## THE MATING GAME

By Marta Hersek

Avian characteristics that are especially fascinating to birders — elaborate song, ornate plumage, striking coloration — have also been the focus of much inquiry and debate among researchers. The Peacock's tail seems to be so burdensome; the bright red of the Cardinal must make it more conspicuous to predators; and the singing and displaying of a Mockingbird at the top of a tree is surely energetically costly. Charles Darwin in *On the Origin of Species* (1859) asked, "Why have such characters evolved?" Today we are still trying to find an answer to that question.

Darwin's suggestion, which most people still agree with, was that such traits have evolved via sexual selection. As under natural selection,* heritable traits that confer an advantage to the bearer of the traits become more common in the next generation. Under sexual selection, the traits confer a reproductive advantage due to the ability to better (1) compete with others of the same sex, or (2) attract individuals of the opposite sex. For example, traits that are important in male-male competition include large male body size, weapons (such as spurs), and song. It is relatively easy to imagine how such features could evolve: the male that dominates during a fight wins the territory or access to the female. He then fathers many offspring, out-reproducing his competitor. He passes on his genes — including those for large size or long spurs — to those offspring, so that his genes are better represented in the next generation than his rival's genes. We call this mode of sexual selection "intrasexual selection."

Traits that make an animal (usually a male) more attractive to the opposite sex include elaborate plumage, ornaments such as wattles and combs, and song (note that song can function in both scenarios, as can many traits). This type of sexual selection is termed epigamic (or intersexual) selection. It is rather more difficult to think about how epigamic selection works. That is, what cues should a female use to choose a mate? What sort of benefit would a female obtain by choosing to mate with, for example, an extravagant, brightly colored male, rather than a dull one? Is it really, as Darwin (1859) suggested, that "a great number of male animals . . . have been rendered beautiful for beauty's sake" ? The paradox that presented itself to Darwin was how an animal that was more

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*Natural selection is the mechanism for evolution which Charles Darwin elucidated. Basically, the theory is that (1) more organisms are produced than survive; (2) there is variation in heritable characteristics which affect survival and/or reproduction; and (3) those animals that have particular characteristics which allow them to survive and/or reproduce better than others will leave more offspring, and hence more of their genes, in the next generation.

vulnerable, or less efficient in its environment, could be preferred as a mate. In this article I'll focus on epigamic selection, and discuss our current understanding of how and why males have evolved gaudy coloration and extravagant ornamentation.

## Cues Available to Choosy Females

First, we must discuss what types of traits or cues females might use when choosing a mating partner. I say females because generally they put more energy into the production of their offspring, and so would be expected to be the "choosier" sex. Females are limited, compared with males, in the number of offspring they can produce, and they invest relatively more in each offspring (including investment in eggs, incubation, etc.). It is imperative, then, for females not to "waste" reproductive effort with a low-quality mate. Males, on the other hand, make many relatively inexpensive sperm, and they often expend little or no effort in caring for young. Their best reproductive strategy is usually to try to mate with as many females as possible; by definition, then, males are often not choosy with respect to mating partners.

So how should females go about choosing a good mate? Mate choice cues available to females are generally placed into three categories: (1) arbitrary traits; (2) indicators of the resources or parenting ability of the male; or (3) indicators of the male's genetic quality.

## Arbitrary Traits

The first possibility, that mate choice is based on some arbitrary trait, seems to fit in with Darwin's "beauty for beauty's sake," and was actually first postulated by him (Darwin 1871). Although aesthetically it is easy to see why females might choose flamboyant males, it's rather harder to understand why such preferences would evolve. That is, why would a female choose a mate that is very conspicuous to predators — especially when her offspring will suffer the same fate? R.A. Fisher (1915, 1958), the famous statistician and population geneticist, came up with an answer. Fisher suggested that if females prefer some trait, for whatever reason, the trait could be adaptive simply because her offspring will possess it, and therefore themselves be attractive to prospective mates.

