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SEXUAL SIZE DIMORPHISM AND ROLES IN RAPTORS – FAT FEMALES, AGILE MALES

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ABSTRACT

Birds of prey are subject to opposing selective pressures for optimal hunting success and the storage of energy reserves. The latter requirement is best met by large size, while small size contributes to better flight performance in catching agile prey. It is argued that breeding raptors need both to store large reserves against food shortages and to hunt efficiently to feed their young. Since these requirements cannot be met individually, the functions of reserve storage and hunting are split between the sexes. Large females hold energy reserves and small, agile males hunt to provision both female and young. This may account for the degree of dimorphism in different species. Those species that hunt the most agile prey have relatively the smallest males because maximum flying performance is needed to hunt agile prey. The same species have relatively the largest females because they probably experience food shortages more often than others.

INTRODUCTION

Unlike most birds, male birds of prey are usually smaller than females and they are relatively smallest in those species that catch the most agile prey. Attempts to explain the function of this reversal have generated a great deal of theoretical literature. However, none of the great many hypotheses reviewed by Mueller & Meyer (1985) and Temeles (1985), has gained wide acceptance. Most ideas have failed to show why females, not males, are the larger sex, why dimorphism should be greatest in those species catching agile prey, or why large predatory birds show reversed dimorphism. Birds of prey have characteristic pa-

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rental roles, in that females generally tend the nest and its contents while males do most of the hunting (Newton 1979). Several ideas have been proposed to account for the partitioning of roles (Andersson & Norberg 1981), but none is really satisfactory. Since differences in size and behaviour are sexual, they are probably related to some functional aspect of reproduction. It is therefore important to establish (a) in what aspect(s) of breeding the sexes adopt different roles, (b) why the roles should differ, and (c) what the consequences are for male and female body size.

This paper incorporates several published ideas into an expanded argument to account for sexual dimorphism and roles in raptors. Andersson & Norberg (1981) demonstrated the importance of small size in catching agile prey, while Snyder & Wiley (1976) and Temeles (1985) suggested that the degree of dimorphism was related to food shortage and prey vulnerability. Marcström & Kenward (1981), Newton et al. (1983) and Hirons (1985) showed that females store substantial fat and protein reserves which buffer them against food shortages. These points are drawn together as follows: (a) body size in raptors is a compromise primarily between selection for large size to store energy reserves against food shortages, and small size for optimal hunting agility; (b) the functions of energy storage and prey capture are split between the sexes because neither requirement can be met individually and efficiently during breeding (except if prey is not agile); (c) females are large to store energy reserves and males are small for optimal flight performance. Available data support most of the predictions based on this argument, suggesting that this hypothesis comes close to accounting for reversed sexual dimorphism, its pattern and direction in terms of prey mobility, and sexual roles in raptors.

ENERGY RESERVES

The requirement to store fat and protein reserves and the need for agility to catch prey are probably the two main determinants of relative sizes of male and female birds of prey. Although other factors, e.g. thermoregulatory requirements and prey size, will also influence body size, I assume here that they affect males and females equally.

The storage of fat and protein is important because these reserves can be metabolized when food availability is reduced or when additional energy is required. Reserves help reduce the effects of sporadic food shortages on birds of prey caused, for example, by adverse weather conditions reducing the availability of prey. Breeding raptors also require additional energy for egg production and rearing nestlings, so reserves accumulated before the onset of breeding are useful in meeting these extra needs. That raptors do indeed store such reserves is shown by measurements of additional fat and protein deposits (Houston 1976. Hirons et al. 1984, Marcström & Kenward 1981) or weight changes that reflect changes in their levels (Figs 1 & 2). The extent of weight change during the year suggests that the quantity of

