Birds and Divorce

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It is often instructive to study the social behavior of birds because, like humans, they routinely provide biparental care and are socially monogamous. And like us, birds divorce. But instead of the complicated emotions that drive our own behavior, birds are presumably motivated by powerful biological forces to divorce. The key to understanding divorce in birds is in understanding their reproductive behavior and the urge to maximize individual lifetime reproductive success, i.e., the total number of young that are successfully fledged over a lifetime. This paper reviews the literature on avian divorce, specifically focusing on the benefits and costs of divorce.

With regard to birds, divorce is generally taken to mean that at least one partner pairs with another individual, even though both partners are still living and residing within the same population. Needless to say, the notion of avian divorce bears little resemblance to what we think of as divorce. The concept is simply a convenient way for ornithologists to measure mate fidelity. By definition, in any given breeding season, the percentage of surviving mates that "divorce" is one hundred minus the percentage of surviving pairs that reunite (Ens *et al.* 1996). Divorce is an active choice by at least one individual within the population rather than some unintended consequence as occurs when partners during one season migrate separately and do not return to the same breeding site. Divorce rates vary widely among species, from no known divorce in the Australian Raven (*Corvus coronoides)* and Wandering Albatross (*Diomedea exultans*) to virtually 100 percent in House Martins (*Delichon urbica*) (Choudhury 1995). Field work done on European tits showed that divorce rates can even vary between populations of the same species (Dhondt and Adriaensen 1994).

There are three principal explanations for why divorce is adaptive in birds: the incompatibility hypothesis, the better-option hypothesis, and the asynchronous arrival of paired birds on the breeding grounds. The incompatibility hypothesis suggests that while neither individual in a pair is inherently of poor quality, their interaction is unsuccessful and they can both improve their reproductive fitness by divorcing and finding another mate, one with whom they are more compatible (Johnston and Ryder 1987, Ens *et al.* 1993, Catry *et al.* 1997). The better-option hypothesis states that divorce takes place when one member of the pair chooses a higher quality mate in order to improve its reproductive success, making the other partner a victim of this decision (Ens *et al.* 1993, Choudhury 1995). The asynchronous-arrival hypothesis argues that the partner that first arrives on the breeding ground will wait only so long for the other partner to return before choosing another mate in order to assure itself of a breeding opportunity that season (Ens *et al.* 1996, Olsson 1998). One version of the asynchronous-arrival hypothesis has been dubbed the "musical chairs hypothesis," the idea being that if a bird arrives too late, it will find its place occupied by another individual (Dhondt and Adriaensen 1994).

It is almost always the female that initiates the divorce. This is true for Blue Tits (*Parus caeruleus*) (Dhondt and Adriaensen 1994), Willow Tits (*Parus montanus*)

(Orell *et al.* 1994), Black-capped Chickadees (*Parus atricapillus*) (Smith 1992), Oystercatchers (*Haematopus ostralegus*) (Ens *et al.* 1993), and Great Skuas (*Catharacta skua*) (Catry *et al.* 1997). A variant of the axiom that male birds attract and females choose appears to hold true in the case of divorce. Females may assess their breeding options using extra-pair copulations and then divorce their present mate if they find a more attractive partner (Cezilly and Nager 1995).

Benefits of Divorce

It is generally accepted that the principal reason for a bird to divorce its partner is to maximize its lifetime reproductive success (Choudhury 1995). For individuals seeking to improve their breeding performance, the basic benefits of divorce could entail finding an older, more experienced mate (Grant and Grant 1987) or a higher quality territory. Divorce would be beneficial if a higher quality territory is available, but only one of the partners wants to move (Lindén 1991).

Let us examine the evidence of the relationship between reproduction and divorce for several species. A study of the Large Cactus Finch (*Geospiza conirostris*) showed that females that divorced younger males within a breeding season and then mated with older males improved their reproductive success because the more experienced males were better providers of parental care, providing more food and more vigorous nest defense than the previous mate (Grant and Grant 1987). Among Willow Tits, females that divorced typically remated with males that were older than their original mate and experienced greater reproductive success after remating. Divorced males had quite the opposite experience, and some were unable to find a mate the breeding season following divorce (Orell *et al.* 1994). Thus, the behavior of Willow Tits supports the better option hypothesis. This is also true for Black-capped Chickadees, where all but one of the individuals initiating a divorce moved up in rank within the flock. Enhanced status within a chickadee flock brings with it greater advantages, notably access to resources (e.g., a breeding territory) and more copulations for alpha males (Smith 1992, Otter and Ratcliffe 1996). Lindén (1991) experimentally manipulated the brood size of Great Tits (*Parus major*) to see whether there was an impact on the divorce rate. He found that those broods that were artificially enlarged had a lower divorce rate than pairs whose brood size was artificially reduced. In a study of divorce in Blue Tits, the researchers used the presence of unhatched eggs in a nest as a measure of the virtue of divorce, and they found that both males and females of the species benefited from divorce by having fewer unhatched eggs in their nests after remating (Kempenaers *et al.* 1998).

