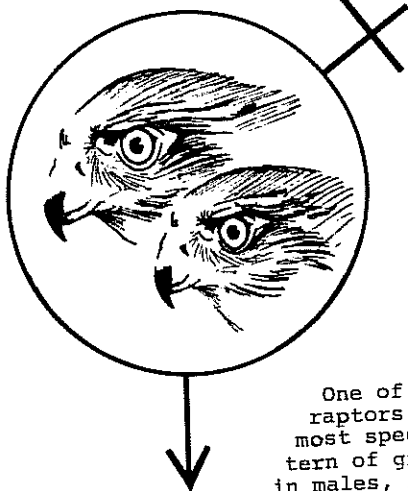


SCIENCE REVIEW

-- is an occasional series in which current or continuing problems in raptor biology, or significant research, are reviewed. Suggestions and contributions are welcome.



Why are females big, or males small ?

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One of the most fascinating questions about raptors is simply this: Why are females in most species larger than their mates? The pattern of greater size in females, or smaller size in males, is called Reversed Sexual size Dimorphism (RSD), because it is the reverse of the usual condition in birds. Attempts to explain the function of RSD have generated more literature than any other theoretical aspect of raptor biology; at least 25 full-length papers or substantial sections in books have addressed this question. Mueller & Meyer (1985) provide the most thorough recent review of all this literature. In this article I will describe the main arguments that have been proposed and then have a stab at a new hypothesis that may be a workable solution. First, however, it is important to describe trends in RSD and to state some basic assumptions.

Although we often talk of raptors as a homogeneous group, they actually consist of a mixed bag of predatory birds that, by convergent evolution, have come to look somewhat similar and do similar things. Thus owls, falcons and accipitrids (hawks, eagles, kites etc) represent unrelated families. RSD however occurs in all these birds, as it does in the unrelated skuas and boobies, indicating that RSD evolved independently several times. Since all these birds are predatory, one might immediately assume that RSD must be associated with behaviour in which a bird goes out and kills its prey. It would seem rather that RSD occurs only in large predatory birds that use flight to pursue their prey, because large seabirds, herons and other birds that land near their prey, or walk up to it, show the normal pattern of size dimorphism.

Sexual size differences vary between species, so that some females weigh almost twice their mates while in other species they are very similar in size. Males are bigger in a few exceptions, notably owls of the genera *Ninox* and *Speotyto*. The degree of size difference is closely related to the agility of preferred prey, those raptors catching avian prey being most dimorphic, followed

and summer, it is clear that energy expenditure per unit time during winter was about 1,4 times that during summer. This finding emphasises the importance of photoperiod and associated differences in activity patterns in the overall energy budget.

The above analysis rests on the assumption that BMR is constant during inactive periods in both winter and summer. Based on continuous nest temperature profiles recorded for occupied nests during these periods, the validity of this assumption is questionable. For example, during midsummer, nighttime temperatures seldom dropped below 28°C with a mean of 30°C, while during mid-winter, temperatures frequently dropped below 20°C, often to 10-11°C. Thus, it seems likely that during summer, birds would remain well within the thermoneutral zone throughout the night. Apart from a possible contribution to metabolism by Specific Dynamic Action (SDA), energy requirements may be quite reliably defined by BMR during this inactive period. During winter, however, it is likely that metabolic rate may increase in response to ambient temperatures below the lower critical temperature. If this occurred, the energetic cost of inactivity would be considerably greater during winter than during summer.

This possibility, in turn, prompted an investigation of body temperature (T_b) of inactive birds removed from nest cavities just before dawn in both winter and summer. These temperatures were then compared with those of captives measured during the day. Body temperature of day-active birds during winter and summer ranged from 38 - 40°C, while for inactive birds removed from nest cavities, T_b was 31 - 33°C during winter and 37 - 38°C during summer. Therefore, it may be concluded that Pygmy Falcons exhibit a moderate hypothermia at night during winter, but maintain a constant T_b during summer. Based on available data for passerines which experience hypothermia, a decrease in T_b of the magnitude observed may reduce BMR by 40 - 50% during nocturnal periods of inactivity.

Although this aspect of the study is being investigated in greater depth, it seems likely that the original assessment of inactivity costs during winter exaggerated the actual costs, while consequently underestimating activity costs. In addition, the energy requirements for breeding Pygmy Falcons are being studied, with special emphasis on the partitioning of energy between male and female and the requirements of developing chicks.

