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ABSTRACT: The adaptive level of a character including a behavioural character, is the level at which the combined effect of predators, climate and all the other selection factors makes the animal's contribution to future generations as large as possible. But how is the animal to know what these adaptive levels are and when they occur? For this it needs information. Even when information is available, the animal still needs characters such as eyes and ears to perceive clues, i.e. items of information, and a nervous system to interpret clues and so infer adaptive levels. Information like weather forecasts is imperfect, so to reduce error animals ought to use as many independent sources of information as possible. But information from companions is not independent, so why do red deer hinds consult their companions and modify their date of oestrus accordingly? Error occurs not only in information but also because of variation in the hind's characters for perceiving clues and inferring adaptive levels. Each individual could improve its estimate by taking the mean of its own estimate with that of one (or more) companions whose estimate was based on the same information. The central limit theorem shows that the variance will be reduced from S^2 to S^2/n. The synchrony of breeding that occurs with predation in other animals shows that animals can perceive from their companions clues that relate to timing of breeding, and where predation does not occur animals will still perceive such clues and thus obtain a closer approach to the adaptive level.

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Iason and Guinness (1985) showed that in herds of wild red deer hinds (Cervus elaphus) oestrus in those non-lactating animals that associate together is synchronized. Why should this be? Synchrony is a distribution of intervals that has a smaller variation than other distributions. Thus the period when people leave a cinema after the film ends will be synchronous compared to the period when the same people arrive at the cinema. But why does synchrony arise in a behavioural character? Here I show that animals need information to regulate their behaviour and that synchrony of oestrus in these hinds could arise because they obtain more information from their companions.

The adaptive level of any character is the level at which the animal's contribution to future generations is kept as large as possible. Because comparison between individuals also acts such that the same state is achieved, the animal's characters naturally evolve to their respective adaptive levels. A selection factor is any variable such as a predator or climate that influences reproduction or survival, and the adaptive level of a character is thus the level at which the aggregate effect of all the selection factors makes the animal's contribution to future generations as large as possible. Thus the adaptive date for oestrus in these red deer hinds is determined by various selection factors.

Selection factors determine the level of a character that is the adaptive level, but how can an animal know what the adaptive levels are and when they occur? For this it needs information. But what is information? Consider a newly hatched Herring Gull chick. It surveys its world and at some moment it sees a red patch near the end of its parent's bill. This red patch is in fact the adaptive place for a chick to peck, and indeed it does so (Tinbergen & Perdeck 1950). But why red spots on yellow backgrounds? Why not white fluffy clouds against blue skies? Clearly the red spots relate to the adaptive occasion and direction for a chick to peck whereas fluffy clouds do not. For this reason (and this reason alone) these red spots are clues for adaptive behaviour. And the general assembly of available clues constitutes information. Note the pivotal role of information: information implies adaptive levels, and without information the animal cannot regulate its behaviour.

Even when information is available, the animal still needs the appropriate characters such as eyes and ears to perceive clues and a nervous system to interpret

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them and so regulate its behaviour at the respective adaptive level.

To distinguish between the environmental variables that relate to adaptive levels (i.e. clues) and the animal's characters that perceive and interpret these clues is very important. Clues imply adaptive levels whereas the animal's characters infer these adaptive levels. Consider that different patterns of day length relate to the different breeding seasons of a large proportion of species including Red Deer (Fletcher 1974). If day length itself had some intrinsic power, influence or necessity that in some way compelled breeding, then all these various species would breed at the same time. But breeding seasons are spread according to the season that is adaptive for each species. So the compulsion lies not in the pattern of day length but rather in the characters of each species, and it is selection that ensured that the characters found in each species today are those that infer the adaptive breeding season for that species.

Returning to synchrony of oestrus in red deer, could it be that the extra information from their companions brings this synchrony about?

Morphological characters vary (Darwin 1859) and so do behavioural characters, which in general differ from morphological characters in that the variation comes not only from the heritable basis of the behaviour pattern but also from the information that the animal uses to regulate its behaviour. All information like weather forecasts is imperfect and for this reason the variation in the behavioural response of an animal certainly will be more than the variation that is largely inherited. Accordingly animals that can perceive and interpret as many independent sources of information as they typically encounter, will be able to reduce that part of the error in their behavioural responses that stems from imperfections in the information. Because the behaviour of these animals will be closer to the adaptive level than the behaviour of other animals that use fewer clues, the characters that perceive and interpret additional clues will spread throughout the population.

