

criteria influence nest-chamber temperature, and in what way this happens.

The nest temperatures in meridian mounds are higher and exceed preferred incubation temperatures of other avian species (35.7°C, Drent 1975) for longer periods of time than conical mounds. Therefore, birds incubating eggs in meridian mounds may have to spend considerably more time, water and energy actively cooling eggs so that lethal egg temperatures are avoided. The more acceptable temperature regime in conical mounds may also result in higher productivity and more rapid development of nestlings.

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## Sexual Size Dimorphism in Raptors: Intrasexual Competition in the Larger Sex for a Scarce Breeding Resource, the Smaller Sex

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Sexual dimorphism in size is a characteristic of many species of birds. Raptors are unusual in the extent of divergence in size between the sexes in many species and the fact that the female is more often the larger sex (reversed sexual dimorphism or RSD). This has elicited much speculation as to the explanation for and adaptive significance of size dimorphism in this group (e.g. Mueller & Meyer 1985).

The most widely accepted explanations for the evolution of avian sexual dimorphism are the avoidance of intersexual competition and sexual selection (Selander 1966, 1972; Trivers 1972; Searcy 1979). The competition avoidance theory, which links the degree of divergence in size between the sexes to differential niche use, has been well explored in its application to raptors (e.g. Newton 1979; Temeles 1985); while it may account for the degree of dimorphism, in general, it offers no explanation for the larger size of the female (Newton 1979; Mueller & Meyer 1985). The theory of sexual selection, on the other hand, attributes the larger size of one sex to the advantage it confers in epigamic display and intrasexual competition (Darwin 1871; Selander 1972; Trivers 1972.).

We believe that, as a consequence of their 'breeding system', intrasexual competition is the primary cause of dimorphism in raptors. We propose that the larger sex (the female in most raptors) competes for a scarce breeding resource (the male in most raptors). To our knowledge, this idea has never been advanced as an explanation for dimorphism in raptors, with the exception of preliminary notes by ourselves (Olsen & Olsen 1983, 1984, 1986).

#### *Aspects of the breeding system of raptors*

Raptors differ from many other birds in what we have termed their 'breeding system'. In particular, the female generally cannot successfully hatch and raise a brood in the absence of a male; the male therefore has a higher investment in the breeding attempt than is the case in many other avian species. The male is often the sole provider for the female, from courtship until several weeks into the nestling period (Newton 1979). Consequently, the male must be a willing provider and a skilled hunter with a good knowledge of his hunting area, particularly in those species that catch agile, fast or otherwise difficult prey. It would be advantageous, though not essential, for the male to hold

a good hunting territory (one with ample, reliable food and a suitable nest site) rather than a mediocre one. Presumably, there is a certain adequate level of provisioning during breeding that can be reached by various combinations of male hunting skill and experience and the available food resources of the territory. For example, a first-year male may be able to provide enough food for successful breeding in a good territory (or season) but would not have acquired the experience necessary for success in a poorer territory that would be adequate for an older male. Because the breeding success of a pair is largely dependent on the ability of the male to supply his mate and offspring with food, the most experienced and efficient male and a female that retains such a male, or at least the bulk of the food that he brings to the nest area, will fledge the greatest number of young.

As is the case with many birds (Selander 1972; Krebs & Davies 1983), the female raptor may select her mate. The male displays to her, feeds her and shows her his nest sites, but she may then leave (Balgooyen 1976; Newton 1979). Courtship feeding, and perhaps the male's displays of flying skill, help the female to select a male that will be a good provider (as suggested for the Common Tern *Sterna hirundo* by Nisbet 1977). Whether she remains with the male or not may depend on physiological factors (an increase in body weight is thought to be necessary for successful breeding, Newton *et al.* 1983) or behavioural factors (the number of presentations of food made by the male, his attentiveness). We do not reject the possibility of male choice; a male choosing a large female will be advantaged by the larger (that is, more attractive) female offspring such a pairing may produce. Selection by either sex and the male as provider are not in themselves predictors of dimorphism, but they set the stage.

#### *Competing females*

During the breeding season, male raptors usually bring food to the nest site or a perch nearby, even in the absence of a female (Newton 1979). It is this area that the female must defend against other females. Larger size would be advantageous even when there is visual confrontation in the absence of combat. As is the case with many species, the importance of large size is illustrated by the raising of feathers in aggressive encounters, apparently in an attempt to bluff the opponent and thus avoiding combat. That competition between females takes place can be inferred from, for example, the number of reports of female-female interaction compared with those between female-male, which is seldom observed (Nelson 1977; Kemp 1978; Picozzi 1984). Newton (pers. comm.) has evidence for competition between female Sparrowhawks *Accipiter nisus* for males; he has also found that larger female Sparrowhawks have a greater lifetime reproductive output than smaller, but not larger broods, and that, although some immature females breed, it is chiefly the larger ones that

do so. Larger females may thus be more successful simply because they are able to retain a mate (and his territory) for more years than smaller females.

Further, females of monogamous raptors are sometimes able to command the territories of two males (e.g. Nelson 1977) and in polygynous raptors the dominant female may command most of the food provided by the male (e.g. Hamerstrom 1969). In some polygynous raptors the female is thought to control the degree of polygyny (Baker-Gabb 1978); females choose to become the second mate of an older male rather than the first mate of a younger male. In raptors, polyandry seems to have evolved in species occupying 'poor' habitats (Newton 1979), when an extra male helps provide sufficient food for successful breeding. Given the supposed advantage of broader niche partitioning in dimorphic raptors (Reynolds 1972), it should benefit an incubating female, particularly in poor habitat, to have a male and another female providing food. Therefore, it is significant that no raptor exhibiting RSD has evolved a mating system with two females sharing a nest or female helpers at the nest. Competition between females may limit such behaviour to the few atypical cases reported.

