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NOTES AND COMMENTS

DIRECTIONAL SELECTION AND CLUTCH SIZE IN BIRDS

Clutch size has been shown both to have significant heritability (Perrins and Jones 1974; van Noordwijk et al. 1981; Flux and Flux 1982; Boag and van Noordwijk 1987; Findlay and Cooke 1987) and to be under directional selection to increase in many populations of birds (Nur 1984; Boyce and Perrins 1987; Rockwell et al. 1987; Gibbs 1988). Nevertheless, several long-term studies on wild populations have failed to find any evidence for evolution of a larger clutch size with time (Boyce and Perrins 1987; Rockwell et al. 1987; Gibbs 1988). Price and Liou (1989) reviewed earlier explanations for this apparent discrepancy and concluded that none is adequate to explain the generality of the phenomenon. They developed, instead, a new explanation based on the model of Price et al. (1988). Price and Liou (1989) suggested that directional selection operates on a correlated, environmentally determined trait (nutritional state). In their model, the genetic component of clutch size could also be subject to selection, but, if clutch size is not evolving, this selection must be nondirectional (e.g., normalizing).

Although we affirm the potential importance of their model, we would like to point out an alternative explanation for the lack of apparent response to selection acting on clutch size. We suggest that components of the genotype may, in fact, be evolving, but the phenotypic expression of the genotype may not change because it depends not only on the individual's genotype but on the deviation of that genotype from the mean of the population. If the population mean is changing with time, this can be considered a change in the individual's environment, which necessarily affects the response to selection. We suggest that such a situation could arise not only for clutch size but for many other traits closely associated with fitness.

We develop this concept starting from the standard univariate equation of quantitative genetics, which decomposes the phenotypic value, P , as

$$P = G + E,$$

where G is the additive genetic value, and E represents the effects of dominance, interaction between loci, and the environment. The values G and E are assumed to

be independent, with the population mean, \bar{E} , equal to zero. Under this model, if the environment remains constant, the change in mean phenotype in response to selection, R , is given by

$$R = h^2 S, \quad (1)$$

where S is the selection differential (the difference between the means of the selected and the unselected populations), and h^2 is the heritability of the trait, measured as the regression coefficient of G on P (Falconer 1981). Clearly, if such a model were applicable to clutch size, then positive values of both h^2 and S should result in an increase in mean clutch size.

However, the assumptions of this model may be violated in two main ways. First, there may be a conditional covariance of G on fitness when P is held constant. This may arise if selection is also operating on other traits that are correlated with the trait under observation. Second, the environment may change with time. The first situation can involve either genetic or environmental correlations and may be treated with the multivariate approach of Lande and Arnold (1983). This case includes the model of Price and Liou (1989) and was discussed by them in detail. Here we consider only the effect of changes in the environment, assuming that the first situation does not apply.

With this assumption, the response, R , is not given by equation (1) but by

$$R = h^2 S + \Delta \bar{E}, \quad (2)$$

where $\Delta \bar{E}$ is the change in the mean environmental component over one generation. The significance of $\Delta \bar{E}$ is well recognized when E refers to the physical environment or derives from the behavior of a predator, prey, or competitor species. For example, if the average nutrient levels in the environment change, we expect an effect on the response to the selective pressures on clutch size. Most studies that take measurements to estimate the effects of selection watch for trends in any of these factors that extend over the period of the study.

Here we point out that some components of the environment may change in a systematic manner but not be readily observed. In particular, the environment of an individual includes other members of the same population. Suppose that the environmental component, E , is partly determined by the mean value of another trait in the same population that is evolving: as its mean value changes, the mean value of E changes.

