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Abstract.—Fitness is a vague, poorly developed concept in ecology and evolutionary biology. Although it is generally recognized that fitness is determined by the complete survival and reproductive schedules of individual organisms, experimental studies have rarely attempted to integrate these into a single measure of individual fitness. Instead, particularly in studies of natural selection, components of fitness are measured as surrogates for fitness. In this article, we develop an integrated measure of fitness based on the philosophical underpinnings provided by the notion of propensity fitness, combined with classical demographic methods. We show how life-history data, collected for an individual, can be formatted as an age-structured population projection matrix, $\mathbf{A}^{(m)}$. The dominant eigenvalue, $\lambda^{(m)}$, of this matrix is an estimate of that individual's propensity fitness. Using life-history data sets on European sparrowhawks and blue tits, we show that the interpretation of analyses of selection can shift radically using the integrated propensity fitness measure instead of components of fitness, such as lifetime reproductive output. Individual fitness, as formulated here, provides an integrated measure of performance that should prove useful in empirical studies in ecology and evolutionary biology.

Darwinian fitness is a central, unifying concept of ecology and evolutionary biology, and it is often the dependent variable of interest in theoretical and empirical studies (Kozłowski 1993). Despite this central role, there is no universally accepted way to measure individual fitness in organisms with age-structured life histories (Stearns 1992; de Jong 1994). Fitness has been equated with population growth rate (Futuyma 1986; Ricklefs 1990), the ability to pass on alleles (Hedrick 1984), an unspecified measure of survival and reproductive prowess (Cockburn 1991), a tendency to leave more or fewer offspring (Begon et al. 1990), or the product of fertility and survival (Ehrlich and Roughgarden 1987). Ecology and evolution texts that show how to calculate fitness (see, e.g., Hedrick 1984; Futuyma 1986; Ehrlich and Roughgarden 1987; Ricklefs 1990) do so for *groups* of individuals (e.g., those with particular life-history traits or with a common genotype or phenotype).

The concept of fitness is even more versatile, and vague, than is indicated by textbook definitions. Endler (1986) described five definitions of fitness that have been developed in the literature, including Darwinian fitness (the above generally fall in this category), the natural selection rate coefficient (Dobzhansky 1968a), adaptedness (Dobzhansky 1968a, 1968b), adaptability (Dobzhansky 1968a, 1968b), and durability (Thoday 1953, 1958). In this article, we focus on fitness as

used in evolutionary genetics, in which it measures the rate of increase of individuals possessing known genotypes or phenotypes (see de Jong 1994 for review). Fitness in this context can be interpreted as a Lyapunov exponent, that is, the asymptotic rate of increase (Metz et al. 1992). As such, it is a demographic parameter, like λ or r, determined by the age- or stage-specific vital rates.

Evolution by natural selection depends on the relationship between individual traits and individual fitness. In the original description of natural selection, Darwin (1859) clearly refers to the advantage accruing to individuals of the traits they possess. Lande and Arnold (1983) and Arnold and Wade (1984a, 1984b) developed powerful tools for analyzing this process in a multivariate manner. They quantify the selection gradient as the function relating the trait(s) and fitness. The response to selection can be projected, knowing the genetic variance-covariance relationships for the set of traits under consideration. Numerous assumptions must be considered before claiming that one understands the forces of evolution with studies employing these methods (see, e.g., Mitchell-Olds and Shaw 1987; Wade and Kalisz 1990; Rausher 1992). However, the general approach, including its close relation, path analysis (Kingsolver and Schemske 1991), is being increasingly used in field studies of natural selection.

These methods of estimating the pattern and strength of selection require some estimate of the fitness of each individual. Demographic parameters are usually estimated for groups of individuals. Hence studies of selection gradients have typically related variation in individual phenotype (or genotype) to components of fitness rather than fitness itself (e.g., offspring production, copulatory success, or survival to maturity) (Arnold and Wade 1984b; Kalisz 1986; Hougen-Eitzman and Rausher 1994; Price and Burley 1994; Schluter and Nychka 1994). These components are relatively easy to measure on individuals, but they cannot always be safely used as surrogates for overall fitness. Attempts to do so ignore important correlations among fitness components that provide explanations for the paradoxes of life-history theory (e.g., negative correlations between fecundity and juvenile survival as an explanation for limited clutch size) (Caswell 1989b; Stearns 1992). Our goal is to provide a way to calculate a more complete demographic estimate of individual fitness that includes both survival and reproduction (amount and timing).

The problem of estimating individual fitness can be described as the problem of estimating the *population growth rate of the individual*. It is the individual that lives, dies, develops, matures, migrates, and reproduces. The translation of such discrete individual events into population rates is standard in demographic analysis. An example is the hazard function, most familiar as the instantaneous mortality rate in life table analysis. The hazard function gives the probability of death in the age interval $(x, x + dx)$, conditional on survival to age x. It is the probability of death that characterizes the survival of an individual, although each individual dies only once.

According to the propensity interpretation of probability (Popper 1959, 1983, 1990), a probability is considered a measure of the strength of "a hidden and not directly observable physical disposition or tendency or propensity" (Popper 1983, p. 286) for an event to occur. Propensities are real and are determined by the

properties of the system in question (e.g., by the genotype, phenotype, and environment of the organism at risk of death). The hazard function can be interpreted as measuring a real physical propensity for individuals to die at each age, as a function of their environment and internal constitution.

