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Directional Selection and the Evolution of Breeding Date in Birds

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In many bird species, those pairs that breed earlier in the season have higher reproductive success than those that breed later. Since breeding date is known to be heritable, it is unclear why it does not evolve to an earlier time. Under assumptions outlined by Fisher, a model is developed that shows how breeding date may have considerable additive genetic variance, appear to be under directional selection, and yet not evolve. These results provide a general explanation for a persistent correlation of fitness with a variety of traits in natural populations.

IN BIRDS OF THE TEMPERATE ZONE clutch size and other measures of reproductive success typically decline as the breeding season progresses (*1–3*). This has led several workers to suggest that natural selection generally favors earlier breeding dates. If this is so, the unanswered question is why such selection has not caused the birds to evolve earlier breeding (*4–6*). One hypothesis is that the evolution of breeding date is constrained by lack of heritable variation (*2*), but this is not supported by several studies that have shown moderate to high heritabilities for breeding date in natural populations (*7*).

Fisher (*9*), in his elaboration of Darwin's theory of sexual selection in monogamous birds, provided an alternative hypothesis. Darwin had proposed that the health and vigor of females influences both the date at which they breed and their fecundity (*10*). Good health causes females to breed early and to raise more offspring, with the result that the earliest breeding individuals tend to be the most fecund. Fisher gave a numerical example in which there is an optimal intermediate breeding date, but in which the early breeding females nevertheless have highest fecundity. He showed that such a pattern could arise from nonheritable variation in female nutritional condition ("health" in Darwin's terminology) if good nutrition simultaneously causes higher fecundity and earlier breeding (*11*). Here we develop a quantitative-genetic model of Fisher's hypothesis which shows how early breeding females can be the most fecund even when the environment favors an intermediate breeding date and there is additive genetic variation for when females breed.

There is now strong empirical evidence that nutrition does affect both fecundity and date of breeding, as suggested by Darwin and Fisher. First, an association of high nutritional state with early breeding is clearly established (*12*). Supplemental feeding advanced breeding date in 12 of 15 studies of natural populations (*13, 14*), and protein reserves of females have been directly measured and correlated with time of breeding in two species (*15*). Second, females in good nutritional condition typically have higher reproductive success. This has been demonstrated by supplemental feeding experiments (*13, 14*), by direct measurements of protein reserves (*16, 17*), and by correlations between food abundance and several measures of reproductive success in natural populations (*16, 18*).

To show that a correlation between fecundity and breeding date is consistent with heritability for breeding date at an evolutionary equilibrium, we develop the following quantitative genetic model. We assume that a female's breeding date b is the sum of three factors: an additive-genetic component, x; a nonheritable component representing nutritional state, n; and a residual nonheritable component due to other environmental factors and nonadditive genetic effects, e. A female's breeding date can therefore be written

$$b = x - n + e \qquad (1)$$

where the sign of n is negative because a higher level of nutrition causes the female to breed earlier. Following the standard assumptions of quantitative genetics (*19*) the components x, n, and e are assumed to be independent and normally distributed, with means $\bar{b}$, 0, and 0, and variances σ_x^2, σ_n^2, and σ_e^2, respectively. We incorporate the positive effect of nutrition on fecundity with the exponential function $W_n(n) \propto \exp(\alpha n)$, where $W_n(n)$ is the fecundity of a female in nutritional state n, and α is a positive constant that scales the strength of the effect of nutrition on fecundity with respect to its effect on breeding date.

First consider the implications of variation in nutrition. From Eq. 1, the covariance between nutrition n and breeding date b is $-\sigma_n^2$. This negative phenotypic covariance implies that earlier breeding females have greater fecundity, since nutrition and fecundity are positively correlated. The covariance between n (nutrition) and x (the additive genetic component of breeding date) is zero, however, and so there is no genetic correlation between breeding date and reproductive fitness. Thus, in the absence of other evolutionary forces, breeding date will not evolve despite a persistent phenotypic correlation between breeding date and fitness. These conclusions can also be deduced from a path diagram (Fig. 1).

