>Charadrius forbesi</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	1
<i>Charadrius hiaticula</i>	63.5	64.7	132	135	14.1	14.5	1	ANA	7	6	10.9	3.8	0	-	0	0	13;13;13;13;15;15;13;13; 13;13;3;13;13; _13;13
<i>Charadrius leschenaultii</i>	-	-	141	144	23.3	23.2	-	ANA	-	-	-	-	-	-	-	-	_10;10;10;10;_13;_13; _13;_13
<i>Charadrius marginatus</i>	48.3	48.3	110	110	17	17	1	-	-	-	-	2	0	-	0	0	1
<i>Charadrius melodus</i>	54.9	55.6	121	120	-	-	1	AA	7	7	9.4	3.3	0	-	0	1	6
<i>Charadrius mongolus</i>	-	-	130	131	18.6	18.6	-	-	-	-	-	-	-	-	-	-	10
<i>Charadrius montanus</i>	102	114	146	149	20.5	22	4	GD	7	0	16.5	3	0	-	0	0	3;3;3;15;15;45;6; 45;45;3;3;46;_6;6
<i>Charadrius obscurus</i>	160	110	159.3	159.1	29	27.5	1	GD	7	7	-	-	-	-	0	0	16;16;13;13;13;13;13;7; 13;13;_13;_13;10;10

<i>Charadrius pallidus</i>	-	-	-	-	-	-	1		7	7	-	-	-	-	0	0	1
<i>Charadrius pecuarius</i>	-	-	106	106	15	15	1	GD	7	7	-	-	-	-	0	0	13
<i>Charadrius rubricollis</i>	-	-	143.2	144.4	17.7	17.6	1	GD	7	7	-	-	-	-	0	0	10;10;10;10;10;7;
<i>Charadrius ruficapillus</i>	37.3	37.6	105.4	105	13.8	13.9	-	ANA	7	7	-	2	-	-	-	-	10;10;10;10;10;10;7;
<i>Charadrius sanctaehelenae</i>	-	-	-	-	-	-	1	-	7	7	10.8	2	0	-	-	-	10;10;10;10;10;10;7;
<i>Charadrius semipalmatus</i>	46.1	47.8	-	-	-	-	1	-	7	5	-	3.94	0	-	0	0	47;47;18;47;19;10;10;
<i>Charadrius tricollaris</i>	-	-	-	-	-	-	1	GD	7	7	-	-	0	-	0	0	6
<i>Charadrius veredus</i>	-	-	166.5	164.5	22.5	22.3	-	-	-	-	-	-	-	-	-	-	1
<i>Charadrius vociferus</i>	92.1	101	167	167	20.2	20.3	1	-	7	7	14.5	4	0	-	0	0	10
<i>Charadrius wilsonia</i>	59	63	116.4	117.6	20.7	20.8	1	-	7	2	12.4	3	0	-	-	-	1;1;1;1;15;15;48;48;48;3;3;3;6;6
<i>Chionis alba</i>	735	638	253	242	34.4	32	1	GD	7	7	45.5	2.2	2	2	0	0	49;49;3;3;3;10;10;10;10;10;10;50;10;50;50;50;50;
<i>Chionis minor</i>	625	551	240	231	-	-	1	GD	7	7	43.1	2.5	2	-	0	0	10;7;10;10;51;51;15;15;15;52;10;52;52;18;10;10;10;10
<i>Chlidonias albostratus</i>	-	-	-	-	-	-	1	-	-	-	-	2	2	-	-	-	12
<i>Chlidonias hybridus</i>	90	86	242	232	31.6	28.5	1	AA	7	7	16	2.74	2	-	0	0	9;9;9;9;9;9;9;9;9;9;9;
<i>Chlidonias leucopterus</i>	-	-	215	212	-	-	1	-	7	7	10.5	2.8	2	-	0	0	9;9;9;9;9;9;9;9;9;9;9;
<i>Chlidonias niger</i>	61.8	58.7	218	213	27.8	26.5	1	ANA	7	7	11	2.83	2	2	0	0	13;13;13;13;13;13;13;13;13;13;13;13;13;13;9;9;9;9
<i>Cladorhynchus leucocephalus</i>	262.8	261	201.5	196.2	71.4	66.3	-	GD	7	7	-	-	0	-	-	-	10;10;10;10;10;10;7;
<i>Coenocorypha aucklandica</i>	101.2	116.1	106.2	109.2	57.5	60.9	1	AA	7	7	23.7	2	2	1	2	0	10;10;10;10;10;10;10;12;12;12;12;12;12;12;54;54;54;54;12;7;12;12