Brandon (1978) and Mills and Beatty (1979) applied the propensity interpretation to fitness (see also Burian 1983; Brandon and Beatty 1984; Sober 1984; Brandon 1990). They view fitness as characterized by its propensities to survive and to produce zero, one, two, and so forth, offspring at each age. If there is a collection of individuals with the same propensities, the individual probabilities are translated into demographic parameters, and the size of the collection increases or decreases at a rate determined by those parameters. Given heritable trait variation, there will be many such collections of individuals. They will increase or decrease in relative frequency depending on their relative rates of growth: natural selection is the statistical result.

In this article, we use the propensity interpretation to measure the fitness of individuals in a way that is consistent with its more familiar calculation for groups of individuals. First, we will formulate a measure of individual fitness as well as other individual demographic parameters, then illustrate the application of these methods with two empirical data sets.

THEORY

We start from the premise that fitness is inherently a demographic concept. All but the most vague definitions of fitness incorporate the idea that the rate of propagation of an individual's genes into the future determines individual fitness (most explicitly developed in Charlesworth 1980). This rate of propagation (summarized by λ, the population growth rate, or $r = \ln \lambda$, the intrinsic rate of increase) depends on the demographic properties—survival and fecundity. The resolution of the paradox that fitness is the "population growth rate of the individual" requires the philosophical basis provided by the propensity fitness concept combined with classical demographic tools.

We use an age-classified population projection matrix (Leslie 1945, 1948; Caswell 1989a) as our demographic model. The Leslie matrix contains age-specific fertilities F_i in the first row and age-specific survival probabilities P_i on the subdiagonal. All other matrix elements are zero. The F_i and P_i are traditionally obtained from a life table representing a summary of life-history data from a collection of individuals. The matrix encapsulates the life histories of the population being studied, and manipulations of the matrix reveal important demographic features, including projected future population size and age structures, the population growth rate (λ), the net reproductive rate (R_o), generation time (T), life expectancy (e_x), sensitivities ($d\lambda/dP_i$, $d\lambda/dF_i$), and elasticities (e_{ij}). All of these quantities are properties of the collection of individuals that have the life history described by the P_i and F_i.

To measure individual fitness, we simply form a population projection matrix for a collection consisting of a single individual. To avoid confusion, we use

subscripts to denote matrix elements and superscripts to denote individuals, so that the matrix for individual m is $A^{(m)}$.

Individual Data

The data for calculating individual fitness consist of the ages at death and the reproductive output at each age of each individual. If individual m dies in year ω of life, we set $P_1^{(m)} = P_2^{(m)} = \cdots = P_{\omega-1}^{(m)} = 1$, and $P_\omega^{(m)} = 0$. This is an estimate of the unknown age-specific survival propensities for individual m.

The realized reproductive output, multiplied by one-half (in sexually reproducing species) to take into account the genetic contribution of each parent to each offspring, provides our estimate of the fertilities $F_i^{(m)}$. For ages after the death of individual m, we set fertility equal to zero. These values estimate the true age-specific propensities to reproduce for the individual under consideration.

Individual Fitness

The survival probabilities and fertilities are used to construct the individual population projection matrix $\mathbf{A}^{(m)}$ for individual m:

$$\mathbf{A}^{(m)} = \begin{matrix} F_1^{(m)} & F_2^{(m)} & \cdots & F_\omega^{(m)} \\ P_1^{(m)} & 0 & \cdots & 0 \\ & \ddots & & \\ 0 & \cdots & P_{\omega-1}^{(m)} & 0 \end{matrix} \qquad (1)$$

Once an individual transition matrix $\mathbf{A}^{(m)}$ is formed, the dominant eigenvalue $\lambda^{(m)}$ of this matrix yields an estimate of the absolute fitness of individual m. The eigenvalue $\lambda^{(m)}$ is a logical measure of fitness because it is an *estimate* of the asymptotic growth rate of a collection of individuals with the propensities to survive and reproduce of individual m; that is, it is an estimate of the propensity fitness of individual m. The value $\lambda^{(m)}$ *is* the population growth rate of the individual, which thereby resolves the paradox of the dual nature of fitness. The individual fitness $\lambda^{(m)}$ is an asymptotic growth rate measure, as fitness measures used in population genetics usually are (see, e.g., Tuljapurkar 1990; Metz et al. 1992).

The fitness $\lambda^{(m)}$ is the largest real root of the characteristic equation of $\mathbf{A}^{(m)}$, which is

$$1 = \sum_{i=1}^{\omega} F_i^{(m)} (\lambda^{(m)})^{-i}, \qquad (2)$$

where the $F_i^{(m)}$ are individual age-specific fertilities.