The relevance of this concept to clutch size can best be illustrated with an example. Following Price and Liou (1989), we assume that clutch size depends at least partly on the nutritional status of the female. Evidence from the literature on several species supports this assumption (Ankney and MacInnes 1978; Dijkstra et al. 1982; Hussell and Quinney 1987; Arcese and Smith 1988). However, unlike Price and Liou, we do not assume that nutritional status affects fitness in any other way—that is, fitness depends only on clutch size. We can then develop a simple model, in which we suppose that clutch size, P (number of eggs), is the

product of three factors,

$$P = P_1 T_2 E_0,$$

where P_1 (number of eggs per unit of area) is determined by the foraging effectiveness of the parent, T_2 is the parental territory size, and E_0 is a random, environmental component (additional factors could be added to the model, such as variation in the proportion of nutrients allocated to eggs, without affecting the basic arguments that follow). For convenience, we use a multiplicative model, which is often appropriate for components of fitness (the standard additive formulation can be derived by taking logarithms of both sides of the equation). We further assume that T_2 is determined by a large number of physical and behavioral traits, which we collect together, for convenience, under the name of aggressiveness and denote by P_2 . Since, in a fixed region, the total area available for territories, A , must remain constant,

$$T_2 = (A/N) P_2 / \bar{P}_2,$$

where N is population size. If we now decompose both of the traits P_i in the standard way, $P_i = G_i E_i$, then clutch size can be written as

$$P = GE, \quad (3)$$

with $G = G_1 G_2$ and $E = E_0 E_1 E_2 A / N \bar{P}_2$. Thus, it is clear that, even if the mean value of each of the environmental subcomponents (E_i) remains one in each generation, E will change in response to changes in \bar{P}_2 . If P_2 increases in the population as a result of, for example, some evolutionary shift in one of its component behavioral strategies, then \bar{P}_2 increases and \bar{E} decreases, making $\Delta \bar{E}$ in equation (2) negative. While this evolutionary change occurs, if P_i does not evolve, it is possible for clutch size, P , to be at equilibrium with $R = 0$ and for $h^2 S$ to be positive.

In the example above, the individual value of P is affected by P_2 in two different ways, positively by the individual value of G_2 and negatively through the population mean \bar{P}_2 (which equals \bar{G}_2 if \bar{E}_2 is zero). Only the second of these is needed to produce a nonzero $\Delta \bar{E}$ and get the above effect.

At any time there must be many traits in the process of evolving, whether adjusting to changes in the environment or to the ongoing effects of an inter- or intraspecific arms race, in a Red Queen fashion (van Valen 1973). Such traits can be expected to have an effect on fitness and often affect characters, such as clutch size, that are closely correlated with fitness. If the individual clutch size (P) depends on the average level of development of a number of such traits in the population, then the environmental component (E) of P is a function of the population means of these traits, and, for as long as any of them evolves, we see a systematic change in \bar{E} .

This generalized model could explain, in part, the absence of observed evolution of clutch size in several long-term studies of bird populations. For example, in

the population of great tits (*Parus major*) at Wytham Woods near Oxford, there is significant heritability of clutch size (Perrins and Jones 1974) and directional selection for greater clutch size (Boyce and Perrins 1987), but there has been no corresponding increase in mean clutch size with time as would be expected if equation (1) applied. Clutch size, both in terms of the number of eggs that can be laid and the number of young that can be raised, depends on the ability of the parents to gather nutrients, which in turn depends on territory quality. As a result, birds with better-quality territories lay larger clutches and raise more young. Thus, there is selection for birds with the best ability to compete for territories. However, as shown above, although the average ability to acquire good territories (\bar{P}_2) increases with time, the average territory quality, and hence the average clutch size, does not change if the population remains constant.

A similar model can also apply to nonterritorial birds, which we can illustrate using as an example the population of lesser snow geese (*Anser caerulescens*) nesting at La Pérouse Bay in Manitoba. In this colony, the selection differential on clutch size is 0.33 eggs, with no evidence for a correlated decrease in longevity or other component of fitness (Rockwell et al. 1987). Based on a heritability of 0.2 (Findlay and Cooke 1987), the predicted response, using equation (1), should be 0.07 eggs per generation, which, allowing for overlapping generations, should have resulted in an average increase in clutch size of 0.20 eggs over the 20 yr of the study (Rockwell et al. 1987). In fact, there has been a significant and systematic decrease in mean clutch size with time (Cooch et al. 1989). Clutch size in snow geese is strongly correlated with the nutrient reserves of the laying female when she arrives at the breeding ground (Ankney and MacInnes 1978). Most of these nutrients are acquired by the birds during migration, when they feed in large flocks. Clearly, selection acts on females to improve their ability to compete for nutrients, thus causing an increase in \bar{P}_2 . This could lead to no change in mean clutch size, despite a positive h^2S . However, the snow goose example is complicated by the fact that the colony size (N) has been increasing with time. A change in either \bar{P}_2 or N affects E (eq. [3]), and thus either could provide an explanation for the lack of an increase (or even a decrease) in mean clutch size, \bar{P} , in spite of a positive h^2S .