(Continued)

APPENDIX. TABLE 1. (Continued)

	Male mass (g)	Female mass (g)	Male wing length (mm)	Female wing length (mm)	Male bill length (mm)	Female bill length (mm)	Social mating system	Male display type	Male care	Female care	Egg mass (g)	Clutch size	Chick feeding	Breeding habitat	Male polygamy	Female polygamy	References
<i>Haematopus fuliginosus</i>	740.3	778.5	290.4	289.9	71.3	81.4	1	AA	7	7	69.5	2	2	-	0	0	15;15;15;15;15;15;62;7; 62;62;3;62;62; _;10;10
<i>Haematopus longirostris</i>	602.3	626.3	274.7	280.9	73.8	84.8	1	AA	7	7	49	2.5	2	-	0	0	10;10;10;10;10;10;62;7; 62;62;18;53;18; _;10;10
<i>Haematopus moquini</i>	668	730	275	279	63.2	71.6	1	AA	7	7	55.8	1.7	2	-	0	0	1;1;1;1;1;1;63;1; 63;63;1;1;1;_;1;1
<i>Haematopus ostralegus</i>	500	536	254	255	69.6	78.4	1	AA	7	7	46.7	2.8	2	2	2	0	8;8;13;13;13;13;64;15; 64;64;43;13;13; 13;13;13
<i>Haematopus palliatus</i>	-	-	254.4	259.5	83	92.3	1	-	7	7	44.9	2.6	2	-	1	0	_;15;15;15;15;3;_ 65;65;18;66;3;_6;6
<i>Haematopus unicolor</i>	717	734	273	279	82.8	91.8	1	AA	7	7	48.2	2.4	2	-	0	0	10;10;10;10;10;10;10;_ 3;3;10;10;10;_;10;10
<i>Himantopus himantopus</i>	164	157	247	232	63.7	61.1	1	ANA	7	7	21.8	3.5	0	2	0	0	10;10;13;13;13;13;13;13; 13;13;43;13;13;13; 13;13
<i>Himantopus mexicanus</i>	170.4	168.7	227	217.5	65.3	63.9	1	GD	7	7	21	3.9	0	-	0	0	6
<i>Himantopus novaezelandiae</i>	219	227	-	-	-	-	1	-	7	7	-	-	0	-	0	0	10;10;_;_;_;_67;_67; 67;_;10;_;10;10
<i>Hydrophasianus chirurgus</i>	126	231	-	-	-	-	3	-	7	0	14.1	4	0	-	0	4	68;68;_;_;_53;_69; 69;3;69;70;_53;53
<i>Ibidorhyncha struthersii</i>	-	-	233.5	255	67.5	74	1	-	7	7	37	4	2	-	-	-	_;3;3;3;3;71;_ 71;71;3;3;3;_;
<i>Irediparra gallinacea</i>	84	143	121.8	141.1	25.4	29.2	3	GD	7	0	7.1	4	0	2	0	4	10;10;10;10;10;10;7;7; 7;7;_;10;7;10;10
<i>Jacana jacana</i>	108.3	142.8	124.9	137.9	31.4	32.6	3	GD	7	0	9.7	3.5	0	-	-	-	3;3;3;3;3;72;73; 72;72;72;73;3;_;