If desired, relative individual fitness can be estimated in the usual ways, as

$$w = \frac{\lambda^{(m)}}{\max \lambda^{(m)}}, \qquad (3)$$

$$w = \frac{\lambda^{(m)}}{\overline{\lambda^{(m)}}}, \qquad (4)$$

or

$$w = \frac{(\lambda^{(m)} - \overline{\lambda^{(m)}})}{\overline{\lambda^{(m)}}}.$$ (5)

This measure of fitness corresponds to the way that fitness is measured in more traditional ways by statistical measurements on collections of individuals. In such studies, a set of individuals that are considered to be experiencing the same propensities is defined. Using clones, it may be possible literally to replicate individuals and thereby estimate probabilities for $P_i^{(m)}$ or means for $F_i^{(m)}$ to obtain estimates of fitness that more closely correspond to the theoretical (propensity) fitness of the individual. Indeed, theoretical life-history studies have defined fitness as the population growth rate of a clone (see, e.g., Stearns and Crandall 1981). Empirical studies have been slow to take advantage of clonality (but see Service and Lenski 1982), despite the fact that many species naturally, or with prodding, can produce such clones through asexual reproduction (e.g., dandelions and aphids; Janzen 1977), vegetative propagation (see, e.g., Antonovics and Primack 1982), or monozygotic sibs (e.g., quadruplets in nine-banded armadillos, twins in humans; Levitan and Montagu 1971) at a certain frequency, which permits such replication. More usually, the individuals consist of a sample of genotypes obtained from a population of interest, and the resulting measure of fitness is a mean over the genotype distribution. In any case, the fates of those individuals are followed over time, and the vital rates (i.e., propensities) estimated by maximum-likelihood methods. The only difference between these approaches and ours is that we are using information from only a single individual.

Individual fitness as measured by $\lambda^{(m)}$ depends on the timing and quantity of reproduction as well as on survival. It integrates these components of fitness into a measure that projects the rate at which individual m would be able to propagate copies of itself (actually its genes) into the future, if its vital rates were to remain the same. We explore the properties of this quantity later with examples.

Other useful quantities can be derived from an individual's life history and the matrix $\mathbf{A}^{(m)}$, as with the elements of the matrix $\mathbf{A}$ for a population. The net reproductive rate can be calculated for an individual as

$$R_0^{(m)} = \sum_i F_i^{(m)} \prod_{j=1}^{i-1} P_j^{(m)},$$ (6)

which for the individual model we have defined reduces to

$$R_0^{(m)} = \sum_i F_i^{(m)},$$ (7)

which is the total offspring production for individual m.

Generation time can be determined by the relation

$$T^{(m)} = \frac{\sum_j jF_j^{(m)} \prod_{k=1}^{j-1} P_k^{(m)}}{\sum_j F_j^{(m)} \prod_{k=1}^{j-1} P_k^{(m)}} \tag{8}$$

$$= \frac{\sum_j jF_j^{(m)}}{\sum_j F_j^{(m)}}, \tag{9}$$

that is, the weighted average age of a parent at the birth of its offspring.

Finally, the reproductive value of individual m is given by the dominant left eigenvector of $\mathbf{A}^{(m)}$:

$$v_1^{(m)} = 1, \tag{10}$$

$$v_2^{(m)} = F_2^{(m)}(\lambda^{(m)})^{-1} + \cdots + F_k^{(m)}(\lambda^{(m)})^{-k+1}, \tag{11}$$

$$\vdots$$

$$v_k^{(m)} = F_k^{(m)}(\lambda^{(m)})^{-1}. \tag{12}$$

Statistical Properties

The projection matrix entries $P_i^{(m)}$ and $F_i^{(m)}$ are nonparametric maximum-likelihood estimates of the vital rates. Thus, $\lambda^{(m)}$, the net reproductive rate, generation time, and other demographic parameters are also maximum-likelihood estimates.

Lenski and Service (1982; Service and Lenski 1982) considered the calculation of individual fitness and showed that the mean $\lambda^{(m)}$ is not equal to the finite rate of increase of the population (λ). This inequality is due to (at least) two reasons. First, $\mathbf{A}^{(m)}$ is not an unbiased estimate of the population matrix $\mathbf{A}$. Although the individual survival probabilities are an unbiased estimate of the population survival probabilities, the fertilities are not, because of the need to set $F_i^{(m)} = 0$ for ages after the death of the individual. An average of the fertilities for a group of individuals would include these zero values and be biased downward from the true population fertility, which is conditional on survival to that age and should not include the zero values. Second, even if the individual $F_i^{(m)}$ and $P_i^{(m)}$ were unbiased estimates of the population values, so that $\mathbf{A}^{(m)}$ was an unbiased estimate of $\mathbf{A}$, the mean of the eigenvalues is not in general equal to the eigenvalue of the mean matrix, so that $\lambda^{(m)}$ would still not be an unbiased estimate of λ.

Lenski and Service (1982) rejected $\lambda^{(m)}$ (which they termed F_i) as an estimator of fitness because of bias. Instead they proposed an estimate that combines individual and population data but that is "unbiased." However, unbiasedness is not a necessary property of a useful estimate. It is no guarantee that an estimate will be in any sense close to the true value, only that the mean of a sufficiently large

number of estimates will be close. (Three statisticians were hunting. The first fired and missed their quarry, 10 ft to the left. The second fired and missed again, 10 ft to the right. "Got him!" cried the third.) Moreover, unbiasedness is not preserved under nonlinear transformations. Thus, even if $\lambda^{(m)}$ were unbiased, the intrinsic rate of increase $r^{(m)} = \ln \lambda^{(m)}$ would not be, and vice versa. Since we do not intend to use the mean of a large number of individual fitness estimates to estimate population growth rate, we do not believe this bias in $\lambda^{(m)}$ to be important. Its consequences, however, have not been investigated.