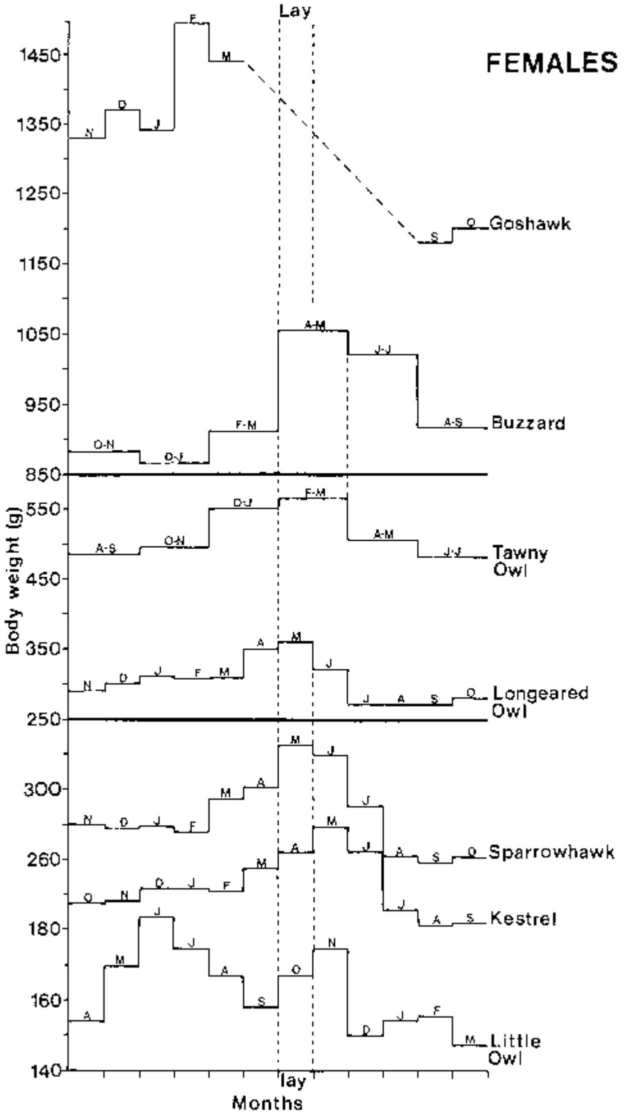

FIGURE 1

Average monthly or bimonthly weights of female Northern Goshawk *A. gentilis*, Common Buzzard *Buteo buteo*, Tawny Owl *Strix aluco*, Long-eared Owl *Asio otus*, European Sparrowhawk *A. nisus*, Common Kestrel *Falco tinnunculus*, and Little Owl *Athene noctua*. The data are plotted with the main month of egg-laying as a point of reference, the actual months being abbreviated as January (J), February (F), etc. Adapted or redrawn from Marcström & Kenward (1981), Cramp & Simmons (1980), Hirons et al. (1984), Wijnandts (1984), Marples (1942), Vulink (1982) and Newton et al. (1983).

RELATIVE BODY SIZES

Selection both for the storage of energy reserves and for agility in flight will have conflicting effects on body size, so the compromised result (as a given size) will depend on how strong each selective factor is in different species and sexes. In considering sexual roles and size dimorphism one must therefore ask (a) whether the respective strengths of the two selective factors are the same for males and females, and (b) how efficiently the requirements of agility and reserve storage will be achieved by a compromised body size?

Both sexes encounter food shortages so both should maximize the storage of reserves. It might be argued that females require added capacity for extra reserves to produce eggs. However, this requirement is not limited to raptors or to other animals showing reversed sexual dimorphism. Furthermore, these additional reserves are required for a relatively short period so the benefits of larger body size would need to balance the costs during the rest of the year. In fact, females probably use a different method of providing most of the extra reserves for egg production: they accumulate reserves but become inactive during the pre-laying period, a relatively short-term cost.

If both sexes maximize the storage of reserves, how might this affect their ability to catch prey? The added weight of reserves would not have any significant effect on the survival of most (see below) non-breeding raptors, because if they were too heavy for efficient flight they could simply use up reserves to lose weight. Most breeding raptors, however, face quite different consequences because their flight performance has to be good to hunt prey to supply their young with food. Moreover, since prey has to be caught regularly, body weight should be as low as possible. For this reason, I suggest that breeding raptors are individually unable to store substantial energy reserves and catch mobile prey simultaneously. Furthermore, since these vital requirements are incompatible, they are best met by splitting the roles between the sexes so that males perform one function efficiently and females the other. The result of such a division of labour is that the two selective pressures are manifested separately and strongly in the two sexes.

