gleanings from the technical literature

Why Some Female Birds are Larger than Males

The Meaning of Reversed Sexual Size Dimorphism

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Among birds, the male of the species is typically larger than the female. The most common explanation for what is termed "normal sexual dimorphism" is Darwin's concept of sexual selection, the idea that males either compete for mates through combat or are chosen by females because they possess an attractive trait. Large body size is one of the most important sexual traits, explained traditionally as beneficial in contests over females and because large males presumably are able to provide better resources than small males, e.g., food and territory (Andersson 1994). Size differences, which often lead to social dominance, can affect access to resources. Typically, males dominate smaller females and gain access to better food resources during the non-breeding season (Temeles 1986).

Females, however, are larger than males in a number of bird species, including many of the predatory species, e.g., hawks, falcons, owls, and jaegers, and also among a number of shorebird and woodpecker species. This relative size reversal is termed "reversed sexual size dimorphism" (RSSD). The greatest degree of RSSD is found among jaçanas, where males may weigh as little as 55 percent of females' weights (Jehl and Murray 1986), and in the genus *Accipiter*—Eurasian Sparrowhawks (*A. nisus*) and Sharp-shinned Hawks (*A. striatus*)—where males average about 58 percent of the size of females (Amadon 1977).

While there is no consensus as to why RSSD exists, there are a significant number of hypotheses that have been proposed to account for it. This article presents some of the major hypotheses regarding the highly controversial question of why females are larger than males in these species. Hypotheses about RSSD fall into three categories: (1) ecological hypotheses, which in general propose that since different-sized predatory birds eat different-sized prey, intersexual competition for food is reduced in mated pairs of different-sized birds; (2) physiological and anatomical hypotheses, all of which focus on the advantages of large size in females, as it affects such issues as egg-laying, incubation, or coping with food deprivation, and of small size in males, which is regarded as efficient because less energy is expended in food provisioning because of their greater agility and ability to capture prey; and (3) behavioral hypotheses, which have to

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In Sharp-shinned Hawks, the most dimorphic of our three accipiters, males average about 58 percent of the size of females. The size difference here is obvious between the smaller male on the left and the female on the right, at the banding operation at Braddock Bay, New York, in May 1996. This species is also the accipiter with the largest percentage (93) of birds consumed as prey items.

do with such issues as nest protection and formation and maintenance of pair bonds (Mueller 1990, Bildstein 1992).

Why Males Might be Smaller than Females

One of the most prevalent hypotheses about RSSD in raptors is related to their ability to capture agile bird prey. The argument is that pursuit of agile birds requires great maneuverability, so the predator had to evolve capacities similar to its prey. Since most aerial prey are smaller than their predators, selection for agile predators led to a decrease in body size among male raptors. Female raptors did not have to evolve small size because they incubated the nestlings while the male provided food during the breeding season. Moreover, females needed to be large so as to have the capacity to fly during the period when they were producing eggs or to endure some food deprivation while incubating. The evidence for this explanation lies in the correlation between RSSD and the importance of birds in the diet of several accipiters. The Northern Goshawk (*A. gentilis*) is the least dimorphic North American accipiter, and birds comprise only 54 percent of its diet; Cooper's Hawk (*A. cooperii*) is somewhat more dimorphic and depends upon birds for 67 percent of its food, while the diet of the Sharp-shinned Hawk, the most dimorphic of the three accipiters, is 93 percent birds (Paton et al. 1994). A long-term study of prey items taken by Sharp-shinned Hawks confirmed that females struck relatively larger prey than males (Mueller et al. 2000). Even so, size dimorphism in raptors does not necessarily imply that they are hunters of elusive bird prey. Red-tailed Hawks (*Buteo jamaicensis*) exhibit about the same degree of sexual dimorphism as Northern Goshawks, although small mammals rather than birds are dominant in the diet of red-tails (Dunning 1993, Preston and Beane 1993).

There are three possible mechanisms through which RSSD could increase the reproductive fitness of small males, assuming a greater availability of small prey as opposed to large prey, and that small raptors take prey more often than larger raptors per unit time (Safina 1984). The first is that females evaluate the hunting abilities of males and choose smaller males because they are more effective foragers. There are a number of species, including Whiskered Screech-Owl (*Otus trichopsis*) and Harpy Eagle (*Harpia harpyja*), in which females appear to provoke males into providing food on demand. Females of these species possess calls or displays that evoke hunting-activity by males. A second mechanism could be selection for smaller males who offer more food during courtship, if that led to a greater receptivity to copulation on the part of females. There is evidence of a relationship between the presentation of food and copulatory behavior among certain raptors, e.g., Peregrine Falcon (*Falco peregrinus*) and Ural Owl (*Strix uralensis*). Those males that return most frequently with food would be most likely to be selected as mates, which would favor smaller males rather than large males that bring back larger prey with less frequency. The implicit assumption is that the capture of large prey less frequently adds up to less food per unit of time. The third mechanism that could favor small males is foraging efficiency. If smaller males are able to capture prey in less time than larger males, then they can spend more time at the nest guarding their young. This benefit could be diminished if small males have to hunt more frequently. Female raptors do not need to be small because they are always at the nest guarding young until their offspring are able to defend themselves.

