Different roles of nutrition in domestic and wild game birds and other animals

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A farm animal converts food that we give it into products that we want. It is conceived at a time we find convenient, and dies when and where we wish it. It may be allowed to breed if it exhibits traits that meet with our approval.

A wild animal finds its own food. It decides what it will, and what it will not, eat. It competes with other animals for food, and tries to avoid being eaten by a predator. If it survives, it chooses its mate and a place to rear its offspring.

The traditional task of nutritional science is to determine the nutrient requirements of domestic animals, so that they will grow flesh, secrete milk and lay eggs as quickly and cheaply as possible. To increase the efficiency of these processes, we modify our domestic stock by selective breeding. They need to be modified because they were not designed, or evolved, for the purposes they now serve. Useless appendages such as horns, or inconvenient traits like seasonal breeding, may be removed.

The task of the wild animal is to survive, and to contribute as many of its offspring as possible to the next generation. Efficiency of production, in the agricultural sense, is irrelevant. If the prodigal use of resources enables an individual to maximize its contribution to the species' gene pool, then natural selection will establish prodigality as a characteristic of that species. Almost all the observed characteristics of a wild animal are functional, and much of our insight into evolution has come from trying to explain the adaptive significance of seemingly odd characteristics.

A group of domestic animals will eat all the food given to them, and then starve unless more is provided. But wild vertebrates usually do not eat all the food available. They often appear to maintain their numbers at a level which is well below that set by potential food supplies. The account which follows outlines some of the ways in which food resources are divided up amongst species and individuals in the wild. Many of the examples are from game birds because I know them best.

Interspecies competition for food

Wild animals often eat certain foods whilst ignoring others which seem to be nutritionally adequate and which are eaten by closely related species or even different populations of the same species. This seems, in part, to be the result of competition amongst species. By specializing, a species may become highly adapted, that is,

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more expert at gathering a restricted range of foods and more efficient at digesting them than if it attempted to take a more catholic diet. In this way, different species have evolved to fit different ecological 'niches' (Elton, 1927) which include not only a particular kind of food but also other resources such as shelter and breeding places.

Interspecies competition for food is illustrated by the foods that different populations of the rock ptarmigan (*Lagopus mutus* (Montin)) choose to eat in winter. This is the only naturally-occurring vertebrate herbivore in Iceland, where its main foods in winter are willow (*Salix* spp.) and birch (*Betula* spp.) (Gardarsson & Moss, 1970; Gardarsson, 1971); of the two it prefers willow to birch, apparently because willow is intrinsically more nutritious. In interior Alaska however, the rock ptarmigan is not alone, as the closely-related willow ptarmigan (*Lagopus lagopus* L.) also occurs on the same wintering grounds. Here, over 90% of the winter diet of the rock ptarmigan consists of birch, even though willow is readily available to it (Moss, 1974). The willow is eaten instead by willow ptarmigan, forming over 90% of their winter food. Willow ptarmigan are quite capable of subsisting on birch, as it makes up more than 90% of their diet in north Norway (S. Myrberget, personal communication), where little willow is available. In Alaska then, it appears that interspecies competition has caused the observed differences in diet. This competition, however, seems to have occurred in the past and is no longer obvious. At present, each species has become adapted to its own particular diet as shown by interspecies differences in bill size (Weeden, 1969), gut lengths and gizzard weights.

Situations such as this make it necessary to refine the concept of 'plane of nutrition', when studying wild animals. Consider two foods, food A providing a higher 'plane of nutrition' than food B, that is, more nutrients and energy per unit weight. When only one species of animal is present, it will be advantageous for it to eat food A. It will spend less time feeding and will develop a smaller digestive system than if it ate food B. The smaller digestive system will require less food to maintain it, and less effort for the animal to carry it. But if two species of animal are present, each will find it advantageous to avoid competition and one of them may adapt to food B. Once it has made the necessary adaptations, it is no longer adapted to food A. Hence, it is likely to perform better on, and to prefer, food B. The optimum 'plane of nutrition' for a wild animal is not necessarily the most concentrated diet, but the diet to which it is best adapted.