Since reserves are required for egg production anyway, females are favoured to maintain substantial reserves "on behalf" of both sexes for as much of the breeding cycle as possible; the magnitude of these reserves is reflected by huge weight changes (Fig. 1, Newton et al. 1983, Village 1983a, Wijnandts 1984). Selection, therefore, favours large size in females. In this role, females can often draw on their reserves so that the maximum quantity of captured prey can be fed to the young to reduce the effects of sporadic food shortages, maintain growth rates and improve survival chances. Female Longeared Owls *Asio otus* decline in weight from about 340 to 250 g during the first 25 days of the nestling period (Wijnandts 1984). This 90 g represents a very substantial amount of energy, and the behaviour of breeding females agrees well with their function as energy reservoirs. In tending the nest they are relatively inactive, allowing energy expenditure and the depletion of their reserves to be minimized. Sapsford & Mendelsohn (1984, unpubl.) found very low rates of water turnover (equivalent to energy expenditure) in female Blackshouldered Kites *Elanus caeruleus* and Martial Eagles *Polemaetus bellicosus* during the incubation and nestling periods. Females probably also do not hunt until their reserves are depleted because the additional weight would reduce their flight performance and hunting efficiency.

Males, by contrast, are selected primarily for their hunting efficiency to provide almost all the food required by both the female and young. Small size is selectively favoured and the weights of breeding males are low (Fig. 2) to maximize flying performance and hunting success. Even if surplus food were available to a breeding male, it would not pay him to accumulate reserves because they would reduce his efficiency in supplying prey to the young. Non-breeding males however can accumulate some reserves to counter food shortages, not having to maximize their hunting success simultaneously to provision their mates and young. Although non-breeding males storing reserves can "afford" to hunt less efficiently than breeding males, they should none the less continually catch prey to maintain their reserves. Since the hunting success of raptors diminishes with increasing prey agility (Temeles 1985), even small reserves are probably detrimental to the hunting success of those raptors that hunt very agile prey.

DEGREE OF DIMORPHISM

The ideas that (a) females are large to store reserves during breeding and (b) that males are small for optimal hunting success during breeding may be extended to account for trends in dimorphism among raptors. Some authors (e.g. Snyder & Wiley 1976) have related the degree of dimorphism to the proportion of birds in the diet, those taking only birds being the most dimorphic. While this holds for raptors that take some avian prey, it cannot explain dimorphism in those that eat no birds. The degree of size dimorphism is more generally related to the mobility of prey (Newton 1979). Mueller & Meyer (1985) show a highly significant correlation between the degree of reversed size dimorphism and prey alertness or elusiveness. This 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 match closely the size and mobility of their prey (Andersson & Norberg 1981). In terms of sexual roles during breeding, males are thus smallest in those species catching the most agile prey. Likewise, females are largest in those species hunting prey that is hardest to catch, where the chances of food shortage are greatest.

PREDICTIONS

Several predictions can be made if dimorphism is the result of a compromise to split the functions of reserve storage and hunting during breeding between the sexes.

(1) If the young could be fed on immobile prey (carrion) or did not need feeding at all (precocial chicks), both parents should accumulate reserves and be similar in size. This is indeed the case in vultures where the sexes are equally large, share in foraging for the young, and both store reserves which are depleted during the breeding cycle (Houston 1976). Similarly, in arctic-nesting geese and cranes, both parents of the precocial young store substantial reserves which they use themselves throughout breeding (Ankney 1982, McLandress & Raveling 1981, Krapu et al. 1985).

(2) Since small size is required for high performance in flight to hunt agile prey, the stronger the selection for agility, and the lower the possibility of accumulating reserves. Thus, if the degree of dimorphism increases as males become relatively smaller, then (a) males of the most dimorphic species should vary least in weight (and thus reserve levels) seasonally, and (b) males that catch the most agile prey should also vary least in weight. Data on monthly or bi-monthly average weights of males in seven species (Fig. 2) provide coefficients of variation for seasonal weight changes. Correlations between indices of sexual size dimorphism and prey agility support these predictions (Fig. 3). Although levels of significance are low, they are dramatically improved if data for Goshawks *Accipiter gentilis* are excluded, weights of this species being available for eight months of the year only (Fig. 2). The most spectacular difference in weight variation is between male Little Owls *Athene noctua* and European Sparrowhawks *Accipiter nisus*. Although comparable in general size, monthly averages (Fig. 2) for the largely insectivorous owl range over 70 g (154-224 g) while those of the sparrowhawk vary just 12 g (143-155 g). The data in Fig. 3 imply that small size and predation on agile prey can be achieved only at the expense of restricting the storage reserves. For this reason then, male Sparrowhawks hunting very agile prey (small passerine birds) can store few reserves, irrespective of the time of year.