More important is the fact that $\lambda^{(m)}$ is a consistent estimate, in the statistical sense that as the sample size is increased, the resulting estimate converges to its true value. It is also consistent in the colloquial sense, in that it is calculated from the life experience of an individual in the same way that a demographic analysis would calculate it in a cohort life table experiment of any size. In such an experiment, the survival rate at age i is estimated as the number of individuals alive at age i divided by the initial cohort size. The fertility is estimated as the total number of offspring produced by the survivors of the cohort at age i divided by the number of survivors, with fertility set to zero after the last individual dies.

EXAMPLE I: EUROPEAN SPARROWHAWK

In this section and the next, we apply our calculations to individual data on two bird species. Newton (1989) has published extensively on his longitudinal life-history data on European sparrowhawks (*Accipiter nisus*) and kindly provided raw data for this analysis. Individual projection matrices were constructed for each bird. For example, individual EB01708 was a female with a life history represented by the matrix

$$\mathbf{A}^{(EB01708)} = \begin{pmatrix} 0 & 0 & 0 & 1.5 & 0 & 0 & 1 & 1.5 \\ 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \end{pmatrix}$$

The top row of the matrix $(F_i^{(m)})$ is 0.5 times the number of offspring produced by sparrowhawk EB01708 in each year of life. The individual thus fledged eight young over its lifetime. The subdiagonal shows that the individual survived to age 8. To compute individual fitness, the solution to the characteristic equation is found ($1 = 1.5[\lambda]^{-4} + [\lambda]^{-7} + [\lambda]^{-8}$), which yields the eigenvalue of the matrix $\mathbf{A}^{(EB01708)}$ (in practice, one of several computer packages such as MATLAB [the Mathworks, Inc.] can be used to determine matrix eigenvalues). The fitness of the individual, derived as the eigenvalue of $\mathbf{A}^{(EB01708)}$, was 1.2667. This procedure was carried out for each individual in the sample population provided.
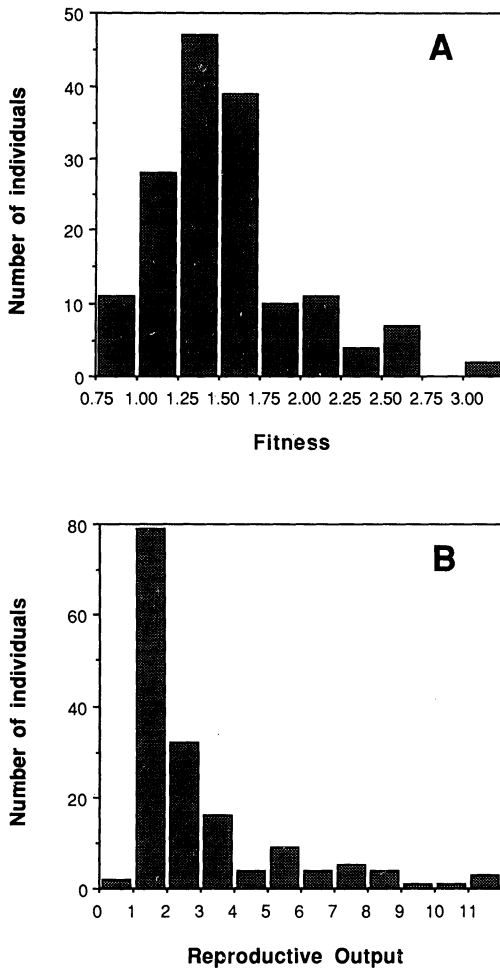
FIG. 1.—Distributions of (A) individual fitness ($\lambda^{(i)}$) and (B) lifetime reproductive output (= 0.5 × total numbers of young fledged in order to yield "genetic" reproductive output) in European sparrowhawks. Only reproductive individuals are shown since clearly the distributions are discontinuous and nonnormal when nonreproductive individuals are included.

In the most thorough studies of life histories, lifetime reproductive output has usually been considered the statistic most closely akin to fitness (Clutton-Brock 1988; Newton 1989). However, in sparrowhawks, fitness and lifetime reproductive output have different statistical properties. Neither statistic is normally distributed (fitness, Shapiro-Wilk $W = 0.89$, $P < .0001$; lifetime reproductive output, $W = 0.77$, $P < .0001$). Both distributions are skewed to the right, reproductive output more so than fitness (fig. 1).