Costs of Divorce

Divorce is not without its costs. Changing mates may have an adverse effect on lifetime breeding success if the time required to remate is long. If the search for another mate takes place while the individual is already mated, the success of current reproductive activity may be jeopardized (Ens *et al.* 1996). Blue tits that divorced laid their eggs later and successfully fledged fewer young in the year preceding divorce than did pairs that remained together (Dhondt and Adriaensen 1994). Among Larids (both gulls and terns), by all relevant measures, recently divorced individuals had

lower reproductive success than continuing pairs: the laying date was always later, the clutch size was smaller, and the number of young fledged was lower (Johnston and Ryder 1987). Barnacle Geese (*Branta leucopsis*) require 3-9 months to find a mate, suggesting that some birds may not breed the following season (Black *et al.* 1996). The Wandering Albatross is a long-lived species (33 years for males, 25 years for females) with a low divorce rate. Mate fidelity may be adaptive for this species because of the length of time required to remate. Widowed males needed 3.2 years, and widowed females 2.3 years to find a new mate, resulting in a decline in the lifetime chick production rate of 14.3 percent for males and 15.2 percent for females (Jouventin *et al.* 1999). Mate change among Great Skuas, another species with a low divorce rate, was also costly because new pairs laid their eggs later in the season and reared fewer young (Catry *et al.* 1997). For these two species divorce may be low because the reproductive costs are too high.

Earlier I said that waiting for a partner to return entails a risk. This is nowhere clearer than in the case of King and Emperor Penguins, the largest penguin species (Olsson 1998; Bried *et al.* 1999). Both are long-lived species, but in contrast to other species with a long-life expectancy, these two have high divorce rates. In neither case was breeding performance a cause of divorce, nor did divorce affect the production of young in the following year. Instead Emperor Penguins divorced because of the asynchronous arrival of mates but only when females returned to the breeding grounds before their previous mates. Asynchrony was also a factor in explaining divorce in the King Penguin colony. Indeed, the greater the asynchrony, the greater the likelihood of divorce. Asynchrony therefore explains part, but not all of divorce. Olsson (1998) proposed the "expensive fat-storing hypothesis" to explain why King Penguins divorced. When the birds arrive on the breeding grounds, both sexes have only about half of their maximum possible fat reserves, and these reserves are close to zero by the time their fast ends. King Penguins whose mates arrive late choose a new one before they exhaust all their fat reserves. While they are capable of storing fat reserves sufficient to allow them to wait for the arrival of their previous mate, they often do not do so, suggesting that the costs of storing additional fat is greater than the benefits derived from mate retention.

The impact of asynchrony was also significant for Common Terns (*Sterna hirundo*) (González-Solís *et al.* 1999). The median arrival asynchrony for divorcing pairs was 7.5 days, while pairs that remained united only arrived 2 days apart. If there was a difference of more than 16 days in the arrival of mates, they always divorced.

Factors Predicting Divorce

Based on what we know about the costs and benefits of avian divorce, it is possible to make a number of predictions about the conditions under which divorce is likely to occur. Populations in which there is substantial variation in quality provide opportunities for individuals to search for mates that will improve their breeding success (Cezilly and Nager 1995). Willingness to wait for the previous partners seems most likely to occur in long-lived species since it is only a small proportion of total lifetime productivity that might be lost. There are a number of studies that have shown

that long-lived and reproductively monogamous species have low divorce rates (Johnston and Ryder 1987, Choudhury 1995). On the other hand, short-lived species do not have the luxury of missing a breeding season, and it is among these species that divorce rates are highest. These species typically have high mortality rates and therefore a low probability that both mates will survive to the next breeding season. Selection may therefore favor divorce and frequent remating (Choudhury 1995). As females grow older, there appears to be a decrease in the likelihood that they will divorce their mates, possibly because there is a direct correlation between age and reproductive success (Orell *et al.* 1994). The number of unpaired individuals in a population will also determine the divorce rate. Unavailability of unmated individuals will impose a constraint on mate switching and increase the costs of divorce. There is evidence that when openings do occur through predation, for example, the divorce rate rises (Ens *et al.* 1993). It has also been suggested that mate retention may be more tied to nest site fidelity than it is to a particular individual. If so, then one would predict a high divorce rate among species with low site fidelity as individuals seek a higher quality site, either to find a better food supply or to cope with frequent habitat changes (Ens *et al.* 1996). Finally, asynchronous arrival at the breeding grounds and uncertainty about a partner's return would encourage divorce if that breeding season was in danger of being lost (Olsson 1998).

Conclusion

There is little doubt that divorce is an adaptive strategy for birds in their effort to maximize lifetime reproductive success. However, this survey of the literature shows that there is no blanket explanation for why birds divorce. The large differences in divorce rates between species are likely explained by the broad range in life histories, and therefore differential costs and benefits associated with divorce. This means that there are several plausible explanations for divorce. Even though we are confident that the ultimate goal is to maximize lifetime reproductive success, it may be that we do not know all of the proximate factors leading to divorce. There is a need for more theoretical work as well as additional field work to study the phenomenon of divorce. In particular there is a need for experimental work to tease apart the complex reasons why divorce occurs.

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