(3) Following similar reasoning, female weights (Fig. 1) should vary most in those species that are highly dimorphic, that hunt agile prey and thus encounter food shortages most frequently. Data in Fig. 3 indicate a weak positive correlation between variation in weight and degree of dimorphism, but not prey agility.

(4) Females should take less agile prey than males. For example, females should take more mammals and males more avian prey. It is hard to test whether preference is for large or less agile prey because size and mobility are usually linked (Andersson & Norberg 1981) and the selection of mammals could depend on the availability of larger prey. Nevertheless, females of three *Accipiter* and two *Circus* spp. catch more mammals than do males (Storer 1966, Nieboer 1973, Kenward

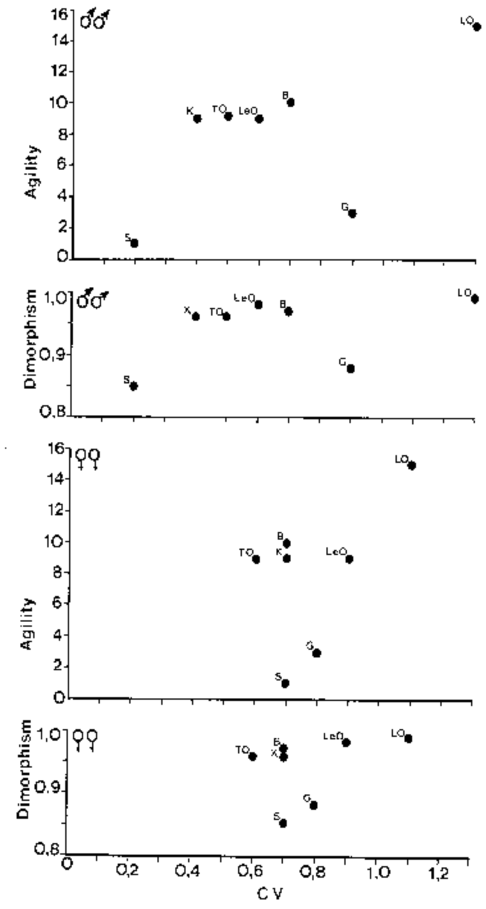

FIGURE 3

Relationships between the coefficients of variation (CV) of average monthly or bimonthly weights of males (from Fig. 2) and females (from Fig. 1) and indices of prey agility and size dimorphism. Prey agility ranks were taken from Mueller & Meyer (1985) or scored using their criteria; size dimorphism was calculated as male wing/female wing length from data in Cramp & Simmons (1980). Abbreviations: G -Goshawk, B - Common Buzzard, TO - Tawny Owl, LeO - Longeared Owl, S - European Sparrowhawk, K - Common Kestrel, LO - Little Owl. Spearman's Rank Correlation Coefficients (from top to bottom):

♂ CV and prey agility: 0,61 $p<0,1$ (without Goshawk (see text) 0,94 $p<0,005$);

♂ CV and wing dimorphism: 0,60 $p<0,1$ (without Goshawk 0,93 $p<0,005$);

♀ CV and prey agility: 0,36 NS (without Goshawk 0,54 NS);

♀ CV and wing dimorphism: 0,58 $p<0,1$ (without Goshawk 0,79 $p<0,05$).

et al. 1981), in accordance with the hypothesis.