The interpretation of selection on life-history traits differs depending on whether $\lambda^{(m)}$ or lifetime reproductive output is used as a measure of fitness. As an example, we show the relationship between age at first reproduction (as a
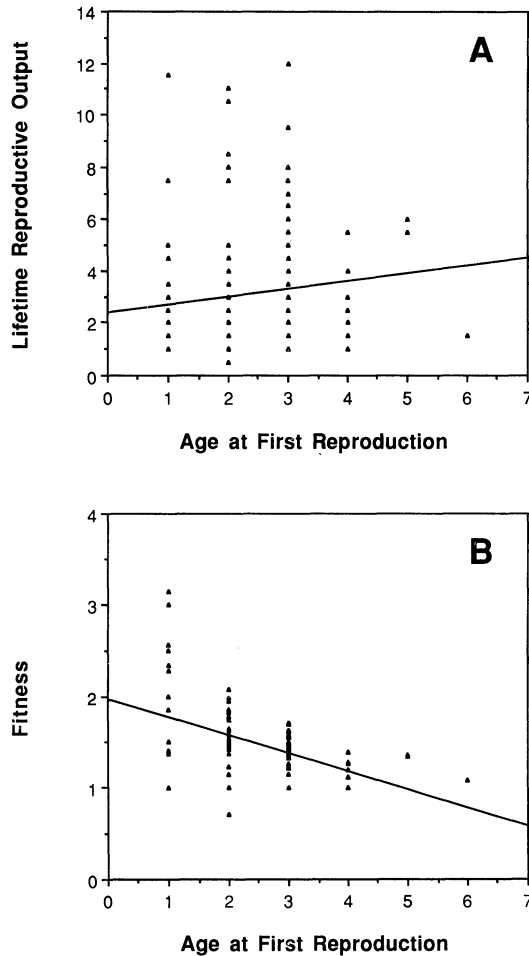
FIG. 2.—Linear regressions of (A) lifetime reproductive output and (B) individual fitness ($\lambda^{(i)}$) on age at first reproduction in European sparrowhawks. Regression was performed only for reproductive individuals since individuals that died before reproducing have no measurable age at first reproduction.

phenotypic trait) and the two measures of fitness (fig. 2). Regressing lifetime reproductive output on age at first reproduction actually shows no relationship (β = 0.32 ± 0.17, P = .06), while the corresponding regression of individual fitness on age at first reproduction yields a significant negative slope (β = −0.20 ± 0.03, P < .0001). The choice of lifetime reproductive output as a surrogate for fitness would clearly lead to contradictory, and misleading, conclusions about the pattern of selection. The importance of timing of reproduction has long been recognized (see, e.g., Cole 1954; Lewontin 1965; Caswell and Hastings 1980; Caswell 1982), and $\lambda^{(m)}$ incorporates the effects of differential timing, while lifetime reproductive output ignores it.

Lifetime reproductive output is in fact a phenotypic trait itself, like age at first reproduction, and with our results we can examine how each of these traits affects fitness. Using the approach of Lande and Arnold (1983), we regressed $\lambda^{(m)}$ on lifetime reproductive output and age at first reproduction to examine the selection surface, both with and without quadratic terms. Not surprisingly, we found significant directional selection on both traits: Selection favored early reproduction (linear regression coefficient, $\beta = -0.23 \pm 0.02$, $P < .0001$ for age at first reproduction) and a large lifetime offspring production ($\beta = 0.10 \pm 0.01$, $P < .0001$ for lifetime reproductive output).

This pattern is consistent with the often-repeated notion that the ideal life history is one in which an organism reproduces immediately after it is born and produces the highest numbers of offspring possible forever. However, the relationship between two phenotypic life-history traits and individual fitness may be nonlinear. When quadratic terms were added to the model, we found evidence for stabilizing selection on lifetime reproduction (coefficient of the second-order term, $\gamma = -0.02 \pm 0.002$, $P < .0001$), disruptive selection on age at first reproduction ($\gamma = 0.09 \pm 0.01$, $P < .0001$), and selection favoring a negative correlation between the two life-history traits ($\gamma = -0.06 \pm 0.008$, $P < .0001$ for cross-product term). These patterns are discernible when viewing the selection surface predicted by the quadratic regression model (fig. 3A). Not all of the terms may be relevant to the sparrowhawk population if there are areas of the surface where no individuals are found (i.e., combinations of the two components that are unrealistic) (Mitchell-Olds and Shaw 1987). Indeed, part of the response surface is not occupied (fig. 3B); however, individuals are clearly found in the region where stabilizing selection is manifested for lifetime reproductive output. A larger sample would be needed to be sure that the correlational selection and disruptive selection parts of the surface are actually operative (i.e., that fitness actually rises with *high* ages at first reproduction as well as low).

EXAMPLE 2: BLUE TIT

Life-history data for males and females from a population of blue tits (*Parus caeruleus*) were provided by Dhondt (1989). Individual 1493900 was typical:

$$
\mathbf{A}^{(1493900)} = \begin{pmatrix} 3.5 & 5 & 5 & 6 & 4.5 \\ 1 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 \end{pmatrix}.
$$

This individual reproduced in its first year, produced 48 young over its lifetime, and had an individual fitness ($\lambda^{(1493900)}$) of 4.82.