<i>Limicola falcinellus</i>	–	–	105	110	30.4	33.5	1	AA	7	4	9.1	3.9	0	2	0	0	13
<i>Limnodromus griseus</i>	111	116	145	144	58.8	56.5	1	ANA	7	3	17.5	4.1	0	–	0	0	13;13;13;13;13;13;3;6; 7;7;3;3;6;6;6
<i>Limnodromus scolopaceus</i>	100	109	141	146	62.1	72.4	1	–	7	2	–	3.9	0	–	–	–	13;13;13;13;13;13;7;7; 7;7;6;6;6;6
<i>Limnodromus semipalmatus</i>	–	–	–	–	–	–	–	–	7	4	–	–	–	–	–	–	115
<i>Limosa fedoa</i>	320	421	228.9	239.9	96.6	114.6	1	–	6	7	44.5	4.1	0	–	0	0	3;3;3;3;15;15;78;7; 78;78;3;3;6;6
<i>Limosa haemastica</i>	222	289	209	217.4	74.5	89.5	1	AA	7	7	37.5	4	0	–	–	–	3;3;3;3;15;15;3;20; 79;79;3;79;3;6;6
<i>Limosa lapponica</i>	313	354	210	223	80.4	97.7	1	AA	7	7	37	3.72	0	–	0	0	13;13;13;13;13;13;13;13; 13;13;13;6;13; 6;13;13
<i>Limosa limosa</i>	264	315	207	218	92.1	107	1	AA	7	7	39	3.9	0	2	0	0	13;13;13;13;15;15;13;13; 80;80;18;13; 13;13;13;13
<i>Lymnocyrtus minimus</i>	53.7	46.7	114	110	40.3	40.1	2	AA	0	7	–	–	–	–	–	–	13
<i>Metopidius indicus</i>	176.2	282.4	162	189	22.5	25.1	3	GD	7	0	11.9	4	–	–	–	–	81;81;81;81;81;3;82; 82;82;3;3;6;6;6
<i>Micropalama himantopus</i>	55.8	60.4	132	134	39.5	41.3	1	AA	7	4	11.2	3.9	0	1	0	0	13;13;13;13;15;15;83;83; 83;83;3;3;13;6;6
<i>Microparra capensis</i>	–	–	86.8	90.6	15.6	16.2	1	GD	7	7	4.5	2.8	0	2	–	–	6;6;1;1;1;1;84;84; 84;84;3;84;19;7;6;6
<i>Numenius americanus</i>	640.1	758.6	279.3	291.3	145.3	184	1	AA	7	4	73	4	0	–	0	0	13;13;13;13;15;15;6;6; 48;48;3;3;19;6;6
<i>Numenius arquata</i>	662	788	292	310	118	137	1	AA	7	6	76	3.9	0	2	0	0	13;13;13;13;15;15;13;13; 85;85;3;13;13;13; 13;13
<i>Numenius borealis</i>	–	–	206.3	203.8	51.3	54.9	–	–	–	–	–	–	–	–	–	–	6
<i>Numenius madagascariensis</i>	697.2	807.9	308.5	310.1	158	179.5	–	–	–	–	–	–	–	–	–	–	12
<i>Numenius minutus</i>	162	182	183	188	41.6	45.3	–	–	–	–	–	–	–	–	–	–	13

(Continued)

APPENDIX. TABLE 1. (Continued)