Over time the trait could become greatly elaborated by what Fisher called runaway selection. The basic idea is that a positive feedback loop would occur; if females prefer a trait, then genes for that preference are passed on to their daughters, while the genes for the preferred trait are passed on to their sons (via their chosen mate). In the next generation, more males should possess the preferred trait, so females might choose to mate with those that are just a bit

more striking than the others — maybe the tail is a bit longer than all the rest, or the breast a bit redder. This leads to an evolutionary arms race, with each generation of males being a bit fancier, and each generation of females preferring the most extreme males. The reason for the initial preference is unimportant in this scenario; it could be based on aesthetics, or the trait could have originally given the female some useful clue about her prospective mate. Overall, this theory is difficult to test; unfortunately, people often simply assume that it has occurred in cases where we see no obvious adaptive value for a trait. The classic example is the elaborate tail of the Peacock. Why would a female mate with a male burdened by such plumage? There is evidence that females do prefer larger tails — they investigate a number of males, and choose to mate with the male with the most feathers in his tail (Petrie et al. 1991). In this case Petrie found that the offspring of males with more elaborate tails actually grow and survive better than offspring of less spectacular males (Petrie 1994), but in most cases it's not at all clear what sort of advantages females obtain from their choices.

**Indicators of Male Ability or Resources**

The second possibility, that females choose males with some necessary resource, is relatively intuitive, and it is well documented for some animals. A female that chooses to mate with a male whose territory is good for raising offspring will obviously do better (i.e., raise more offspring to fledging) than a female that mates with a male in an unsuitable area. For example, Indigo Bunting females prefer to settle in territories that contain good food resources, even if it means sharing the territory with another female (Carey and Nolan 1975). Females might be able to judge how good of a provider a male will be by listening to his song, or estimating his body size, and so those characteristics come to be cues used in mate choice. Furthermore, in many cases older males tend to be larger, so females can judge experience using body size. One elaboration of this idea, called the *handicapping principle*, suggests that by selecting for males that have outrageous traits, and the problems that go along with them, females are able to choose males that can live and flourish *despite* a handicap (Zahavi 1975). These males must be of extremely high quality, and therefore should be chosen as mates.

Studies of plumage patterns in birds have recently produced interesting insights into the "male quality" hypothesis for female choice. First, work by Hill on House Finches has shown that plumage brightness and color can be reliable indicators of male quality and foraging ability. Hill (1994, 1995) found that females prefer more brightly colored males, and that the brightness of a male's plumage depends upon his diet. The red pigment is derived from carotenoids which the male obtains from his food (the same pigments which give carrots

their orange color), so the brightness of the male indicates something about his ability to find food, and possibly about his overall level of health.

Furthermore, this is a signal that cannot be faked — a male cannot have red feathers without having a proper diet. Work done by Slagsvold and colleagues with European Pied Flycatchers shows that females can use plumage coloration as an indication of other male characteristics (Sætre et al. 1994, Dale and T.Slagsvold 1996). In this species, females prefer brighter males, and brighter males tend to be larger, older, and more experienced. They also tend to disappear more often, apparently due to predation by Eurasian Sparrowhawks. This is an interesting point — there is a cost to being attractive to females, and probably not all males can sustain that cost. Females can therefore use these "honest" cues to reliably determine male quality.

**Good Genes**

The third possible type of cue used by females is the most controversial. Can females really choose a male with "good genes," based on some external cue? Wouldn't all males advertise "good genes," whether or not they had them? In 1982 Hamilton and Zuk wrote a provocative paper which has influenced many studies of sexual selection ever since. They suggested that one set of "good genes" that should be very important to prospective mates is the genes that confer resistance to parasites. In domestic poultry, for example, genetic resistance to one important parasite is known to be heritable (Johnson and Edgar 1982). Since parasitic infections are often very important in the life-history of animals, and since they are often debilitating, females should select mates that carry resistance genes whenever possible. General good health and freedom from parasites is important for the maintenance of healthy plumage, especially when it is brightly colored, so Hamilton and Zuk suggested that bright coloration could be used as a cue to an animal's health. They reasoned that this type of cue should be especially important in species that face heavy parasitism, so they hypothesized, and found, a positive relationship between how brightly colored various bird species were and how much parasitism they faced. They also predicted that within a species, birds with lower parasite loads would be better able to maintain their brightly colored plumage, and other elaborate traits, than more parasitized birds. In one test of this hypothesis, Møller (1991) studied male Barn Swallows, which attract mates by singing and displaying their long tails. He found that increasing their parasite load decreased their singing rate, indicating that parasitic infections can take a toll on birds, and that females might be able to use song as a cue about the male's health. Since then, many other studies have looked at how individual characteristics vary with individual parasite loads, and whether females use such information during mate choice. A number of examples follow.