Exclusive of nonreproductive individuals, the distribution of fitnesses of both males and females was not significantly different from normal (Shapiro-Wilk W-test, $P > .05$; distributions of lifetime reproduction did deviate from normality
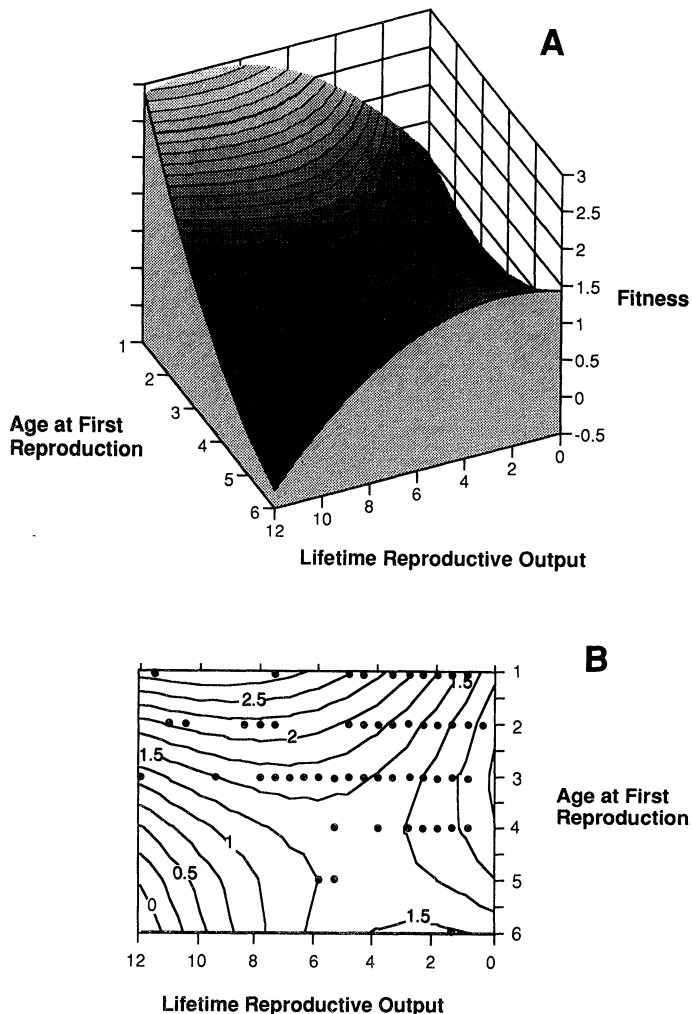
FIG. 3.—*A,* Selective surface showing the joint relationship of age at first reproduction and lifetime reproductive output to fitness using multiple regression including quadratic (second-order and cross-product) terms for European sparrowhawk data. *B,* Bird's-eye view of the selection surface, showing the portion of the character space occupied by individuals (shown by dots) in the sparrowhawk population.

for both males and females, $P < .01$). Including nonreproductive individuals, males and females were not significantly different in mean individual fitness (ANOVA, $P = .80$), as expected, since they were from the same population. However, their distributions were qualitatively different, with two males having a much higher fitness than any females (fig. 4).

As with the sparrowhawks, no selection on age at first reproduction was evident if lifetime reproductive output was used as the measure of fitness in the regression ($\beta = -0.67 \pm 2.66$, $P = 0.80$). However, directional selection favoring early
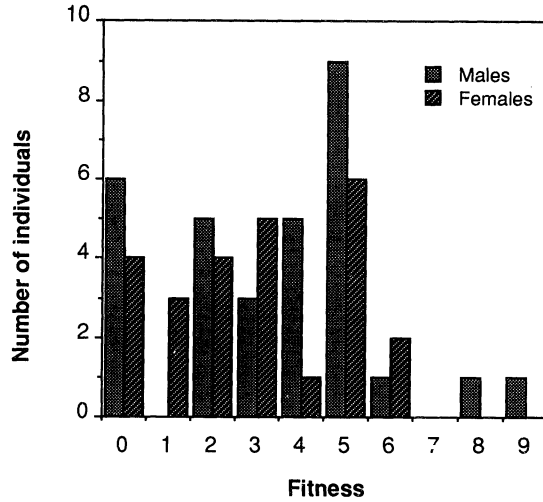
Fig. 4.—Distribution of male and female individual fitness ($\lambda^{(i)}$) in a population of blue tits.

reproduction was evident when individual fitness was regressed on age at first reproduction ($\beta = -1.59 \pm 0.71$, $P = .03$). The regression model including both age at first reproduction and lifetime reproductive output as characters related to fitness showed significant directional selection on both ($\beta = -1.49 \pm 0.61$, $P = .02$, and $\beta = 0.14 \pm 0.04$, $P = .0003$, respectively) in the same pattern as with sparrowhawks. When quadratic terms were included in the model, stabilizing selection was evident on lifetime reproductive output (fig. 5A) ($\gamma = -0.019 \pm 0.003$, $P < .0001$), which did occur in regions of character space actually occupied by individual blue tits (fig. 5B).

DISCUSSION

The measurement of components of fitness and the use of those measurements to make inferences about selection are not new. However, we have shown that it is possible to integrate survival and fertility into a single demographic measure of individual fitness. Our examples rely on life-history data on individuals followed throughout their lifetimes.

