

The reproductive behavior of birds

# Nest of Discord

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**Dr. Dariusz Bukaciński and Dr. Monika Bukacińska study the behavior and ecology of gulls, and have spent 20 years uncovering the secrets of colonies of gulls' species**

**The ostensible ideal of the “harmonious” family life enjoyed by birds fails to account for the real story: forced compromises and the constant battle by each gender to secure advantages and dominance over the other**

Which mate to choose? Is this particular mate the right one to have children with? If not, then who is? And how should the parenting duties be divided so that healthy off-

spring are raised, but neither parent “works themselves to death” in the process? These are dilemmas that plague not just humans, but also the close to 92% of the world’s bird species that lead “monogamous” lives (note that monogamy is defined somewhat more liberally for birds than for humans, as a bond between a single male and a single female that lasts for at least 20–25% of their reproductive period). Similar dilemmas are likewise faced by the far less numerous “polygamous” species, which maintain long-term relationships with several partners at the same time. Only the few species that have not been found to maintain any lasting inter-gender bonds are exempt from such parenting and relationship conundrums.

Until recently, reproductive behavior in monogamous pairs of birds was viewed in terms of “harmonious cooperation between



**Harmonious cooperation between parents for the good of the species? Forget it! Research shows a “gender conflict” is something practically inevitable**

Robert Dejrowski

Childrearing parents  
are not always  
the genetic parents  
of all the nestlings  
in their brood



Andrzej Różycki

the two genders for the good of the species.” This view could only be adjusted once it was grasped that natural selection, including its mechanisms aimed towards maximizing reproductive success, operates on the level of the individual specimen (or even on the level of its genes). A pair of birds attending to a clutch of eggs in fact constitute two individual specimens, each of which has the option of acting against their opposite gender, and each of which are using their mate to for the purpose of helping spread their genes to the maximum possible extent. This may indeed result in behavior that does serve “the good of the species,” but exclusively as a side effect of serving the individual’s own interests. If we view the “domestic life” of birds from this standpoint, it becomes clear that a gender conflict is practically inevitable – at every stage of procreation, from choosing a mate to rearing the young.

### Monogamy pays off

The different sizes of the gametes produced by the two genders and their consequentially different initial investment in producing offspring necessitate different strategies for maximizing their reproductive success. Here we already have our first “bone of contention” – and at the very outset of the parenthood process. The production of sperm is not very costly in relative terms for males, and so they can increase their reproductive success by copulating with many females. Females, producing incomparably larger gametes, can achieve the same aim chiefly by raising the quality of their offspring.

Now for something surprising: despite these lopsided interests, monogamy frequently remains the most favorable solution for both genders. This is especially true for species where nestlings need to be fed by their parents. For most sea and predatory birds, where both parents brood the eggs and cooperate in

rearing the young, the death or absence of one of the mates spells complete reproductive disaster. For other species (such as the sparrow family), the disappearance of one of the mates may not necessarily lead to the loss of the brood, but it will strongly curtail the reproductive success of each of the genders. Research that involved removing the male from the picture during the brooding period has shown that breeding success then dropped by 35% for the seaside sparrow (*Ammoramus maritimus*) and by nearly 70% for the dark-eyed junco (*Junco hyemalis*), as compared to pairs where both parents raised their young together.

Sometimes there is an even stronger argument for remaining monogamous: the males’ limited ability to maintain stable ties with more than one female. Fierce competition among males frequently prevents them from winning over a second female. Moreover, a female stands to lose by losing her monopoly on the male’s assistance. As a consequence, birds most frequently remain paired as they rear their young, although each of the genders can indeed maximize their reproductive success in more subtle ways. How? For example, by means of *extra-pair fertilization* (EPF), or by depositing some of their own eggs into the nests of other pairs, known as *intraspecific brood parasitism* (ISBP).

Males that follow such a mixed strategy can increase their reproductive success by increasing the number of their own offspring. What do females stand to gain? If fertilization occurs as a result of rape, then not much. But a female actively involved in copulation “on the side,” controlling the frequency of intercourse and her choice of males, can not only increase her certainty of fertilization but also raise the genetic diversity of broods and the quality of her offspring.

The large disparity observed between the frequencies of extra-pair copulation (EPC) and

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consequent extra-pair fertilization, females' ability to prevent sperm from entering the reproductive canal, and their ability to store sperm from various males for an extended duration, all indicate that females are able to manipulate the reproductive process to a significant extent. This is also why males usually have limited trust in the females they maintain long-term relationships with, and take measures to guard their own fatherhood. During the fertile period they stick very close to their partners (known as *mate guarding*), or they copulate with them as frequently as possible, especially right after one of them returns from an absence.