(5) If increasing body size reduces flight performance we should expect raptors, particularly breeding males, to behave in ways that minimize their flying weights. Some raptors cache prey, continue hunting and return to the hidden food later. This has obvious costs, for a cached item could be lost to a scavenger, so the benefits of caching should be substantial to outweigh the potential loss of food. Rijnsdorp et al. (1981) show that breeding male Common Kestrels *Falco tinnunculus* eat a greater proportion of food at dusk than at other times of the day, much of this being food cached earlier. Breeding females, by contrast, consume food at a roughly constant level throughout the day. Their data also indicate that breeding males retrieve prey more frequently at dusk than they do at other times of the year when cached food is often eaten earlier in the day. These findings suggest that hunting birds actively maintain low weights during the day, particularly while hunting to provision their mates and young. This circumstantial evidence is consistent with the idea that low weight helps to improve agility. Low weight also reduces the energy costs of flight during hunting; Rijnsdorp et al. (1981) estimated that 7% of daily energy expenditure would be saved by a kestrel postponing consumption of a 22-g mouse until evening. Energy saving as a result of small male size has previously been used to explain size dimorphism (Mosher & Matray 1974). However, this alone does not explain why males should be smaller than females, and it implies that raptors that hunt in flight should be the most dimorphic, a prediction not supported by available data (Mueller & Meyer 1985).

(6) If the storage of energy reserves and efficient prey capture were compatible in predators of agile prey, males should accumulate reserves before the onset of breeding and maintain these as long as possible. This clearly does not happen because weights of those species that undergo substantial annual changes are much lower before breeding than at other times of the year (Fig. 2). Presumably males do have small reserves before breeding and these probably become exhausted as the cycle progresses, as suggested by a slight decline in average weight.

(7) Raptors that hunt large prey should be more dimorphic since those taking small but more or less equally mobile prey probably feed more predictably and have less need for reserves. Von Schantz & Nilsson (1981) show a positive correlation between the degree of dimorphism and relative prey weight, although Mueller & Meyer (1985) question the validity of their data and conclusion. Actual prey size does not relate to the degree of dimorphism, because large eagles feeding on large mammals are no more dimorphic than those taking smaller ones. Among bird-eaters, the smallest accipiters catching the smallest birds are more dimorphic than those taking larger birds.

DISCUSSION

Several other predictions could be tested if adequate information was available. For example, because the degree of reversed size dimorphism is so closely related to prey agility, some species, as judged from their diet, differ from the general pattern in raptors. These deviations are probably due to factors that restrict the ability of females to store reserves. If the nature of the prey is such that males are unable to provision their mates, females will be required to maintain efficient flying performance and small female size will be favoured. These conditions may hold for Bat Hawks *Macheiramphus alcinus* in which males are probably unable to catch sufficient prey to feed their mates during the short periods of optimal hunting time. Accordingly both sexes incubate, the females hunt for themselves (Hustler 1983) and the degree of dimorphism is less than expected of a predator hunting aerial vertebrates (Mueller & Meyer 1985). Similarly, if nests are frequently visited by predators, effective defence by females may require agility in flight and low body weights, allowing few reserves to be stored. The degree of reversed size dimorphism in other large predatory birds, e.g. skuas and sulids, will probably also be related to the degree that males and females perform the roles of provisioning and reserve-storage respectively. Female Longtailed Skuas *Stercorarius longicaudus* store greater reserves than do males, do most of the incubation and are often fed by their mates (de Korte 1985).

Several hypotheses have related sexual dimorphism in raptors to a scarcity of food resources (Temeles 1985, Mueller & Meyer 1985). Size differences between males and females enable a wider food base to be exploited, reducing intersexual competition for food and increasing the range of potential prey to feed to nestlings. Evidence supporting this relationship is provided by Temeles (1985) who found that the degree of dimorphism was related to hunting success, this being an indication of prey vulnerability and, ultimately, scarcity. Similarly, Snyder & Wiley (1976) indicated that the degree of dimorphism in raptors is directly related to the frequency of food shortage during the nestling period. These are probably effects of the two main selective pressures that I have put forward in this paper. Thus, poor hunting success is probably related to the need (a) for male agility in hunting mobile prey, and (b) for substantial reserves to offset the effects of temporary food shortages.

The diverse literature on size dimorphism in raptors suggests many other advantages of small size in males or large size in females (Mueller & Meyer 1985). Most of these are probably incidental effects, but other factors might have selective benefits further contributing to the degree of dimorphism. For example, if females are already large to store reserves, they should produce larger eggs and/or clutches, defend their nests more powerfully, better protect their follicles, incubate and tear-up food for their young more efficiently, and perhaps dominate their mates more effectively. Other advantages may accrue to small males: they will incur reduced absolute energy costs, greater agility in flight may be an advantage in territorial contests (Widen 1984), and better hunting success could improve fitness by allowing males to provide food readily during courtship, guard females more effectively, and stimulate reproductive synchrony with their mates (Safina 1984). Furthermore, both sexes may benefit by partitioning and reducing competition for prey. However, no single theory based on these assumptions explains the direction or degree of dimorphism in raptors.