Even in organisms for which it is practically impossible to follow individuals over their lifetimes, the individual fitness concept can be helpful. For example, if it is feasible to empirically determine the fertility schedule for a portion of the life span, that individual information could be embedded in simulated or artificial data on the other vital rates. The resulting calculations would show the relationship of the measured component to overall fitness, given the hypotheses about the rest of the life cycle. Alternatively, simple parametric models might be estimated from information less detailed than a complete record of the life of the individual. For example, λ can be calculated from a model with three parameters:
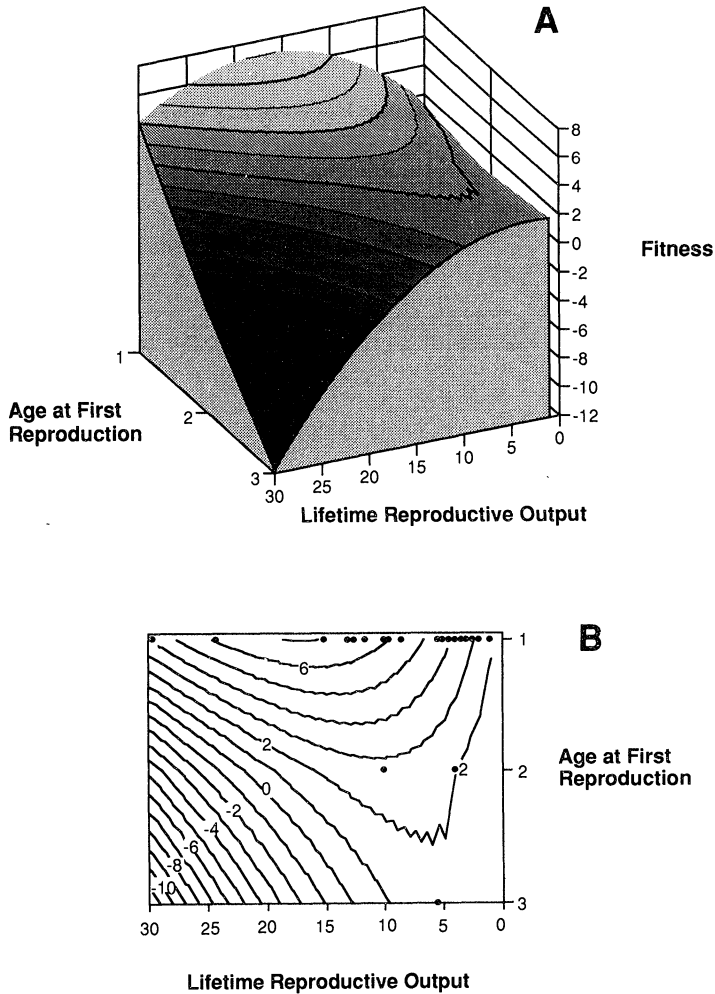
FIG. 5.—*A*, Selective surface showing the joint relationship of age at first reproduction and lifetime reproductive output to fitness using multiple regression including quadratic (second-order and cross-product) terms for blue tit data. *B*, Bird's-eye view of the selective surface, showing the portion of character space occupied by individuals (shown by dots) in the blue tit population.

an age-independent mortality rate, an age at maturity, and an age-independent adult fertility. The mortality rate can be estimated from the age at death, the age at maturity can be observed (or may vary little among individuals), and the adult fertility can be estimated from even a few observations of reproduction. Such a model is, of course, only an approximation to the full age-classified model, but it would permit the calculation of λ from fragmentary data.

As formulated here, $\lambda^{(m)}$ is an estimate of individual fitness. Its accuracy as a propensity measure would, of course, be improved if it could be estimated not

from a single individual but from a set of individuals, all with the same propensi-
ties to survive and reproduce. While these individuals would all have the same
fitness propensity, each would no doubt have a slightly different life.

This line of reasoning shows that even with an integrated measure of fit-
ness, if the estimate is based on a sample of one, it will be affected by the
environment, including both deterministic effects and stochastic events oc-
curring therein. A detailed discussion of the "environment" is beyond the
scope of this article (but see Antonovics et al. 1988 and Brandon 1990). However,
we must be aware that when an individual's life history is observed, it is one of
many possible lives that individual might have lived. Therefore, our measure will
be an imperfect estimate of an individual's propensity fitness. In sparrowhawks
and blue tits, a sizable portion of the population had an individual fitness of zero
by our measure. However, the true fitness propensities are very unlikely to be
zero for any given individual, except in the case of inviability due to lethal mu-
tation.

Two strategies, one experimental and one statistical, may provide ways to
obtain estimates of individual fitness that more closely correspond to the propen-
sity fitness notion. One approach to improving the individual fitness estimate is
to clone individual genotypes, a procedure that is presently possible in only a
limited number of organisms. Presumably, since all members of a clone have the
same genotype, they will have the same innate propensity to survive and repro-
duce in a given environment, and, thus, they will have the same propensity fit-
ness. An advantage of using clones is that not only can mean individual fitnesses
be determined for these units but variances in fitness as well, which may them-
selves be subject to evolutionary pressures (Gillespie 1977).

An alternative to cloning is possible if we take the view (as regression or path
analysis techniques do) that selection acts on the phenotype. With data about
ecologically relevant aspects of the individual's multivariate phenotype, it would
be possible to estimate the propensities to survive and reproduce, based on infor-
mation from a group of individuals or the population as a whole. For example,
regression of survival (0 or 1) on bug thorax width for the population (Lande and
Arnold 1983) will yield a function that can be used to determine the propensity
for a specific individual with a known thorax width to survive. Combined with
knowledge about the fertility propensity (obtained in a similar manner), it would
be possible, in the context of an appropriate demographic model for the species,
to determine a nonzero fitness ($\lambda^{(m)}$) even for individuals that died without repro-
ducing. The greater the number of ecologically relevant traits that are included,
the more potent this strategy becomes. Obviously, this is not readily done for
individuals that die so early that their traits are not expressed; this is the problem
of the "invisible fraction" in analyses of selection (Grafen 1988; Bennington and
McGraw 1995).