### Taking a good look at "fidelity"

Mindful of the benefits and potential costs of maintaining a relationship with a single partner, let's take a closer look at how "fidelity" looks in practice among theoretically monogamous bird species. As it turns out, the species within this group vary greatly. Even though "extramarital" copulation does sometimes occur among birds such as the northern fulmar (*Fulmarus glacialis*), merlin (*Falco columbarius*), and barnacle goose (*Branta leucopsis*), here monogamous social patterns overall coincide with strict genetic monogamy. But among the common gull (*Larus canus*) population we studied on the Vistula River,

15-35% of the observed females engaged in EPC each year. Still, despite these considerable endeavors on the part of "foreign" males, only 3.6% of nestlings, from 8.3% of nests, were in fact sired by a "foreign" father. Research using considerably more extensive data nevertheless shows that the frequency of EPF may range up to twice this figure in certain years. Such "extra-pair fathers" are most frequently neighbors (shouldn't we expect?) or a female's former partner in previous years - which just goes to prove the old adage that old loves are never forgotten. Nevertheless, the least faithful "monogamous" species were found to be the red bunting, yellowhammer, American redstart, and tree swallow, for which 37-54% of nestlings, from 59-86% of nests (!), were found to be result of EPF. Moreover, as many as 97% of red bunting females engaged in EPC!

The practice of planting eggs in foreign nests is neither as frequent or as widespread as EPF. Female starlings (*Sturnus vulgaris*) are among the leaders here, laying eggs in 5-40% of the nests of other females. American winter wren (*Troglodytes t. hiemalis*) seek a "free ride" for their young in up to 30% of nests. Female cliff swallows (*Hirundo pyrrhonota*) are even able to carry already-laid eggs from their own nests and deposit them in the nests of other females (!), thereby reducing their own parenting costs.

### Not to get taken for a ride

Another source of conflict between avian pairs is the division of labor in caring for the brood. Models of parental behavior most frequently involve two opposing scenarios. The first assumes that parents should adapt their current contribution so as to minimize the likelihood of "wasting" the effort they have already invested. In line with this logic, birds that have already invested a lot in a given brood should continue to make a high degree of effort. The other scenario works entirely in the reverse: greater parental investments during an earlier stage of childrearing will result in providing worse care during the remainder of the breeding season. How do things look in practice? Birds that have short life-spans (such as some of the sparrow family), for whom every season might be their last, usually strive to make a maximal investment in each brood, especially if this involves relatively low-cost efforts. Birds which enjoy longer life-spans, in turn, hav-

Rape does occur among birds, but females are able to prevent sperm from entering their reproductive canal



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Some bird species maximize their reproductive success by depositing some of their own eggs into the nests of other pairs (as in the case of this black-headed gull's nest)



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In case of smaller, short-lived birds (like these black redstarts), each of parents will increase their own effort to compensate for their "delinquent spouse," who doesn't work hard enough

ing an interest in ensuring that their current efforts should have the smallest impact on their own fertility, success, and survival in subsequent years, usually behave otherwise.

We can again take the common gull as an example. Females which we induced to lay an additional egg (by taking away the first egg immediately after it was laid) offered significantly worse care to their offspring, while brooding their eggs and especially after the nestlings hatched. How should their partner behave in such a situation? Theories of cooperation between the pair envision that the optimal reaction of the other parent in such a situation should be to increase their own effort to compensate for the "delinquent" parent, albeit not to up the same level of care as would be ensured if their partner was "doing his or her job." And indeed, the male partners of such "delinquent" common gull females were seen to work so hard during the incubation stage and first weeks of hatchling life that they almost compensated fully for the poorer care being provided by the females. In consequence, the offspring survival rate was comparable to that seen among the control group. However, during the later chick development stage, if the females continued to work less hard than those which had laid their eggs normally, the males likewise began to take poorer care of the young. The growth and survival of young from these nests was as a consequence worse than in the control nests. Our research results also show that cooperation between pairs is a very dynamic process, where each of the parents tailors their current efforts to the intensity of care being provided by their partner.

### Dispelling illusions

The analysis of parental behavior among birds leads to conclusions that differ quite significantly from our intuitive impressions. Instead of concerted, honest, hardworking behavior on the part of both parents, we frequently see the pursuit of individual interests, very limited trust, and partners constantly keeping an eye on one other. Moreover, due to the occurrence of "marital infidelity" and the practice of depositing eggs with foreign parents, hatchlings from the same nest are not always genetic siblings. This may give rise to more conflicts, this time between parents and their offspring, or among the siblings themselves. Under such conditions, is there any room for any sort of unselfish action? Probably not, one has to assume. Even the cases of chick adoption that we observed in gull colonies were hard to interpret in terms of "pure altruism." Conflicts (as well as individual interests) seem to be a constant element of all social behavior, and not just among birds. The trick lies in being able to resolve these conflicts well. ■

#### Further reading:

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