SAPSFORD CW & MENDELSON JM. 1984. An evaluation of the use of tritium for estimating daily energy expenditure for wild Black-shouldered Kites *Elanus caeruleus* and Greater Kestrels *Falco rupicoloides*. In MENDELSON JM & SAPSFORD CW (eds.) Proc. 2nd Symp. Afr. Pred. Birds. Durban: Natal Bird Club.

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by predators of mammals, fish, reptiles, insects and carrion (Newton 1979). Mueller & Meyer (1985) examine this relationship statistically and show it to be highly significant ($p \ll 0.0001$).

An obvious assumption, but one seldom recognised, is that RSD is related to reproduction. Although many people may be surprised, males and females exist only because of a need to reproduce sexually (not the other way around), so any structural differences are very likely due to their respective reproductive functions. Given this, it is instructive to consider the roles of male and female raptors during breeding. Interestingly, their roles vary little between species, males doing the hunting to provide all the food from the pre-laying stage to the late nestling period. Females are aerially inactive during these stages, performing all the incubation, brooding and feeding of the young. Because parental roles follow this pattern in probably all raptors that show RSD, I assume that sexual roles and size dimorphism are causally related. The same roles and patterns of dimorphism have evolved independently in large predatory birds that pursue their prey in flight.

Mueller & Meyer (1985) distinguish 15 different hypotheses which have been used in various combinations to account for RSD in raptors. I shall briefly discuss the basic concepts of these ideas, but will not criticise them individually. Most hypotheses fail to adequately explain RSD because they do not show 1) why females, not males, are bigger; 2) why RSD occurs only in large predators that hunt their prey in flight; and 3) why the degree of RSD should vary with diet in the way that it does. The hypotheses fall into three broad categories: a) Prey availability - RSD allows exploitation of a greater range of prey sizes, leading to reduced intersexual competition for food and a greater potential prey base. Since females often start hunting during the late stages of the nestling period, their bigger size is claimed to be adaptive because they can catch larger prey when the nestlings' food requirements are perhaps greatest. During the early stages of breeding it is better for one parent to hunt alone, as two hunters might interfere with each others' efforts by frightening alert prey. b) Sexual roles - At least eight hypotheses depend on the assumption that the roles of males and females during breeding are fixed, and that RSD is due to the need to perform these roles effectively. Large females therefore lay bigger eggs, cover eggs better during incubation, provide better protection for developing follicles, tear up food more effectively for their young, and protect their nests better against predators. Colonial species are claimed to be less dimorphic because communal defence against predators reduces the need for large females. On the other hand, small males defend territories better than large, less agile ones, use less energy during foraging, and have greater hunting success because small prey is most abundant. c) Dominance factors - Females are said to be large so that they can prevent their mates from eating their young, force males to provide food, and help to form and maintain pair bonds. These bizarre ideas could only have had their origins in the female liberation movements of the 1960's and 1970's.

I have attempted to develop different ideas to explain RSD and the potential roles of raptors (Mendelsohn in press). They de-