Males also compete with each other but it is for territories (Newton 1979), whereas we propose that in females competition is for the complete package of the food provider and his territory.

#### *The male as a scarce resource*

Not all male raptors are created equal in terms of breeding success. In general, older more experienced males are more likely to be good food-providers, have mates, and produce a greater number of offspring than other males; females, on the other hand, are often likely to breed at a younger age than males and successful breeding does not seem to be as age-dependent as in males (Hagar 1969; Newton 1979; Baker-Gabb 1981; Picozzi 1984; Village 1985). Thus the 'operational' sex ratio (the sex ratio of those capable and available for breeding, Krebs & Davies 1983) is likely to be biased in favour of females. There is also evidence that the number of females may be greater than that of males in some populations, for example, females removed from nest sites are more quickly, and more likely, to be replaced than males (Hagar 1969; Newton *et al.* 1983; Picozzi 1984). In addition to being experienced, an 'operational' male must also hold a breeding territory, a further limiting factor to the number of males available to a female.

We will not attempt to review other hypotheses on dimorphism, some of which are not refuted by our hypothesis and which we would see as possible enhancers of the main selective force, competition for a scarce breeding resource (e.g. Widen 1984); several, sometimes opposing, forces influence body size. Nor is this article intended as a comprehensive justification or development of our ideas.

Nevertheless some further points are relevant.

Von Schantz & Nilsson (1981) rejected intrasexual competition as the mechanism for the evolution of RSD in raptors on the grounds that most raptors are monogamous and therefore do not conform to the observation that dimorphism is usually greatest in polygamous species (as a result of stronger intrasexual competition between, usually, the larger males). However polygyny is not a prerequisite for dimorphism so its rarity in raptors (and that of its correspondent in the case of species with RSD, polyandry) does not eliminate the possibility of intrasexual selection. We would argue that the male is a scarce resource in both polygynous and polyandrous raptors. In the former species (e.g. Harriers) nesting habitat is often restricted or localised, and in the latter (e.g. Harris Hawk *Parabuteo unicinctus* and Galapagos Hawk *Buteo galapagoensis*) the breeding habitat is 'poor'.

A number of authors invoke intrasexual selection for smaller males as the cause of dimorphism in raptors (e.g. Safina 1984; Widen 1984). However, they fail to explain, in particular, how raptors with 'normal' dimorphism fit their theories. Our discussion has so far been confined to raptors with RSD. A number of owls exhibit 'normal' dimorphism, most notably a number of Hawk Owls of the genus *Ninox* and the Burrowing Owl *Speotyto cunicularia*. In *Ninox* the degree of dimorphism corresponds with differences in diet between the species (insect eaters are less dimorphic than bird eaters, Schodde & Mason 1980) as it does in raptors with RSD. Although little is known about *Ninox*, the roles of the sexes appear to be somewhat reversed to those of raptors with RSD. The (usually) smaller female holds the territory, advertises for a male by hooting and shows him her nest hollow(s) (Schodde & Mason 1980). The male Burrowing Owl is said to compete for the female and males outnumbered females at least in one population under observation (Thomsen 1971). As would be predicted by our theory, this indicates that the larger male competes for the scarce resource, the smaller territory holding female.

While we argue that the male is the scarce resource in most raptors because he must be a skilled hunter and hold a breeding territory (i.e. his contribution to the breeding attempt is great), the male is also a scarce resource in those species where he hatches and raises the chicks alone and may also hold the territory (his contribution is also great in such species). Examples include Southern Cassowary *Casuarius casuarius*, Button Quail *Turnix* sp., and Emu *Dromaius novaehollandiae*, all of which exhibit RSD. Raptors would be unable to support this type of polyandry because of the need for one bird to incubate while the other hunts.

It is tempting to speculate on the relevance of our theory to the degree of dimorphism. For example, in species that

prey on slow, readily available prey it may be easier for a female to find an adequate, competent male than in species that catch difficult prey. Therefore, females of the former species may be under less competitive pressure than those of the latter and would tend to be closer to the size of their male. That is, hunters of difficult prey would be more dimorphic than hunters of easily caught, readily available prey, as is in fact the case.

As an example, Eleonora's Falcon *Falco eleonorae* is weakly dimorphic and, according to our theory, competent males do not need to be such skilled hunters as, say, those of the more dimorphic Peregrine Falcon *F. peregrinus*. Eleonora's Falcons hunt the large numbers of migrating passerines that fly over their islands (readily available prey) and they do so in co-operation with other hunting males. There is also a great deal of piracy (Walter 1979). In such a situation the most skilled hunters are not necessarily the best providers, i.e. there are more competent males available, males are not such a scarce resource and competition for them among females may be less intense than in Peregrines. In monomorphic raptors, e.g. some vultures, male hunting skill would not greatly limit the number of 'operational' males, thus a competent male would not be as scarce a resource as in highly dimorphic raptors, and competition between females would be correspondingly less. (This is not an argument against selection for small males in hunters of prey that is difficult to catch.)

A prediction arising from our ideas is that when females of species with RSD are removed from breeding territories they will tend to be replaced by one of the larger members of the non-breeding population, but no such trend should be apparent in males or for non-dimorphic raptors. Further, in seasons when food is severely limited, larger females (not necessarily fatter) should be more prevalent in the breeding population than in poor seasons.

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