Much of the argument in this paper should also apply to small insectivorous passerines and non-passerines that catch agile prey to feed their young. There are however at least two probable reasons why these females are relatively small, their size not being strongly selected for the storage of large reserves. First, the allometric scaling exponents that determine quantities of reserves and energy expenditure according to body weight indicate that the energetic and survival value of reserves improves disproportionately as body size increases. This means that a 10% increase in the size of a small bird (and thus reserve capacity) will have comparatively little additional value in enabling it to withstand food shortages (C.W. Sapsford pers. comm.). Selective pressures for the storage of reserves are thus probably weak among small insectivores. Second, small birds face a greater risk of predation than larger ones. If they stored reserves to the same extent, their increased weight should lower their manoeuvrability and therefore ability to escape from predators (Lima 1986).

I have so far suggested that opposing directional selection drives male and female body sizes apart. However, the respective strengths of the selective factors may differ, so that the degree of dimorphism is determined to a greater extent by the size of the male, female size being more conservative. Firstly, the roles of females of different species during breeding vary little. All produce eggs, and most of those larger than their mates do nearly all the incubation and brooding, only helping to provision the young during the latter half of the nestling period, irrespective of diet (Newton 1979, Mueller & Meyer 1985). In performing this predictable role, females should maximize their capacity equally to store reserves because all breeding raptors are likely to encounter at least some food shortages. Secondly, the predictive evidence in support of directional selection of small males as prey agility increases is relatively robust. That for females, by contrast, is perhaps rather weak and inconsistent *(Predictions* 3 & 7). Finally, among the seven species for which data on weight variation are available, males show greater variability than females (Fig. 3). The coefficients of variation for male weights range from 0,2 and 1,3, while those for females lie between 0,6 and 1,1, suggesting that their body size is more conservative.

The main points made here depend strongly on the assumption that it is as important to store adequate reserves as it is to be an efficient hunter. Traditionally, greater emphasis is placed on feeding success than on the maintenance of adequate reserves. Although the two strategies ultimately serve the same purpose of balancing energy budgets, the accumulation of reserves will be at the expense of flight performance, while hunting efficiency will improve as reserves (i.e. weight) are lost. What are some of the costs of large size for females and small size for males? How does a large female manage to catch agile prey and how does a small male survive without substantial reserves? I will not consider these questions here, but simply suggest that differences between non-breeding males and females in behaviour, habitat selection, and prey choice may reflect each sex's attempt to avoid the costs and exploit the benefits of their respective body sizes. Such differences are usually explained within the context of competition theory, but it may be more useful to first consider the constraints imposed by body size on males and females, in the same way that allometric principles account for interspecific differences.

The relative importance of strategies to maximise hunting success or store reserves should be manifested in other aspects of raptor biology. For example, much of the individual variation in activity budgets might be related to the size of reserves. Raptors may switch from one type of prey to another in different seasons, there may be regional differences in the mobility of available prey, and the need for reserves may vary in different ways. In species that hunt both in flight and from perches, individuals with large reserves should do more of their hunting from perches than those with lower weights. Village (1983b) found that Common Kestrels used less expensive foraging methods in winter than during the breeding season and suggested that these differences were related to the respective needs to conserve energy or obtain prey rapidly. There are obviously many testable predictions about the conflicting consequences of conserving reserves or hunting efficiently, but these are outside the scope of this paper. However, any study that can successfully monitor changes in the weights and behaviour of individuals will provide many of the data needed to test these ideas.

The general ideas presented here are attempts to identify the pressures selecting for size dimorphism. Other factors are probably involved, and those highlighted in this paper are likely to vary under different circumstances. There is a great need for better data to study changes in reserve levels and prey agility. Much of what has been said depends on body weights, often collected in different ways from only a few species. It is not clear how faithfully body weights reflect reserves (Marcström & Kenward 1981), what reserves are involved, and just how efficient different kinds of reserves are. Clearly, more needs to be learned about nutrition and hunting ability to understand the breeding strategies of raptors.

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