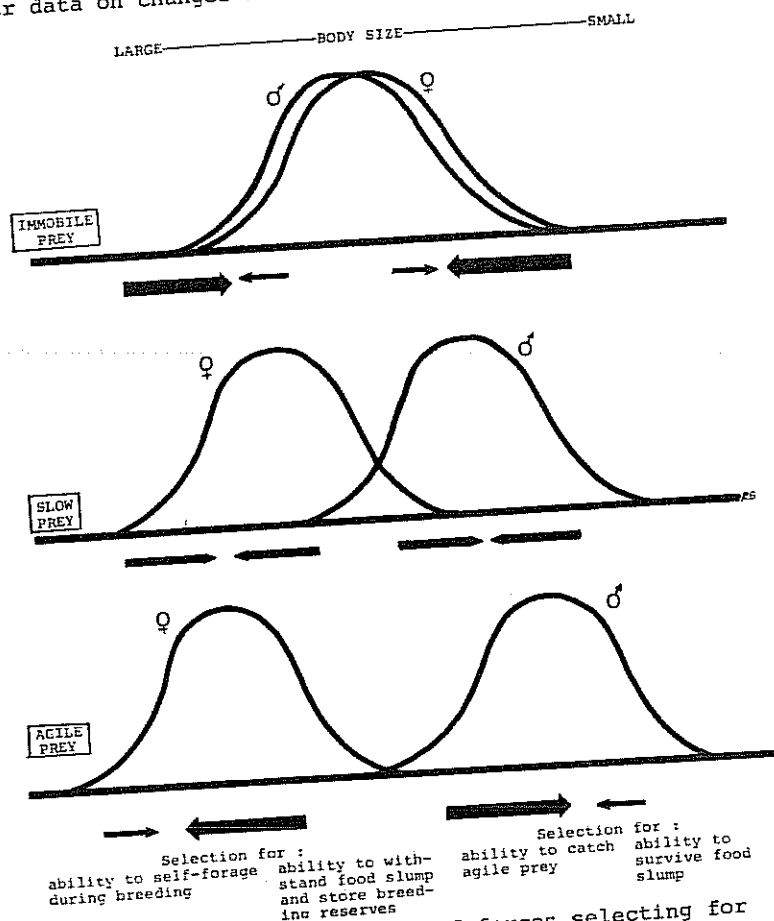
pend strongly on the following hypotheses and observations. Andersson & Norberg (1981) showed on theoretical grounds that small size is optimal for catching agile prey in flight; Snyder & Wiley (1976) and Temeles (1985) indicate that the degree of RSD relates to food shortage and vulnerability, and Marcstrom & Kenward (1981), Newton et al. (1983) and Hiron (1985) show that female raptors store substantial fat and protein reserves during breeding to counter sporadic food shortages. As a result of these findings, I consider that two selective factors are the main determinants of relative size: 1) the need for females to store energy reserves and 2) the need for males to be agile predators. Further, as a general strategy, it is probably as important to provide energy reserves to meet occasional food shortages as it is to hunt successfully.

Newton (1979) reviews a great deal of evidence that raptors often encounter food shortages, so strategies to counter the effects are very important. Large body size allows the storage of disproportionately bigger reserves (Linstedt & Boyce 1985), and therefore a better capacity to draw on them and survive for long periods. However, large predators that rely on manoeuvrability, acceleration and speed in flight to catch prey are less efficient than smaller ones (Andersson & Norberg 1981). Thus, the two selective pressures on body size are in direct opposition. The compromised result of this conflict, a given body size, probably depends on the relative strengths of selection for reserve storage or hunting success. During breeding, these vital requirements cannot be met individually and efficiently (unless prey is not agile), so the functions are split between the sexes. Females store the maximum quantity of reserves and, accordingly, are large and conserve these as much as possible by remaining inactive near the nest. The small males store no reserves during breeding (Newton et al. 1983, Hiron 1985), so their body weights are as low as possible, enhancing flight agility and hunting success. Extending these ideas can explain how RSD relates to diet. Prey agility should reflect the degree of difficulty with which prey is caught (Temeles 1985) and, hence, the need for a) good flight performance and b) substantial energy reserves. Those raptors hunting the most mobile prey should be as small as possible to closely match the size and mobility of their prey. In terms of sexual function during breeding, males should be smallest in those species catching the most agile prey. Likewise, females should be largest in those species hunting prey which is hardest to catch, where the chances of food shortage are greatest.

These ideas are supported by a number of observations and predictions (Mendelsohn in press), and a few examples are given here. If prey is not agile, both sexes should incubate, forage and store reserves during the breeding season. This is indeed the case in vultures (Houston 1976). An apparent exception is the Bat Hawk *Nachieramphus alcinus*, which is less dimorphic than expected on the grounds of its diet. However, both sexes incubate and hunt for themselves (Hustler 1983). This may be due to the restricted time available for hunting bats; males may not have sufficient time to hunt on behalf of their mates.

During the breeding season, male raptors should behave in ways that minimise their body weights while hunting. Rijnsdorp et al. (1981) show that breeding male Common Kestrels *Falco tinnunculus* consume a greater proportion of food at dusk than at other times of the day, much of this being cached earlier. Breeding females, by contrast, consume food at a roughly constant level during the day. Their data also indicate that males retrieve prey more frequently at dusk while breeding than at other times of the year.

I have attempted to describe the general trends in Reversed Sexual Dimorphism and the effects of parental roles in raptors. Other factors are doubtless involved, and those highlighted here are likely to vary with circumstances. A great number of questions relate to the probable trade-off between the needs to hunt and to store reserves efficiently. There is a particular need for better data on changes in reserve levels and hunting success. I



Diagrammatic representation of forces selecting for Reversed Sexual Dimorphism in raptors.

predict that such information will go a long way toward explaining behavioural differences between the sexes, different seasons of the year (see Village 1983), various habitat and prey preferences, different patterns of daily activity and hunting behaviour.

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