Several variables in the environment relate to the adaptive date for oestrus and so are clues. They include food and weather (Mitchell & Lincoln 1973), day length (Fletcher 1974), possibly temperature, and, as demonstrated by Iason and Guinness (ibid), companions. But surely the information from companions is not independent, but rather is completely redundant so could not help animals regulate behaviour at a closer approach to the adaptive level. Why does each hind not rely on its own perception and interpretation of food and weather, day length, and temperature? Why do these hinds consult thair companions and modify their date of oestrus accordingly?

When a hind interprets these variables, the variance in its ability to interpret, as well as the variance in the information available prevent it from estimating the date for oestrus precisely at the adaptive level. It is not possible to reduce the variance in the external information of day length, food and temperature. But could a hind reduce the variance in its ability to interpret? As with any other character its estimate of the date for oestrus will have a mean at the adaptive level and a variance about this mean. An individual could improve its estimate by taking the mean of its own estimate with that of one (or more) companions whose estimate was based on the same variables. The Central Limit Theorem (e.g. Clarke 1969) shows that the variance would be reduced from S^2 to S^2/n. In any regime subject to selection such information could not be ignored. But surely the appropriate detail from their companions must be hardly perceptible if at all. Is it possible that the animal's characters could evolve to perceive and interpret such fine detail?

Elsewhere predation has been shown to be important in determining synchrony in breeding. But predation is a selection factor. In what way does predation impose synchrony on breeding? And what does this imply for synchrony of oestrus in red deer hinds?

The timing of nesting by some, if not all, species of gulls is determined largely by seasonal abundance of food and seasonal weather. When Darling (1938) studied the breeding success of Herring Gulls and Lesser Black-backed Gulls (L. fuscus) he found that pairs in larger colonies were more successful in rearing young than those in smaller colonies. He thought that this was because predation was more severe in smaller colonies. If the number of predators stayed the same, then in large colonies the same number of acts of predation would be spread over a larger number of pairs of gulls than would occur in smaller colonies. This advantage would be more if breeding was synchronous (see also Parsons 1971). For Black-headed Gulls (L. ridibundus), Patterson (1965) found that predation itself was decreased by the increased mobbing over the denser parts of colonies, an advantage that would also be enhanced by synchronous breeding.

In such circumstances it will then pay individuals to adjust their timing of breeding to the mean for the local population. For some individuals this involves starting to breed earlier than their condition and experience dictates. Then they may increase the risk to themselves and their offspring because they may have to face the following winter in poor condition. Conversely, other individuals may need to delay breeding later than the point appropriate to their condition and experience. Then they too get less benefit in this case from their better body condition and experience. For each set, the advantage of reduced predation no doubt exceeds the disadvantage of synchronization. Thus when predation is important, the timing of breeding that is adaptive will depend to some extent on the rest of the local group. When predation is not present the adaptive timing depends only on other factors such as time of year and availability of food.

A selection factor such as predation may determine the adaptive level of breeding to be synchronous compared to similar circumstances without predation. But where is the information to regulate such synchrony? It can only come from the behaviour of companions, even though it is difficult to identify precisely which clue from their companions these animals do perceive (see e.g. Brown 1967: Southern 1974).

The selection factors cited by Iason and Guinness (op cit) that determine the date of oestrus are: availability of food (Lack 1968), inclement weather (Stewart 1982), risk of predation (Sinclair 1977) and the increased vigilance that predation entails (Arman et al. 1974, Clutton-Brock et al. 1982). Of these, only the incidence of predation or the need for vigilance select for synchrony. However, Iason and Guinness point out that on giving birth hinds disperse and hide their calves, behaviour that supports their view that neither predation nor vigilance affects the timing of oestrus. The synchrony of breeding that occurs with predation shows that some animals can indeed obtain information about time of breeding from their companions. Where predation does not occur then animals will still use such information from their companions because any closer approach to an adaptive level results in a larger contribution to future generations. I think that this is why oestrus in red deer hinds is synchronized.

What all this means is that when several individuals experience the same information, then each could improve its performance by adjusting its estimate towards the estimates of its companions. This improvement will occur even in the absence of factors selecting for synchrony such as predation and vigilance.

This has been most elegantly demonstrated by Iason and Guinness (op cit) for the timing of oestrus in non-lactating red deer hinds.

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