	Male mass (g)	Female mass (g)	Male wing length (mm)	Female wing length (mm)	Male bill length (mm)	Female bill length (mm)	Social mating system	Male display type	Male care	Female care	Egg mass (g)	Clutch size	Chick feeding	Breeding habitat	Male polygamy	Female polygamy	References
<i>Numenius phaeopus</i>	368	398	242	251	78.6	86.9	1	AA	7	6	50	3.9	0	–	0	0	13;13;13;13;15;15;13;15; 85;85;18;13;13; _;13;13
<i>Numenius tahitiensis</i>	378	489	230	245	82.8	77.2	1	AA	7	5	54.8	4	0	–	0	0	3;3;3;3;15;15;8;6;6; 86;86;3;3;6;_6;6
<i>Numenius tenuirostris</i>	–	–	251	262	72.9	89.9	–	–	–	–	–	–	–	–	–	–	13
<i>Pagophila eburnea</i>	617	507	345	336	35.3	32.7	1	GD	7	7	–	1.69	2	1	0	0	13;13;13;13;13;13;13;13; 13;13;_;13;6;13;13; 13
<i>Pedionomus torquatus</i>	54	72.4	88.9	96.5	12.3	12.8	3	GD	7	0	10	3.6	0	0.5	0	3	16;16;10;10;10;10;88;10; 88;88;18;88;10;7; 10;10
<i>Peltohyas australis</i>	80	88.2	141.8	140	17.2	17	1	–	7	7	–	–	–	–	–	–	10
<i>Phalaropus fulicaria</i>	50.8	61	129	137	21.6	22.8	3	ANA	7	0	7.5	3.8	0	–	0	2	13;13;13;13;15;15;13;13; 89;89;3;13;13;_6;6
<i>Phalaropus lobatus</i>	32.4	37.4	108	114	21.1	21.4	3	ANA	7	0	6.3	4	0	2	0	3	13;13;13;13;15;15;13;13; 90;90;3;13;13;13;6;6
<i>Philomachus pugnax</i>	199	118	191	158	35	30.9	2	GD	0	7	21	3.7	1	2	4	0	13;13;13;13;13;13;13;13; 13;13;3;13;13;13; 13;13
<i>Pluvialis apricaria</i>	175	176	190	190	21.8	21.6	1	ANA	7	6	32.8	3.9	0	1	0	0	13;13;13;13;15;15;13;13; 43;43;3;13;13;13; 13;13
<i>Pluvialis dominica</i>	145	146	182	182	23.2	23.3	1	–	7	7	26	4	0	–	0	0	3;3;3;15;15;9;1;_; 91;91;18;3;91;_6;6
<i>Pluvialis fulva</i>	130	140	165.9	168.7	24.1	23.5	1	–	7	6	–	–	0	–	0	0	6;6;10;10;10;10;6;_; _;_6;_6;6

APPENDIX. TABLE 1. (Continued)

	Male mass (g)	Female mass (g)	Male wing length (mm)	Female wing length (mm)	Male bill length (mm)	Female bill length (mm)	Social mating system	Male display type	Male care	Female care	Egg mass (g)	Clutch size	Chick feeding	Breeding habitat	Male polygamy	Female polygamy	References
<i>Scolopax rusticola</i>	306	313	202	200	70.9	73.5	2	ANA	0	7	24.5	3.8	1	1	4	0	13;13;13;13;15;15;100;- 13; 100;100;13;13; 13;13;_
<i>Steganopus tricolor</i>	50.2	68.1	125	136	30.7	33.6	3	GD	7	0	9.4	4	0	-	0	3	13;13;13;13;15;15;101;6; 102;102;3;3;6;_6;6 _;13;_13;13
<i>Stercorarius longicaudus</i>	269.9	307.2	30.6	28.4	-	-	1	-	-	-	39.2	-	2	-	0	0	6;6;6;_6;_6;_6;_6; _;13;_13;13
<i>Stercorarius parasiticus</i>	361	408	315	321	31.1	31.8	1	AA	7	7	-	2	2	1.5	0	0	13;13;13;13;13;13;13;13; 13;13;13;13;13;7; 13;13
<i>Stercorarius pomarinus</i>	648	740	363	373	39.8	40.9	1	AA	7	7	66	1.95	2	-	0	0	13;13;13;13;13;13;15; 13;13;13;13; _;13;13
<i>Sterna albifrons</i>	60	55	181	175	30.2	28.7	1	-	7	7	10	2.05	2	-	0	0	9;9;9;9;9;_; 13;13;9;9;13;_9;9
<i>Sterna aleutica</i>	-	-	271.8	271.5	-	32.9	1	GD/ ANA	-	-	19.6	-	2	-	-	-	6
<i>Sterna anaethetus</i>	-	-	261.8	258.6	-	-	1	-	7	7	20	1	2	-	0	0	_;12;12;_6;_; 12;12;9;1;12;_9;9
<i>Sterna antillarum</i>	46.9	49.3	166.9	166.4	28.2	26.7	1	ANA	7	7	8.1		2	1.5	0	0	6;6;6;6;6;6;6;6;6; _6;7;6;6
<i>Sterna balaenarum</i>	-	-	171	171	29.3	29.3	1	-	7	7	-	1	2	-	0	0	1
<i>Sterna bengalensis</i>	-	-	-	-	-	-	1	-	7	7	35	1	2	-	-	-	_;_;_;_;_12;_;
<i>Sterna bergii</i>	-	-	351.1	344.2	61.2	57.7	1	ANA	7	7	-	1	2	-	0	0	1;1;9;1;12;_;
<i>Sterna caspia</i>	680	588	421	412	72.4	67.8	1	ANA	7	7	65	1.54	2	2	0	0	_;12;12;12;12;9;12; 9;9;_1;12;_9;9
<i>Sterna dougallii</i>	-	-	236	233	-	-	1	ANA	7	7	20.4	1.43	2	-	0	0	_;9;9;_12;12; 9;9;9;1;9;_12;12

