

NOTES AND COMMENTS

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ECOLOGICAL VERSUS EVOLUTIONARY HYPOTHESES: DEMOGRAPHIC STASIS AND THE MURRAY-NOLAN CLUTCH SIZE EQUATION

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In explaining patterns of phenotypic variation in and among natural populations, it is important for evolutionary biologists to consider alternative hypotheses. In particular, basic ecological principles may often offer parsimonious explanations of patterns observed in nature and should always be considered when examining putative evidence for specific evolutionary hypotheses. As an example we will draw on Murray's (1979, 1985; Murray and Nolan, 1989; Murray et al., 1989) hypothesis that natural selection "favors females that lay as few eggs as are necessary for replacement" (Murray and Nolan, 1989 p. 1699). Specifically, we will focus on an equation (most recently presented in Murray and Nolan, 1989 and Murray et al., 1989) which, given survivorship and the number of successful clutches laid per year, predicts clutch size in two quasi-stable avian populations. Murray and his colleagues conclude that the match between the predictions of this equation and the data supports the hypothesis that clutch size has evolved to be the minimum required to offset mortality.

We demonstrate that the Murray-Nolan (M-N) equation predicting clutch size can be derived from the Lotka-Euler (L-E) equation for a population that is neither growing nor shrinking (Lotka, 1925; Euler, 1970) without considering phenotypic evolution at all. We argue that an alternative hypothesis for the apparent success of the M-N equation is that it reflects the simple fact that in a static population, birth rate on average equals death rate. We argue that, regardless of the evolutionary factors that influence clutch size, the M-N equation will always correctly predict clutch size, given that demographic assumptions are met. We should point out that in this note we are not attempting to criticize or evaluate in any detail the many facets of Murray's theory of clutch size evolution, but instead are developing an alternative rationale for why the M-N equation might be valid. Indeed we agree with Murray's view that considering detailed age-specific fecundity and survivorship schedules for different genotypes may be of great importance in understanding the evolution

of many traits. However, we do question Murray's proposal that natural selection "favors females that lay as few eggs as are required for replacement." In our alternative nonselective hypothesis, we might pose a parallel statement: In a persistent population, on average, births match deaths, so females will be observed on average to lay as few eggs (and as many) as are needed for replacement. We feel that Murray's hypothesis may implicitly (albeit not explicitly) make an assumption about demographic stability.

Murray and Nolan (1989) present the following equation predicting clutch size (CS):

$$CS = \mu_s / (P_1 + P_2 + \dots + P_i) \quad (1)$$

where μ_s (which is assumed to be independent of age) represents the annual number of eggs laid in successful nests per female, and P_i represents the probability of successfully fledging at least i broods in a breeding season. Note that the sum of the P_i 's is simply the average number of successful broods per year per female (which we denote B_s below). They then note that μ_s can be expressed as

$$\mu_s = (a + 1) \left/ \sum_{\alpha}^{\omega} \lambda_x \right.$$

where λ_x represents survivorship to age x of individuals hatched only from eggs in nests that successfully produce a brood (i.e., at least one fledgling), a represents the primary sex ratio (i.e., # males/# females), α is the average age at first reproduction, and ω is the age at last reproduction. These equations predict clutch sizes approximating observed clutches in Prairie Warblers, *Dendroica discolor*, (Murray and Nolan, 1989) and Florida Scrub Jays, *Aphelocoma c. coerulescens* (Murray et al., 1989).

The clutch size equation (1) can be derived from the L-E equation, which Murray and Nolan (1989) write as:

$$1 = \sum \lambda_x \mu_x e^{-\rho x}$$

where λ_x is probability of surviving from birth to age class x , μ_x is the average number of female eggs produced by a female while a member of age class x , e is the base of natural logarithms, and ρ is the annual rate of increase. This equation contains no assumptions of

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how its various parameters have evolved; rather, it is a statement of how the population parameters are mathematically interrelated. If one assumes a population that is neither increasing nor decreasing on average (i.e., $\rho = 0$), then the L-E equation becomes:

$$1 = \sum \lambda_x \mu_x.$$

By assuming constant age-specific fecundity (μ) beginning with the age of first reproduction (α) and ending at the age of last reproduction (ω), this equation can be rearranged to

$$1 = \mu \sum_{\alpha}^{\omega} \lambda_x, \text{ or}$$

$$\mu = 1 / \sum_{\alpha}^{\omega} \lambda_x.$$

By tradition, the basic L-E equation only accounts for females. Because females also lay eggs that produce males, the female replacement rate can be adjusted by the primary sex ratio, a :

$$\mu = (a + 1) / \sum_{\alpha}^{\omega} \lambda_x. \quad (2)$$

Because average annual fecundity (μ), or total number of eggs laid per year, is just the product of average clutch size and the average number of clutches attempted (B), clutch size can be expressed as:

$$CS = \mu/B. \quad (3)$$

Murray and Nolan's (1989) use of only eggs in nests which successfully fledge at least one young is mathematically equivalent to the more common practice of using all eggs laid, and this adjustment can be made by multiplying λ_x and B by the probability of fledging at least one young from a nest, c . Then equation (1) follows from equations (2) and (3):

$$CS = \left(c[a + 1] / \sum_{\alpha}^{\omega} \lambda_x \right) / cB = c\mu/cB = \mu_s/B_s.$$