Smith (1982) offered a persuasive theory regarding the behavior of raptors that tied together their deadly weapons (talons and bill) and their monogamous mating system. During the early part of the breeding season, female birds in general are usually dominant in monogamous species. In non-predatory species this dominance can be exercised through male-female aggression without serious consequences. But in predatory species, such encounters have the potential of injuring if not killing at least one of the pair because of raptor weaponry. By being substantially larger, females can settle any aggressive interaction quickly without a lot of lengthy or violent escalation of the encounter.

One of the more standard arguments is that both the direction and degree of sexual dimorphism in birds of prey can be explained by the requirements of

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There is evidence of a relationship between the presentation of food and mating among Peregrine Falcons. A male that returns most frequently with food may be most likely to be selected as a mate; this activity actually favors smaller males rather than large males that bring back larger prey but with less frequency. This bird was photographed at Jones Beach, New York, in February 1992.

territorial defense. The argument is that in species which perform territorial aerial display flights, small size and agility are favored. This idea is consistent with the behavior of birds of prey in which the male has the major responsibility for advertising and territorial defense. Logic then suggests that in order for this hypothesis to be valid, sexual dimorphism should be greatest in solitary breeders as well as highly territorial species (Widen 1984). Sexual dimorphism should be trivial or absent in birds of prey that are colonial breeders—that is, those species that would defend only a small area around their nest. A study of 12 species of birds of prey (Falconiformes) supported the conclusion that "interspecific differences in degree of sexual size dimorphism are explicable in terms of the territorial-defense hypothesis" (Widen 1984). Jehl and Murray (1986) hypothesized that RSSD evolved as a consequence of sexual selection for small size in males that were agile in performing aerial displays. Their work, which focused on shorebirds, found that RSSD was present in both monogamous and polygynous species in which aerial displays were used to establish territories or to attract a mate. When males compete for females through aerial displays, rather than contests conducted on the ground, it is the smaller and more agile individuals that are able to outcompete larger, less agile individuals, leading to selection for small males among species where courtship displays take place in the air.

They also found RSSD in polyandrous shorebird species—that is, species in which one female mates with more than one male. Their argument is that in cases where males outnumber females and cannot find a mate, males can increase the probability of mating not by engaging in aggressive competition with other males, but rather by abandoning aggressive behavior and turning to polyandry. In this case, evolution would favor those females that attain dominance, which in turn favors large female size and thus leads to reversed sexual size dimorphism.

Why Females Might be Larger than Males

There are at least three important hypotheses for why female raptors are large. A number of researchers have suggested that large females can more easily deter potential predators than smaller individuals (e.g., Andersson and Norberg 1981). This includes defending the nest from male raptors, a task made easier by reversed size dimorphism. Wheeler and Greenwood (1983) pointed out that female raptors gain weight just before egg-laying. This extra weight might reduce their capacity to hunt prey, especially in those species hunting agile prey. They suggested that larger females would be better able to absorb this weight increase without reducing their hunting prowess. It is also very likely that because incubation reduces the time for hunting and thereby increases the potential for starvation, larger females that bulk up can better withstand food deprivation.

Large size confers other advantages on females where there is RSSD. Among Northern Harriers (*Circus cyaneus*), another sexually dimorphic species, during the non-breeding season females dominate access to the preferred resources of high-vegetation areas, and the smaller males (as well as subordinate females) are forced to forage in less desirable areas. Foraging behavior among harriers is also affected by size differences. Males fly much faster when hunting than do females in areas where both sexes hunt together. One explanation is that males may use fast flight as a strategy to avoid being noticed by females (Temeles 1986). There may well be reason for smaller males to fear encroaching on the territories of females. In the sexually dimorphic Eurasian Sparrowhawk the larger females frequently kill and eat their smaller male counterparts outside of the breeding season (Marquiss and Newton 1982). While small raptor males may be endangered by larger females, it should be pointed out that fast flight may also reflect different hunting strategies by males or the pursuit of prey different from that pursued by females.