<i>Sterna elegans</i>	-	-	316.9	312.7	64.3	60.8	-	-	-	-	36.48	1.02	2	2	-	-	1;20;20;6;6;1;1;
<i>Sterna fuscata</i>	-	-	294	287	-	-	1	-	7	7	40.2	1	2	-	0	0	6;6;6;7;1;
<i>Sterna hirundo</i>	124	126	272	270	37.1	35.2	1	ANA	7	7	21	2.65	2	2	0	0	9;9;1;6;1;
<i>Sterna maxima</i>	-	-	-	-	-	-	1	-	7	7	-	1	-	-	0	0	6;6;12;6;6;12;12
<i>Sterna nereis</i>	72.2	72.4	186.8	182.4	-	-	-	-	7	7	10.2	1.77	2	-	-	-	13;13;13;13;13;13;9;9;
<i>Sterna nilotica</i>	-	-	-	-	-	-	-	-	-	-	-	2	-	-	0	0	9;9;13;13;6;9;9;
<i>Sterna paradisea</i>	112	117	279	274	-	-	1	ANA	7	7	19	-	2	-	0	0	1;1;1;1;1;1;6;6;1;1;
<i>Sterna repressa</i>	-	-	247	250	37.4	35.7	-	-	-	-	19	2.4	2	-	0	0	9;9;9;9;1;1;9;1;1;
<i>Sterna sandvicensis</i>	-	-	309	304	-	-	1	-	7	7	35	2	2	-	0	0	1;1;1;1;9;9;9;9;1;9;
<i>Sterna saundersi</i>	-	-	168	165	29.6	28.3	1	-	-	-	-	-	-	-	0	0	9;9;
<i>Sterna striata</i>	125.8	131.9	282.1	277.5	-	-	1	ANA	7	7	-	1.07	2	-	0	0	1
<i>Sterna sumatrana</i>	106	106	228.1	228.6	-	-	1	ANA	7	7	16.1	1.5	2	-	0	0	12
<i>Sterna vittata</i>	-	-	-	-	-	-	1	-	7	7	20	1.29	2	-	0	0	12
<i>Stilia isabella</i>	66	65	203.3	194.7	17.2	16.7	1	GD	7	7	7	1.86	2	-	-	-	12
<i>Synthliboramphus antiquus</i>	206.3	205.7	141.4	142	-	-	1	-	7	7	-	-	2	-	-	-	6
<i>Synthliboramphus hypoleucos</i>	166.1	173.2	120.3	122.5	17	18	1	-	7	7	37.2	-	2	-	-	-	6;6;5;5;5;5;6;1; 5;5;5;1;5;
<i>Thinocorus orbignyianus</i>	134	125	139.9	135.8	16.1	15.9	1	ANA	0	7	15.5	4	0	-	-	-	1;1;1;
<i>Thinocorus rumicivorus</i>	49	60	114	115.6	14	14.3	1	ANA	0	7	8	4	0	0	-	-	103;103;103;103;15;15; 103;103;103;103;18; 103;103;1;1;
<i>Thinornis novaeseelandiae</i>	-	-	121.2	121.1	23.9	22.7	1	AA	7	7	-	-	-	-	0	0	103;103;103;103;15;15; 103;103;103;103;18; 103;103;7;1;
																	1;10;10;10;10;10;7; 10;10;1;1;1;10;10