Intraspecies competition for food

Individuals of the same species also compete with each other. It is unusual for animals to fight directly over food. Instead, vertebrates exist within a social system, one function of which is to provide a dominance ordering of some kind. Animals which die usually do so because they are at the bottom end of the dominance order. The proximate cause of death may be starvation, as in wood-pigeons (*Columba palumbus* L.) in East Anglia where there is not enough food to support the entire population over winter. Here, the dominant wood-pigeons get enough food and survive, whereas the sub-dominant starve (Murton, Isaacson & Westwood, 1966).

Sub-dominant animals may also die in the presence of a large excess of potential food. This is probably true for most Tetraonids (birds of the grouse family) and is well documented for the red grouse (*Lagopus lagopus scoticus* (Lath.)). Red grouse are territorial and monogamous; cocks take up territories in autumn and maintain them throughout the winter and spring until after the hens have laid their eggs (Watson & Jenkins, 1964). About half the birds fail to get territories in the autumn and these all die over winter from a variety of proximate causes. However, grouse eat only a few per cent of the available shoots of heather (*Calluna vulgaris* L. (Hull)), which makes up their main food (Savory, 1974). The mortality which occurs is not due to lack of food, but to the workings of the social system: a bird dies because it does not have a territory (Watson, 1967).

Thus, in agricultural terms, red grouse are remarkably inefficient at utilizing their food. Why are they not more efficient? But one can as well ask: why should they be? After all, it is of no advantage to the individual cock to take a smaller territory. The only benefit would be to his neighbours, with whom he is competing. It is probably advantageous for a cock to take a big territory so that he can get the maximum scope for food selection, and thus provide the best possible diet for himself and his mate.

Even though red grouse eat only a minute proportion of the available heather, they are nonetheless greatly affected by variations in the quantity and quality of the food available to them. Indeed, grouse numbers seem to be continually responding to changes in food supplies, which affect the number of young reared, the density of breeding birds and the proportion of territorial cocks which remain unmated for the breeding season and do not pair up with a hen (Watson & Moss, 1972). This paradox may be explained by noting that grouse are very selective feeders (Moss, 1972*a*; Moss, Miller & Allen, 1972), so that only a small proportion of the available food may be both of optimum nutritive value and readily accessible (i.e. at a convenient height) to the feeding bird.

But this explanation conflicts to some extent with the earlier statement that grouse eat only a small proportion of the available food. If very little of the available heather is of optimum quality, then this small fraction of the heather may be used quite efficiently. This may well be so, but the question remains: why is the suboptimum but nonetheless adequate food so inefficiently utilized? One explanation is that an individual who tried to use this food would probably need a bigger digestive tract to do so (Moss, 1972*b*) and this would be a disadvantage when it was competing with its more selectively feeding and fitter neighbours.

Distribution of food supplies in relation to social systems

The food available to red grouse is fairly uniformly distributed and readily available at all times of year. This has allowed grouse to be sedentary and to evolve a territorial social system. A more patchy distribution of food, both in time and in space, is associated with different forms of social organization.

Many birds are territorial in the breeding season, but flock in the winter when food is scarcer. It is thought that one reason for flocking is that flocks may discover localized patches of food more effectively than single birds or pairs (Ward & Zahavi, 1973).

The food of California quail (*Lophortyx californicus* (Shaw)), which live in the desert, is adequate for breeding only in years when enough rain falls (Francis, 1970). The social system of the birds reflects this. When not breeding they flock, but when breeding they take territories, and may also breed at an unusually early age when food is plentiful. The first chicks hatched in a year of abundant food will breed in the same year. In other words, California quail are adapted to exploiting sporadic but plentiful food supplies as quickly as possible, whereas the social system of red grouse is adapted to utilizing a more stable and predictable supply of food.

One of the advantages of being territorial is that a food supply is thereby ensured for the owner, usually the male, and thus for his mate and offspring. But if hen and offspring can find adequate food without the aid of the cock, then there may be no reason for maintaining the pair bond. In its absence, other social systems may evolve, and this has occurred in nine of the ten genera of Tetraonids. Of these nine, five have 'leks' where groups of males display together in the breeding season. As the hens come to the leks only to be mated, and then rear the young themselves, the pair bond here is confined virtually to copulation. In the four remaining genera, individual cocks display at sites dispersed evenly throughout the available habitat. The hens are similarly dispersed, but again only associate with a cock for copulation.