Hence we have derived the M-N clutch size equation from an assumption of demographic stasis (an ecological hypothesis) rather than an assumption about the direction of selection (an evolutionary hypothesis).

What happens if the observed equation relating clutch size to the other demographic parameters is not met by a data set? One possibility is of course sampling error. Leaving this aside, by our purely demographic hypothesis, then the population should either be declining or increasing in size. By contrast, in Murray's hypothesis, if the M-N equation is not met, the population is presumably not in evolutionary equilibrium, so that different subpopulations (corresponding to different genotype/phenotype classes) are growing at different rates.

In our opinion, Murray and Nolan's (1989) assumptions that clutch size evolves to the minimum needed for replacement and that a population has reached evolutionary stasis imply a population that is neither growing nor shrinking. By measuring mortality rates to "predict" a birth rate (i.e., clutch size) that will offset the mortality rate, population stasis again seems

to be assumed. If the population truly is neither increasing nor decreasing on average, the "predicted" mean birth rate *must* equal the observed mean birth rate (within the range of sampling error). Thus, clutch size is simply the missing variable given survivorship, sex ratio and average number of broods.

According to our demographic hypothesis, a reasonable fit to the M-N equation requires a population to have a ρ near zero. Murray et al. (1989) report that $\rho = -0.0111$ in the Scrub Jay and we have calculated $\rho = -0.0229$ from the Prairie Warbler data in Murray and Nolan (1989). We would argue that these conditions of near-stasis account for the reasonably close correspondence between the data sets and the M-N equation. Hence, observing such a match does not necessarily express "the consequences of selection favoring females that lay as few eggs as possible in a clutch while still replacing themselves" (Murray and Nolan, 1989 p. 1704). The M-N equation would still predict clutch size well for a near-static population if, for example, clutch size evolved to that which maximized the number of young fledged, with density-dependent compensatory mortality to maintain a static population, as Lack (1947) suggested. The models and analyses of Ricklefs (1977) suggest that many of the patterns of covariation observed in bird life histories can be the result of density-dependent effects on mortality and fecundity, not due to the evolutionary adjustment of fecundity to adult survival. The L-E equation dictates a necessary connection between each of the variables it contains, but it assumes nothing about the ecological or evolutionary factors that determine them. In a near-static population, the same is true for the M-N equation. In fact, Murray and Nolan (1989 p. 1704) "... recognize the possibility that equation [1] is no more than a description of a dynamic relationship that has evolved in some other way," but Murray's papers do not otherwise reflect this statement.

The critical portion of Murray's theory of clutch size evolution is that clutch size is minimized by natural selection to meet the needs of replacement. Because an alternative, nonevolutionary hypothesis is available, matches between data and the M-N equation do not constitute tests of this critical assumption.

What would constitute a critical test of this hypothesis? It is instructive to compare tests provided by the M-N equation with other tests of clutch size models. Quantitative predictions about clutch size and empirical tests have been made repeatedly (e.g., Lack, 1947, 1948; Nur, 1984; Boyce and Perrins, 1987; Reid, 1987; Rockwell et al., 1987; Pettifor et al., 1988). These, together with many other quantitative models (e.g., Williams, 1966; Charnov and Krebs, 1974; Ricklefs, 1977; Schaffer, 1974; Winkler and Wallin, 1987), have all proceeded in a similar manner: they posit 1) variation in clutch size, 2) explicit costs and benefits (in the form of parental survivorship and offspring production) associated with this variation in clutch size, and 3) some explicit measure of fitness compounded from parental survival and offspring production. Given these assumptions, the predicted clutch size is then the one having optimal (usually maximal) fitness. The quantitative, empirical tests of these models rely on comparisons among alternative phenotypes in a common environment. The empirical test provided by the M-N equation, as used in Murray and Nolan (1989) and

Murray et al. (1989), is concerned instead with the average phenotype of an entire population.

