

# sex & the single plover



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Life on earth managed without sex for more than two billion years, but it was only after sex evolved some 1.2 billion years ago that we saw the rapid diversification of life forms. The main advantage of sexual reproduction is that combining genes from two parents greatly enhances the genetic diversity of the next generation. Sex literally provides the variation on which natural selection operates.

This might seem a long way from the sex life of plovers, but bear with me. If the main advantage of sex – with all its distracting angst and aggression – is to create diversity, it stands to reason that promiscuity should be the norm. All other things being equal, you should

*above White-fronted Plovers are unusual among plovers in not being known to divorce during the chick-rearing period to pursue breeding opportunities with other individuals.*

have sex with many different individuals to increase the likelihood that at least some of your offspring will survive, whatever hurdles are presented by an ever-changing world.

Because humans are largely monogamous, we tend to forget this fundamental premise of sex. But it is humans who are unusual; most animals and plants are promiscuous. For example, more than 90 per cent of mammals are polygamous. Monogamy is thought to have evolved among humans because it benefited males to remain with their partners to protect their offspring, largely from infanticide by other males.

Birds too are unusual in being largely monogamous. This results from the high degree of parental care needed to raise a brood of chicks to independence. Of course we now know that many birds are only socially monogamous; like humans, both sexes might seek out extra-pair

mating opportunities but remain with a social partner for the sake of the children. Such cuckoldry only adds further tension to an already tricky partnership.

Mating systems among birds become more varied as the amount of parental care decreases. For example, in birds with precocial chicks that can feed themselves, there is the opportunity for one partner to desert the family to start a new breeding attempt once the chicks hatch. And if one bird can both incubate and rear the chicks, then the options for unequal parental investment are even greater.

Shorebirds provide one of the classic case studies of the diversity of mating systems as they exhibit the full range, from polygamy (for example, Ruff and Pectoral Sandpiper) through monogamy to polyandry (for example, Spotted Sandpiper and some jacanas, phalaropes and painted-snipes). As



expected, species with chicks that are unable to feed themselves, such as oystercatchers and thick-knees, are socially monogamous, whereas species with more 'exotic' mating systems have chicks that require little parental care.

In nature, all marriages tend to be expedient. As soon as one partner can raise more offspring by deserting the pair bond, selection favours that option. This rather begs the question, why don't all shorebirds with precocial chicks that feed themselves experience strong competition between the sexes, pushing towards either polygyny or polyandry? In order to tease apart the factors underpinning different mating choices, it is informative to study the intermediate cases, where individuals vary in their choices.

That brings us to the plovers. Most of the 33 plover species in the subfamily Charadriinae are regarded as socially

monogamous. Pairs defend breeding territories, share incubation duties and work together to protect the chicks from predation during the vulnerable nestling period. However, it is not essential for both parents to assist with chick rearing. This opens the door for one member of the pair to leave its mate literally holding the babies while it absconds to breed with another partner.

In the 1980s, studies of individually marked Kentish Plovers found that serial polygamy is fairly common in this species. The factors underpinning the decision to abandon an existing brood are complex. Each parent has to consider the needs of its current brood and the likelihood of the chicks surviving to fledge (with and without both parents present), the behaviour of its partner, its condition (is it ready to breed again?) and most importantly, the chances of finding a new mate.

*A White-fronted Plover raises its wings in an attempt to intimidate an intruder venturing too close to its nest. Most plovers share incubation duties and nest defence, but in some species once the chicks hatch one member of the pair leaves to pursue other breeding opportunities.*

A detailed study of Snowy Plovers in Mexico by Krisztina Kupán et al. (2019, *bioRxiv* doi: 10.1101/2019.12.19.880856) found that parents are more likely to desert small broods, often leaving immediately after the death of a chick. This makes sense because the evolutionary 'reward' from their current breeding attempt has just decreased. Parents are also more likely to abscond early in the breeding season, when there is still enough time to undertake another breeding attempt. Parents that abandon their broods raise more chicks than those that remain with their partner, which runs >





the short breeding season limits the options for multiple attempts.

The only species where no divorces have been recorded is the White-fronted Plover. This is not just a consequence of a small sample size. Thanks to Penn Lloyd's long-running study of White-fronted Plovers breeding on the west coast of the Cape Peninsula, we have more data on mate fidelity for White-fronted Plovers than for any other plover species. Quite why they remain together through thick and thin is unclear, but as we'll see shortly, they are also unusual in other ways.