In Red Jungle Fowl, Zuk and colleagues (1990a, 1990b, 1990c) found that females prefer to mate with males that have large, brightly colored combs, and that comb size and color are decreased when the animal is burdened by nematode parasites. Since bare skin reflects the current state of the animal (while feathers reflect the bird's health at the time of molting and new feather growth), its coloration and general appearance can be reliable cues about the male's present state. At a recent scientific meeting (Animal Behaviour Society 1997), Zuk presented more evidence that comb color and size may indicate male genetic quality. She showed that males with larger combs have stronger immune responses, indicating their better ability to fight off disease and infection. This is especially interesting in light of the fact that most male secondary sexual characteristics are under the control of the male hormone testosterone, which tends to suppress the immune system (e.g., Folstad and Karter 1992). So while we might expect a "macho" male to have a suppressed immune system, he is actually strong enough to maintain his immune system and, therefore, his health. Saino and Møller (1994) found a similar relationship between parasites and testosterone in Barn Swallows. They found that males with longer tails (which are preferred by females) had higher levels of testosterone, but they had fewer lice. Finally, Buchholz (1995) found that female Turkeys prefer males with larger, brighter ornaments, and those males also had lower parasite loads. In general, these studies indicate that females apparently are able to use external cues to choose mates that are healthy and able to fend off parasites, and that such resistance may be a reflection of genetic quality.

Of course, things can't be that simple, with each system providing more evidence for our theories! In 1993 Davidar and Morton were studying Purple Martins, and they found that females preferred older, brighter males over younger ones. So far, so good. They also found that Purple Martins have fairly high levels of blood parasites (Davidar and Morton 1993). Unlike the above studies, however, the older, preferred males were more likely to be parasitized than the younger, nonpreferred males. Although this finding seems exactly opposite to the hypotheses outlined above, Davidar and Morton provided the following explanation. They suggested that although many animals attempt to avoid parasitism, another way to approach the problem is to evolve ways of living with the parasites. That is, instead of resistance genes, these birds would have some "coping" genes. They suggested that the reason so many older males have parasites is that they have lived through the initial, virulent infection to which many younger birds succumb. In a sense, these males have been "tested" and found able to live with a chronic infection. Furthermore, infection does not decrease a male's ability to guard his mate, or provision his young (Wagner et al. 1997). Adult Purple Martins have glossy purple feathers, and those males that can maintain such plumage, often in the face of chronic parasitic infection, are the ones females prefer to mate with.

Finally, a recent study calls into question the original Hamilton and Zuk finding of a relationship between species-typical coloration and the amount of parasitism the species is subject to. Garvin and Remsen (1997) suggest that there is an important factor that few researchers have considered with respect to parasitism. They point out that nest height is positively related to overall parasitism — those birds that nest in the canopy face significantly more parasitism than those that nest on the ground. Furthermore, canopy dwellers also tend to be more brightly colored. Therefore, the relationship between bright coloration and parasites might be a by-product of the relationships between nest height and coloration, and nest height and parasitism.

## In Conclusion

Although it might be obvious to most listeners that a male Winter Wren is singing a love song, it probably isn't so evident that we're eavesdropping on a very complex system. Not only is the male trying to keep other males away and gain the attention of a female, he may also be demonstrating his good health and parenting ability. When you next flush a Ring-necked Pheasant and are considering the weight of his tail, you might imagine that it really could make him more vulnerable to predators; perhaps then you'll be impressed that he's managed to survive at all, given such a handicap. And next time you're birding and you see a flash of red as a Scarlet Tanager flies through the forest, you'll wonder if there's a well-informed female nearby, and just what choices she's making. . . .

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**Marta Hersek** is a professor at Boston University and the Features department head for *Bird Observer*.