We suggest that future tests of Murray's proposal that clutch size is minimized by natural selection to meet the needs of replacement incorporate comparisons of alternative phenotypes in shared selective environments, or investigate the changes of a population's traits in response to a perturbation of its environment that causes an alteration in its replacement rate. For example, House Finches (*Carpodacus mexicanus*) were introduced from a population exhibiting static dynamics ($r = -0.001$, T. Wootton, unpubl.) in southern California into a new environment in the northeastern United States (Elliot and Arbib, 1953; Aldrich and Weske, 1978). The introduced population grew exponentially with a doubling time of less than three years (Wootton, 1987), experienced reduced fledging mortality, and consequently exhibited a change in its mean clutch size (Wootton, 1986). Although the available data are not detailed enough to provide a quantitative prediction of the clutch size at replacement using the M-N equation, the pattern of rapid exponential growth clearly shows that the population is reproducing far above its replacement rate. Therefore, we can make a strong qualitative prediction about the direction that the clutch size should change if the assumption that clutch size evolves to the minimum required for replacement is true. In this case, the clutch size increased (Wootton, 1986), rather than decreased to match the lower replacement rate as would be predicted by Murray's hypothesis of clutch size evolution.

We should point out that Murray's proposal may in one sense describe the product of natural selection when a population is in both demographic and evolutionary equilibrium, even if it inaccurately characterizes its causes. Because the population is in demographic equilibrium, the average female lays a clutch size such that on average she just replaces herself regardless of the factors that influenced the evolution of clutch size. Because the population is in an evolutionarily stable state, genetic variants that have a clutch size different from this average have a lower expected fitness, so such deviants will lay a clutch of a size that on average does not replace themselves. However, we remain to be convinced that this description of the end product of both evolution and demography enhances our understanding of the forces that actually determine the evolutionarily stable clutch size in the first place.

In conclusion, we believe it is important for evolutionary biologists to consider whether the phenotypic patterns they observe within and between populations can be explained parsimoniously by ecological processes without resorting to evolutionary explanations. This warning is particularly germane to the study of life history traits, which exhibit unusually great phenotypic plasticity (i.e., low heritability) in response to environmental changes (e.g., Winkler, 1985; Hailman, 1986; Mousseau and Roff, 1987), and relate intimately to the dynamics exhibited by ecological populations. Thus ecological relationships may explain not only the patterns observed by Murray and Nolan (1989) and Murray et al. (1989), but also the strong correlation between various components of fecundity and mortality observed in mammals (Harvey and Zammuto, 1985; Sutherland et al., 1986; Read and Harvey, 1989), and the positive relationship frequently observed be-

tween fecundity and adult survivorship in birds (e.g., Smith, 1981; Price et al., 1988; Cooke et al., 1990).

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CORRELATIONS BETWEEN HETEROZYGOSITY AND PHENOTYPIC VARIABILITY IN *COTTUS* (TELEOSTEI: COTTIDAE): CHARACTER COMPONENTS

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A substantial body of theory and empirical investigation has been devoted to understanding the relationship between levels of variability in polygenic morphological traits and the levels of heterozygosity of the genes contributing to them. The rationale for such correlations among individuals dates primarily from Lerner's (1954) reviews of genetic homeostasis, which predicted that high individual heterozygosity should result in low morphological variance due to the developmental buffering effects of heterosis. Individual heterozygosity has since been suggested to be a general effective buffering mechanism even in natural populations (Mitton and Grant, 1984; Mitton and Koehn, 1985; Zouros, 1987; Zouros and Foltz, 1987), although the relationship is by no means clear or universal (Handford, 1980; Booth et al., 1990).

The corresponding prediction for the relationship between heterozygosity and morphological variability among populations, species, and higher taxa remains problematic (Zink et al., 1985). If Lerner's hypothesized negative correlation within populations is simply extrapolated to higher levels of organization, then a

negative correlation between heterozygosity and morphological variance should be observed among populations and species. However, if the morphological and genetic variances are merely two operationally independent estimates of total genetic variation, then a positive correlation should be observed because they represent different aspects of the same underlying phenomenon. Empirical studies have detected associations ranging from nonexistent to moderately significant, both positive and negative (citations in Zink et al., 1985 and Strauss, 1989).

In contrast to most previous studies, a surprisingly strong positive correlation between mean heterozygosity and total size-independent morphological variance ($r = 0.73$, $P < 0.001$) was discovered among 32 samples, representing eight nominal taxa, of eastern North American freshwater sculpins (*Cottus*) (Strauss, 1989). These cottids are small (<15 cm) bottom dwelling fishes of marine ancestry that have secondarily invaded Holarctic freshwaters, and in North America and Asia have undergone significant Pliocene-Pleistocene radiation. They are characterized by patchy,