Oddly, when one plover absconds, it is the female that is more likely to desert her mate. Female Snowy Plovers are three times more likely than males to abandon their broods to pursue other breeding opportunities, and similar female-biased divorce occurs in most other plover species. The Killdeer is the only species studied to date where males might be more likely than females to leave their broods. Females also go to great lengths to find new mates, with some Kentish Plovers moving more than 100 kilometres between successive breeding attempts. By

counter to the general pattern of divorce in birds. However, plovers typically retain the same mate if the nest fails before the chicks hatch, because re-laying intervals tend to be shorter when they remain with the same mate.

Expanding on this research, Naerhulan Halimubieke and colleagues (2020, *Scientific Reports* 10: 15576) report levels of brood abandonment and divorce among eight species of plovers from around the world. Divorce rates range from 0 to 78 per cent, with the highest levels in Snowy and Kentish plovers. However, there is considerable variation

in divorce rates among different populations of Kentish Plovers, ranging from 24 per cent on the Cape Verde Islands to 80 per cent in China. The likelihood of divorce increases with breeding success and decreases at higher latitudes, where



above A male White-fronted Plover broods his one-day-old chick. The chicks can feed themselves within hours of hatching, but continue to benefit from parental protection.

right Unlike most plovers, where females are more likely to abscond and leave the male to raise the chicks, the much faster re-mating time for male than female Kittlitz's Plovers suggests that they may be serially polygamous. As in humans, the availability of other breeding opportunities is a key factor determining mate fidelity in plovers.

comparison, divorcing males seldom move far when they take up with a new partner.

The tendency towards female-biased divorce, and thus serial polyandry, has evolved in at least seven plover species. It reaches its peak in the Eurasian Dotterel, where females are larger and more brightly coloured than males. Females compete aggressively for access to mates and most play little role in incubation or chick rearing. However, the degree of female investment varies among populations and a female can be induced to take on all the incubation duties if her mate is removed. Such within-species flexibility is mirrored in Greater Painted-snipes, which typically are polyandrous but can be monogamous at low population densities, such as occur in much of southern Africa, presumably because they lack the opportunity to move on to another male.

Quite why females tend to hold the balance of power among most plover species is still debated. In most birds (and humans), males are more likely to leave their partners. This pattern is thought to result from the reduced initial investment by males in each breeding effort (eggs cost a lot more to produce than sperm). This allows males to 'blackmail' females into supporting the chicks through to fledging. Plovers might buck this trend if there is an excess of males in the adult population. Theoretical models show that females are more likely to abscond when there are many more males than females, making it easy for them to find a new mate.

There is little information on sex ratios among plovers. In one well-studied population of Kentish Plovers in southern Turkey, the sex ratio among chicks is equal at hatching, but for unknown reasons becomes increasingly male-biased as the chicks approach independence. This imbalance probably persists into adulthood, because females re-mate within a few days after the experimental removal of their partners, whereas males typically take a few weeks to find a new mate (Székely 2019, *Journal of Ornithology* 160: 923–933). However,



re-mating intervals for Kittlitz's Plovers who had their partner temporarily removed are shorter for males than females, suggesting an excess of females in this species. This inference is supported by males having higher adult survival rates than females.

Once again, the White-fronted Plover is anomalous. In the same experiment as that conducted on the Kittlitz's Plovers, both sexes rapidly obtained new partners within a few days after the removal of their mate and did so while remaining on their original territory, irrespective of the sex of the bird removed. However, they all reverted to their original partners once the mates were released from their temporary captivity. By comparison, all Kittlitz's Plovers remained with their new partners, even after their original partners were released.

If females are likely to shirk their parental duties, they need to reassure their mates that they have not been cuckolded. A male is more likely to continue to care for a brood of chicks if he is confident that he is the biological father. And

*Despite its wide distribution, surprisingly little is known about the breeding biology of the Three-banded Plover. As far as is known, it appears to be entirely monogamous.*

indeed the rate of extra-pair paternity among plovers is very low, occurring in only 0–4 per cent of chicks, irrespective of mating system (Maher et al. 2017, *Journal of Avian Biology* 48: 910–920). By avoiding extra-pair behaviour early in the marriage, females increase their chances of stepping out later on!

It has been argued that the diversity of shorebird mating strategies is an adaptive response to the often rather variable habitats in which they breed. And the fact that mating systems vary within species gives some hope that shorebirds can adapt rapidly to changing conditions. Sadly, however, their rapid decline in many parts of the world suggests that they are struggling to cope with the swift pace of global change. ♦

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