Now consider how breeding date will evolve if the environment favors some

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breeding dates over others. Factors such as inclement weather (which can reduce the reproductive success of females that breed early in the season) and declining food resources (which can lower success late in the season) commonly result in an overall pattern of stabilizing natural selection favoring an intermediate breeding date (*1, 2, 4, 13*). This form of selection can be approximated by a Gaussian fitness function $W_b(b)$ with optimum breeding date θ and width ω^2 (so that small ω^2 implies strong stabilizing selection). If this selection and the effects of nutrition on breeding date are independent, then the overall fitness of a female with nutritional status n that breeds on date b is

$$W(n, b) = W_n(n)W_b(b) \propto \exp(\alpha n) \exp\{-(\theta - b)^2/2\omega^2\} \quad (2)$$

The net effect of selection on the heritable component of breeding date is calculated by substituting the expression for breeding date b from Eq. 1 into both sides of Eq. 2, then integrating over n and e to determine female fitness as a function of the additive genetic component x.

The evolutionary equilibrium for the mean breeding date, which is the optimum for this fitness function, is found to be $\hat{b} = \theta + \alpha\sigma_n^2$. This is not at the optimum breeding date, θ, but is displaced to a later date. The displacement is equal to the strength of the effect of nutrition on fecundity, α, multiplied by the variance in nutrition, σ_n^2. The mechanism thus causes the mean of a heritable trait to evolve to an equilibrium which differs from the ecological optimum (*20*). This outcome is adaptive, however, in the sense that the equilibrium maximizes the mean population fitness (*21*) (Fig. 2).

It is not known whether the average breeding date actually is later than the ecologically optimal time for raising young in natural populations. Lack (*4*) and Perrins (*1*) have argued that variation in nutritional condition does have a strong effect on breeding date and that a large proportion of females breed later than the optimal time in some species. These studies, however, confound the effects of the environment (our W_b function) and the effects of nutrition (our W_n function) on female fecundity, so the question remains unanswered. It will be critical to distinguish between these two effects whenever selection on breeding date or the adaptive significance of the timing of breeding is under investigation.

A correlation between a heritable trait and fitness can persist at an evolutionary equilibrium whenever a nonheritable trait, such as nutritional state, simultaneously affects both the expression of a character and fitness through separate pathways (Fig. 1). Two examples show that this may be widespread. First, clutch size in birds usually appears to be under directional selection with larger clutches leaving more surviving young than smaller clutches (*3, 12, 22*). Clutch size and the ability to raise young are both likely to be positively correlated with a female's nutritional state. Second, plant germination time appears to be under directional selection (*23*), and this could be caused by a nonheritable nutritional effect from the maternal endosperm. These examples were chosen because they have been subject to recent in-depth analyses (*3, 22, 23*). Many other characters which have yet to be as thoroughly investigated may show a similar persistent correlation with fitness.

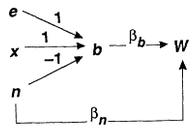

Fig. 1. A correlation between fecundity and breeding date persists even at evolutionary equilibrium in the Darwin-Fisher model. Breeding date is determined by an additive genetic component, x; a nutritional state, n; and a residual nonadditive effect, e. Fitness is denoted by w. At equilibrium, direct selection on breeding date, β_b, vanishes but a correlation between nutritional condition and fecundity generates a selective force, β_n, that is responsible for the correlation between breeding date and fitness.

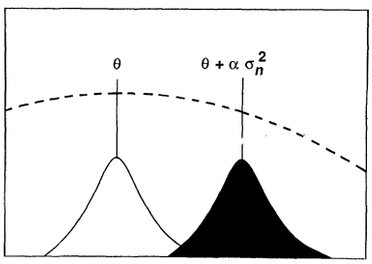

Fig. 2. Given variation in female nutrition affecting both fecundity and breeding date, the average breeding date in the population will be later than the ecologically optimum time. The selection function arising out of variation in environmental conditions is shown by the dotted curve. The solid (right) normal curve shows the distribution of female breeding dates at equilibrium. The open (left) normal curve shows the distribution of female breeding dates, weighted by each female's fecundity: the mean of this weighted distribution coincides with the optimum breeding date (θ). Thus, the mean hatch date of young falls on the optimum date. In adjusting the breeding dates toward the optimum, selection gives more weight to females in high nutritional condition because they are more fecund. Since these individuals breed earlier, the majority of the population is shifted to dates later than the optimum.

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21. Female fecundity will decline throughout the breeding season if the stabilizing selection on breeding date is sufficiently weak relative to the strength of the effect of nutrition on fecundity [approximately, if $\omega_b^2 > (2\sigma_b^3/\alpha\,\sigma_n^2) - \sigma_b^2$, where σ_b^2 is the variance in breeding dates]. Numerical analysis shows that the conclusions are qualitatively robust to the assumption of normal distributions and a Gaussian selection function.
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