An obvious question here is why, having abandoned the pair bond, have some species evolved the lek system and others a system of dispersed display sites? The evolution of leks has often been explained by suggesting that groups of displaying cocks are more likely to attract hens than lone individuals. There is no generally accepted explanation of the evolution of the dispersed display system. However, all four genera of Tetraonids using the dispersed system live in thick forests, while four of the five genera which display at leks do so in open country. It is likely that a group of displaying cocks is especially attractive to predators, as well as to hens, and that it is only safe to lek in open country, where the predators can be spotted at a safe distance from the lek. The exception to this rule is the capercaillie (*Tetrao urogallus* L.) which leks in forests. However, the cock capercaillie is so large that it is much less vulnerable to many predators than the other forest-dwelling species.

Similar ideas are currently being formulated to explain differences in the social systems of wading birds (Pitelka, Holmes & MacLean, 1974), primates including man (Michael & Crook, 1973) and ungulates (Geist, 1974). Many of these ideas are purely speculative and this subject, the study of factors which determine different social systems, is in its infancy. Nonetheless, it is already clear that the distribution of food supplies in time and space is an important determinant of social organization.

Once a society has evolved, it is status within that system that determines whether an animal has access to the best food or not. Status is generally achieved by competitive display. Spectacular plumages and organs such as horns and antlers have evolved to lend emphasis to such displays. These displays and their associated organs are functional in the wild because they enable the animal to get access to food, mates and other resources, but they are just a nuisance to the prospective farmer.

Bringing wild animals into captivity

Studies of the sort just outlined offer explanations for some of the difficulties that people find in attempting to domesticate wild animals: for example, although it is easy to breed some game birds in captivity, others are difficult. If pairs of birds are caged, then territorial, monogamous species such as the red grouse will adopt the cage as their territory and breed readily, whereas lek species like the capercaillie or black grouse (*Lyrurus tetrix* L.) will breed only in a large aviary with several males present.

But this is an anthropocentric viewpoint. The title of this symposium implies a proposal to take new species of animals from the wild and to put them and their descendants into captivity. As scientists, we are not allowed to credit the animal with a viewpoint, or we will be laughed at. Nonetheless, we can ask the question: what are we doing to a wild animal by bringing it into captivity, and in particular into modern, intensive farming conditions?

Intensive farming uses the animal for only one function: production. But the wild animal has a complex nervous system which has evolved to allow it to respond continuously and effectively to its physical and social environment. We are only just beginning to appreciate the complexities of animal societies. But we know enough to say that in bringing a wild animal into captivity, we are depriving its nervous system of many of the stimuli to which it is adapted and preventing the animal from fulfilling many of its normal functions.

We do more than bring an animal into captivity. We select for certain traits and create a new 'domestic' animal from the original stock. Domestic animals have smaller brains than their wild counterparts, and the more recently evolved ('higher') parts of their brain have degenerated most (Herre & Röhrs, 1973). They have lost many of the wild animal's abilities. Many of the behaviour patterns which remain are mere fragments of once-integrated displays or once-coordinated sequences of activity. A domestic animal has a degraded nervous system, and a behavioural repertoire which can only be described as a caricature of its origin.

Any extrapolation beyond this point is a matter of personal taste. Nonetheless, ethical and aesthetic aspects of bringing wild animals into captivity, and especially into intensive farming conditions, should be thought about carefully.

Many recent attempts at domestication (grouse, partridge, quail, trout, plaice, turtle, crocodile) have been aimed at producing high-cost products intended for the luxury market. Some of these projects have made money, but economics should not be the only consideration affecting our actions. If we harden ourselves to the prospect of degrading new species of animals into 'new farm animals', we may also be degrading ourselves.

Summary

Aspects of the nutrition of wild animals are briefly outlined using game birds as examples. Wild animals are contrasted with farm animals. For wild animals, making the maximum possible use of available resources, i.e. efficiency in the agricultural sense, is irrelevant. It is more important for the individual to maximize its ability

to compete with other animals. Competition takes place within a social organization in which a dominance ordering occurs, and the most dominant animals gain access to the resources at the expense of subdominants. The form of an animal society is determined, in part, by the pattern of distribution of food supplies in time and space. Ethical considerations are raised about the propriety of bringing 'new farm animals' into captivity.

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