(Continued)

APPENDIX. TABLE 1. (Continued)

	Male mass (g)	Female mass (g)	Male wing length (mm)	Female wing length (mm)	Male bill length (mm)	Female bill length (mm)	Social mating system	Male display type	Male care	Female care	Egg mass (g)	Clutch size	Chick feeding	Breeding habitat	Male polygamy	Female polygamy	References
<i>Tringa cinerea</i>	69.4	74.8	132	137	45.2	49.2	1	–	–	–	–	–	–	–	0	0	13
<i>Tringa erythropus</i>	142	161	167	170	57.4	59.8	1	AA	7	3	24.5	4	0	–	0	1	13;13;13;13;13;13;13;13;13;13;104;104;3;[51];13;_13;13
<i>Tringa flavipes</i>	80	83.7	159	163	36	36.5	1	AA	7	7	17.4	4	0	–	0	0	13;13;13;13;13;13;13;6;57;6;6;6;_6;_6;6
<i>Tringa glareola</i>	62	73	126	129	28.3	29.3	1	AA	7	4	13.5	4	0	–	0	0	13;13;13;13;13;13;13;13;13;13;13;13;3;8;13;_13;13
<i>Tringa hypoleucos</i>	45.5	50	112	112	24.6	24.5	1	ANA	7	5	12.5	3.9	0	2	0	1	13;13;13;13;15;15;13;13;105;105;3;43;13;13;13;13
<i>Tringa incana</i>	101	116	163	165	38.5	39.9	–	–	7	7	–	–	0	–	–	–	12;12;12;12;12;12;_1;_1;6;_1;_6;_1;_1;_1
<i>Tringa macularia</i>	36.9	48	105	109	23.2	24.1	3	GD	7	0	9	4	0	2	0	4	13;13;13;13;15;15;13;15;106;106;3;13;13;13;13;13
<i>Tringa melanoleuca</i>	164	176	196	199	55.8	56.7	1	AA	7	7	27.9	3.7	0	–	–	–	6;6;13;13;13;13;6;57;6;6;6;6;_1;_1;_1
<i>Tringa nebularia</i>	172	175	191	193	55.1	57	1	AA	7	6	30.5	3.9	0	–	1	0	13;13;13;13;13;13;3;13;43;43;3;13;13;_1;13;13
<i>Tringa ochropus</i>	75	85	144	146	34.5	34.6	1	AA	7	4	15.5	3.9	0	–	0	0	3;3;13;13;13;13;13;13;107;107;3;43;13;_1;13;13
<i>Tringa solitaria</i>	45.1	52.1	131	136	29.2	29.6	1	AA	–	–	–	–	–	–	0	0	13;13;13;13;13;13;6;6;_1;_1;_1;_1;_1;_1;6;6
<i>Tringa stagnatilis</i>	67.1	76	139	142	39.5	40.4	1	AA	7	7	14	4	0	–	0	0	13;13;13;13;13;13;13;13;13;13;13;13;107;13;_1;13;13

APPENDIX. TABLE 1. (Continued)