While raptors start out with intrasexual size differences, there is at least one case in which RSSD emerges as a consequence of the life cycle of the species. RSSD confers advantages on females of a much smaller species, the Ruby-throated Hummingbird (*Archilocus colubris*). A study done over nearly three decades showed that the adult female:male ratio of hummingbirds rises throughout the year, suggesting that males do not survive as well as females and that this may be connected to RSSD. While females maintain their weight between May and August, males lose a great deal of weight during the breeding season because of metabolic stress, and they do not recover this weight loss in July. As a consequence, their risk of death may rise during the self-imposed nocturnal fast that all hummingbirds endure, or they may become vulnerable during periods of harsh weather (Mulvihill et al. 1992). In this instance, RSSD translates into a higher survival rate for female hummingbirds.

Virtually all the work that has been done on RSSD concerns the behavior of breeding birds. But some effort has been made to determine why RSSD might be adaptive at other times. Bildstein (1992) argued that RSSD evolved in raptors as a way to quicken the development of juvenile males. Male raptors, which provide virtually all of the prey for their mates and young for a large part of the breeding season, must become skillful hunters and develop their skills as soon as possible. In almost all raptor species, males fledge before females, in larger eagles by a week or more (Bildstein, pers. comm.). Because their talons are so deadly, there is no need for them to develop large size. Indeed, if males were larger than females, their more rapid growth might pose a threat to female siblings in the nest as potential victims of siblicide. The smaller size of males has the dual benefit of reducing the risk of siblicide and speeding up their development. Bildstein called this phenomenon the Head Start Hypothesis. Males are themselves not at risk from potentially siblicidal females because by developing more quickly, males are always ahead of their larger female siblings; males trade size for advanced coordination.

RSSD in Owls

While most of the empirical and theoretical work involving RSSD has been done on Falconiformes, there has been some empirical work on the evolution of RSSD in owls, notably by Mueller (1986, 1989). Female owls are larger than their male counterparts in all owl species (Dunning 1993). After considering twenty major hypotheses used to explain RSSD in Falconiformes, Mueller (1986) concluded that only the behavioral hypotheses applied to owls. In particular, the degree of female social dominance in owls appears to be

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In larger eagles, males fledge before females, sometimes by a week or more. The smaller size of males has the benefit of reducing the risk of siblicide. Males are not at risk from potentially siblicidal females because by developing more quickly, males are always ahead of their larger female siblings and will leave the nest sooner. You can barely see the young Bald Eagles in this nest at Cape Coral, Florida, in March of last year.

highly correlated with RSSD. For example, during the breeding season, the female Eurasian Pygmy-Owl (*Glaucidium passerinum*) will chase the male away from the nest if he hangs around without bringing food for hungry young, although this also occurs within some species with regular dimorphism as well. The Boreal Owl (*Aegolius funereus*) female will even leave the nest and chase the male for some time if he does not bring enough food for young (Mueller 1989). Such behavior patterns suggest that RSSD may have evolved as a way to assist in pair maintenance in owls. Most of the other hypotheses that were proposed for Falconiformes were rejected by Mueller as being inapplicable to owls. For example, Jehl and Murray (1986) predicted that aerial displays would be found in owls. While it is true that a number of owl species do perform aerial displays, some quite elaborate, the empirical evidence does not suggest a strong direct correlation between RSSD and the "complexity, variety, and frequency of aerial displays in...European owls" (Mueller 1989).

RSSD in Woodpeckers

RSSD also exists among a number of woodpecker species; the tail length of females is longer than that of males. Short (1970) offered two functional explanations for these differences. In those woodpecker species in which the male does most of the excavating of nesting cavities in the spring the shorter tail of the male may serve as a supporting mechanism. As a corollary, he suggested that the longer tail of certain female woodpeckers, e.g., Nuttall's Woodpecker (*Picoides nuttallii*) and Ladder-backed Woodpecker (*P. scalaris*), may be associated with the fact that many females are much more likely to probe and glean from the surface of smaller branches and consequently may require a longer tail to help them keep their balance while they are feeding.

Conclusion

At this point it should be obvious that explaining RSSD is extremely complicated, if not ultimately impossible. At a minimum, none of the hypotheses has universal applicability to all species in which reversed size dimorphism exists. This fact does not diminish the value of the hypotheses, but rather reflects the fact that in the murky world of evolutionary ecology there are frequently no certainties.

In all of the arguments that are made, it is important to make the distinction between cause and consequence, and this is not always done. Do small, agile males perform more aerial displays because they can, or are aerial displays somehow advantageous so that small males really perform better? Is the ability of Northern Harrier females to dominate foraging areas a cause or a consequence of RSSD? Much of the evidence offered by ornithologists is derived from finding a correlation between two phenomena. But correlation is not causation. In spite of a large body of creative scholarship, the main issues in this area of inquiry remain largely unresolved. There is still a great deal more to be learned about the causes of RSSD by conducting research in the field and with museum collections.

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