One possible implication of this model is that the competitive ability of birds has been improving systematically with time, such that modern birds should be competitively superior to birds from several hundred generations ago. This hypothesis is not, in fact, unreasonable, because new mutations arise continually that may allow novel ways of exploiting the environment (Hill and Keightley 1988). Over the short term, it may even be possible to measure this by comparing the fitness of daughters from the same monogamous mother over a period of, for example, 10 yr, after correcting for effects due to age. Even over such a short period, there might be a sufficient improvement in the population mean of a number of traits that the later offspring will have lower fitness.

It is worth noting, however, that this systematic improvement over time is not a necessary consequence of the model. Traits such as competitive ability (P_2) are determined by the deviation of many other traits from their optimal values. The

individuals that most closely approach these optima have the greatest competitive ability. Random fluctuations in the biotic or physical environment may alter these optimal values; thus, the population evolves continuously to track these fluctuations. For example, competitive ability may be influenced by resistance to parasites. Changes in the parasite community (possibly in response to the evolution of the organism) alter the optimal combination of traits providing resistance to the parasites, which, in turn, affect competitive ability. Continuous improvements in resistance are necessary even to maintain a constant parasite load, as suggested by the Red Queen hypothesis (van Valen 1973). Similarly, suppose that foraging efficiency is a function of deviation from the optimal bill size. The population could be continuously evolving to approach this optimum if the optimal bill size fluctuates with changes in the vegetation.

Although we suggest that the ability to acquire nutrients influences clutch size, we are not implying with this model that clutch size necessarily increases continuously in the presence of unlimited nutrients. Large clutches could have lower fitness if the parents cannot adequately incubate the eggs or raise the offspring or if the nests suffer high predation. In addition, environmental constraints may limit the time available for egg laying, thus limiting the total number of eggs that can be laid. Furthermore, although factors such as the ability to acquire nutrients may be under selection to increase, other factors may be under different selection regimes. For example, genes controlling the proportion of available nutrients allocated to egg production may be under normalizing selection because sufficient reserves must be retained for the parents to survive incubation and caring for the young.

Although this model has been developed with the example of clutch size in birds, it is potentially applicable to many traits, including other components of fitness. For example, consider the mating success of males in a population in which females choose mates. The mating success of a male (P) depends on the value of various characters that females find attractive (P_2). Characters that increase the attractiveness of a male are under directional selection, resulting in a continual increase in the attractiveness of males (within the constraints of other forms of selection). However, the mating success of a male depends not only on his own attractiveness, P_2 , but on the average attractiveness of the other males in the population, \bar{P}_2 . As a result, the average mating success \bar{P} does not change as \bar{P}_2 evolves but depends only on the number of males and females in the population.

This model is, in many respects, an extension of the models described by Fisher (1930) and Wright (1949) for fitness itself. According to Fisher's fundamental theorem of natural selection (Crow and Kimura 1970, pp. 206–225), any genetic variability in fitness results in an increase in mean fitness. A number of important assumptions are necessary for this to hold. One set of assumptions, which we make here, includes random mating and absence of overdominance, epistasis, or linkage effects on fitness. Another important assumption is a lack of frequency dependence (Wright 1949). In our model, if we identify clutch size (P) with fitness, absolute fitness ($P_1P_2E_0$) is frequency-independent and should follow Fisher's theorem, increasing when there is genetic variance; but relative fitness $P =$

$P_1T_2E_0$, which is what is typically measured, is frequency-dependent and should be unchanged.

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