	Male mass (g)	Female mass (g)	Male wing length (mm)	Female wing length (mm)	Male bill length (mm)	Female bill length (mm)	Social mating system	Male display type	Male care	Female care	Egg mass (g)	Clutch size	Chick feeding	Breeding habitat	Male polygamy	Female polygamy	References
<i>Vanellus miles</i>	264.2	252.8	227.2	223.2	36.1	35.2	1	ANA	7	7	32	3.7	0	–	0	0	10;10;10;10;10;113;7; 113;113;3;113;113; _;10;10
<i>Vanellus senegallus</i>	–	–	236	237	34	33.9	1	–	7	7	23.3	3	0	–	0	0	1;1;1;1;1;1;1;_; 114;114;1;1;1;_;1;1
<i>Vanellus spinosus</i>	191.5	183.8	203	200.7	27.2	26.7	1	ANA	7	7	16.4	4	0	2	0	0	13;13;13;13;13;13;13;13; 13;13;3;13;13;13;13; 13
<i>Vanellus superciliosus</i>	–	–	–	–	–	–	1	GD	7	7	–	–	–	–	0	0	1
<i>Vanellus tectus</i>	–	–	191	190	24.3	23.3	1	–	–	–	–	–	–	–	0	0	1
<i>Vanellus tricolor</i>	–	–	196.3	193.4	22.5	23	1	ANA	7	7	21.6	3.75	0	–	0	0	_;10;10;10;10;10;7; 10;10;10;10;10; _;10;10
<i>Vanellus vanellus</i>	211	226	229	224	24.1	23.9	2	AA	7	6	25.5	3.9	0	2	1	1	13;13;13;13;13;13;13;13; 43;43;13;13;13; 13;13;13
<i>Xema sabini</i>	194	177	276	267	24.9	24.1	1	ANA	7	7	–	2	1	2	0	0	13

^aScored variables are defined as follows: social mating system (1, monogamous; 2, polygynous; 3, polyandrous); male display type (GD, ground display; ANA, aerial nonacrobatic; AA, aerial acrobatic); male care and female care (scored independently for males and females: 0, no care; 1–3, provides care during incubation; 4–6, provides post-hatching care; 7, full care until hatching; see Székely and Reynolds, 1995 and Reynolds and Székely, 1997 for full details); chick feeding (0, chicks self-feed from hatching; 1, chicks self-feed after approximately 7–10 days; 2, chicks fed by parents until fledging); breeding habitat (0, desert and

semidesert; 1, dry grassland and tundra, and dry forest; 2, wetland, marsh, seashore, lake, and river); male and female polygamy (scored independently for males and females: 0, monogamous; 1, rare polygamy (<1% or only anecdotal reports of polygamy); 2, occasional polygamy (1–5%, polygamy is known to occur but it is infrequent); 3, moderate polygamy (6–20%, polygamy is well known but is not regarded as typical of the species); 4, frequent polygamy (>20%, polygamy is considered the main mating system for the species); Underscores in reference column indicate no data available; see [Thomas *et al.* \(2006\)](#) for full details).

(1) [Urban *et al.* \(1986\)](#); (2) [Tarboton \(1976\)](#); (3) [Johnsgard \(1981\)](#); (4) [Pitman \(1960\)](#); (5) [Gaston and Jones \(1998\)](#); (6) [Poole and Gill \(1992–2003\)](#); (7) [del Hoyo *et al.* \(1996\)](#); (8) [Dementiev and Gladkov \(1969\)](#); (9) [Cramp \(1985\)](#); (10) [Marchant and Higgins \(1993\)](#); (11) [Hay \(1979\)](#); (12) [Higgins and Davies \(1996\)](#); (13) [Cramp and Simmons \(1983\)](#); (14) [Nettleship \(1973\)](#); (15) [Jehl and Murray \(1986\)](#); (16) [Dunning \(1993\)](#); (17) [Handel and Gill \(2000\)](#); (18) [Schönwetter \(1967\)](#); (19) [Walters \(1984\)](#); (20) [Blake \(1977\)](#); (21) [Hayman *et al.* \(1986\)](#); (22) [Anderson \(1991\)](#); (23) [Westwood \(1983\)](#); (24) [Brown \(1948\)](#); (25) [Ali and Ripley \(1996\)](#); (26) [Myers *et al.* \(1982\)](#); (27) [Parmelee and Payne \(1973\)](#); (28) [Soikkeli \(1967\)](#); (29) [Nettleship and Maher \(1973\)](#); (30) [Holmes and Pitelka \(1964\)](#); (31) [Parmelee *et al.* \(1968\)](#); (32) [Holmes \(1973\)](#); (33) [Holmes \(1972\)](#); (34) [Pitelka \(1959\)](#); (35) [Miller \(1985\)](#); (36) [Miller \(1983\)](#); (37) [Prater *et al.* \(1977\)](#); (38) [Gratto-Trevor \(1991\)](#); (39) [Tomkovich \(1989\)](#); (40) [Hildén \(1975\)](#); (41) [Howe \(1982\)](#); (42) [Szekely and Lessells \(1993\)](#); (43) [Nethersole-Thompson and Nethersole-Thompson \(1986\)](#); (44) [Reiser and Hein \(1974\)](#); (45) [Graul \(1973b\)](#); (46) [Graul \(1975\)](#); (47) [McCulloch \(1992\)](#); (48) [Lenington \(1984\)](#); (49) [Bergstrom \(1981\)](#); (50) [Jones \(1963\)](#); (51) [von Blotzheim *et al.* \(1975\)](#); (52) [Burger \(1981\)](#); (53) [Pringle \(1987\)](#); (54) [Miskelly \(1990\)](#); (55) [Pullainen \(1970\)](#); (56) [Tomkovich \(1990\)](#); (57) [Figueroa \(1999\)](#); (58) [Tuck \(1972\)](#); (59) [Saether *et al.* \(1986\)](#); (60) [Webster \(1941\)](#); (61) [Groves \(1984\)](#); (62) [Wakefield \(1988\)](#); (63) [Summers and Cooper \(1977\)](#); (64) [Harris \(1967\)](#); (65) [Nol \(1985\)](#); (66) [Nol *et al.* \(1984\)](#); (67) [Pierce \(1986\)](#); (68) [Thong-aree *et al.* \(1995\)](#); (69) [Hoffman \(1949\)](#); (70) [Roberts \(1991\)](#); (71) [Kelso \(1972\)](#); (72) [Osborne \(1982\)](#); (73) [Osborne and Bourne \(1977\)](#); (74) [Jenni and Collier \(1972\)](#); (75) [Jenni and Betts \(1978\)](#); (76) [Moynihan \(1962\)](#); (77) [Kitchinski and Flint \(1973\)](#); (78) [Nowicki \(1973\)](#); (79) [Hagar \(1968\)](#); (80) [Lind \(1961\)](#); (81) [Butchart \(2000\)](#); (82) [Mathew \(1964\)](#); (83) [Jehl \(1973\)](#); (84) [Tarboton and Fry \(1986\)](#); (85) [Grant, M.C. \(in literature\)](#); (86) [Gill *et al.* \(1991\)](#); (87) [Baker-Gabb *et al.* \(1990\)](#); (88) [Bennett \(1983\)](#); (89) [Kistchinski \(1975\)](#); (90) [Hildén and Vuolanto \(1972\)](#); (91) [Parmelee *et al.* \(1967\)](#); (92) [Jehl \(1975\)](#); (93) [Gibson \(1971\)](#); (94) [Brown \(1950\)](#); (95) [Maclean \(1967\)](#); (96) [Kobayashi \(1955\)](#); (97) [Höhn \(1975\)](#); (98) [Burger and Gochfeld \(1990\)](#); (99) [Mendall and Aldous \(1943\)](#); (100) [Hirons \(1983\)](#); (101) [Colwell \(1986\)](#); (102) [Höhn \(1967\)](#); (103) [Maclean \(1969\)](#); (104) [Hildén \(1979\)](#); (105) [Yalden and Holland \(1992\)](#); (106) [Oring \(1986\)](#); (107) [Glutz von Blotzheim *et al.* \(1977\)](#); (108) [Pitelka *et al.* \(1974\)](#); (109) [Hall \(1964\)](#); (110) [Walters \(1982\)](#); (111) [Ward \(1989\)](#); (112) [Tuljapurkar \(1986\)](#); (113) [Barlow *et al.* \(1972\)](#); (114) [Little \(1967\)](#); (115) [Melnikov, J. I. \(personal communication\)](#).

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