Clearly an empirical determination of $\lambda^{(m)}$ applies only to the environment
in which the life history is measured (Antonovics et al. 1988; Brandon 1990).
Additional issues add to the complexity of estimating fitness in temporally fluctu-
ating (Tuljapurkar 1990) or spatially varying environments (Houston and McNa-

mara 1992; Kawecki and Stearns 1993). For example, recent work has shown that the optimal life history (using r or λ to measure fitness) may differ if the dispersal of offspring among environments is possible (Houston and McNamara 1992).

The intricacies of procuring complete life-history data to estimate fitness will pose formidable experimental challenges for many species. In hermaphroditic plants, for example, fertility ($F_i^{(m)}$) cannot simply be measured by seed production of an individual as this ignores the male component of reproduction (Primack and Kang 1989). Indeed, for plants and animals with separate sexes, accurately determining male reproductive success ($F_i^{(m)}$) may require the use of genetic markers in combination with sophisticated paternity analysis techniques because of the uncertainty of parenthood without such verification (Meagher 1986; Meagher and Thompson 1987). Complex breeding systems, which may change the genetic relationship between parent and offspring (e.g., partial selfing in plants) or result in viability differences in offspring (e.g., inbreeding effects), would require special consideration (Gregorius 1984). We have also not addressed the calculation of inclusive fitness (Hamilton 1964), which may be important in analyses of selection on behavioral traits in some species. These issues create interesting experimental and conceptual problems for the measurement of fitness.

CONCLUSIONS

In this study, we demonstrate the use of individual survival and fertility data to estimate individual fitness on a demographic basis. This estimate, $\lambda^{(m)}$, synthesizes knowledge of individual survival and fertility propensities into a single measure. The individual fitness measure can be used in studies of selection in natural or experimental populations.

Our analysis of selection on life-history traits in birds shows that, in age-structured populations, components of fitness are inadequate surrogates for individual fitness. However, the implications go beyond this context. In ecological studies, one often wishes to know the effects of environmental variation, natural or that resulting from experimental treatments, on performance. Interpretations are frequently ambiguous because alternative performance measures (e.g., survival, reproduction, growth, etc.) will respond to the environment in differing ways. A more complete performance measure is required. Where the principal interest is in the fitness response of individuals, we suggest that the concept of individual fitness, as set out above, provides such a measure.

LITERATURE CITED

Antonovics, J., and R. B. Primack. 1982. Experimental ecological genetics of *Plantago*. VI. The demography of seedling transplants of *P. lanceolata*. Journal of Ecology 70:55–76.

Antonovics, J., N. C. Ellstrand, and R. N. Brandon 1988. Genetic variation and environmental variation: expectations and experiments. Pages 275–303 *in* L. D. Gottlieb and S. K. Jain, eds. Plant evolutionary biology. Chapman & Hall, New York.

Arnold, S. J., and M. J. Wade. 1984a. On the measurement of natural and sexual selection: theory. Evolution 38:709–719.

———. 1984b. On the measurement of natural and sexual selection: applications. Evolution 38: 720–734.

Begon, M., J. L. Harper, and C. R. Townsend. 1990. Ecology: individuals, populations and communities. Blackwell, Boston.

Bennington, C. C., and J. B. McGraw. 1995. Phenotypic selection in an artificial population of *Impatiens pallida:* the importance of the invisible fraction. Evolution 49:317–324.

Brandon, R. N. 1978. Adaptation and evolutionary theory. Studies in the History and Philosophy of Science 9:181–206.

———. 1990. Adaptation and environment. Princeton University Press, Princeton, N.J.

Brandon, R. N., and J. Beatty. 1984. The propensity interpretation of "fitness"—no interpretation is no substitute. Philosophy of Science 51:342–347.

Burian, R. 1983. Adaptation. Pages 287–314 *in* M. Greene, ed. Dimensions of Darwinism. Cambridge University Press, Cambridge, Mass.

Caswell, H. 1982. Life history theory and the equilibrium status of populations. American Naturalist 120:317–339.

———. 1989a. Matrix population models. Sinauer, Sunderland, Mass.

———. 1989b. Life history strategies. Pages 285–308 *in* J. M. Cherrett, ed. Ecological concepts. Blackwell, Oxford.

Caswell, H., and A. Hastings. 1980. Fecundity, developmental time, and population growth rate: an analytical solution. Theoretical Population Biology 17:71–79.

Charlesworth, B. 1980. Evolution in age-structured populations. Cambridge University Press, Cambridge.

Clutton-Brock, T. H. 1988. Reproductive success. University of Chicago Press, Chicago.

Cockburn, A. 1991. An introduction to evolutionary ecology. Blackwell Scientific, London.

Cole, L. C. 1954. The population consequences of life history phenomena. Quarterly Review of Biology 20:103–137.

Darwin, C. 1859. On the origin of species by means of natural selection. J. Murray, London.

de Jong, G. 1994. The fitness of fitness concepts and the description of natural selection. Quarterly Review of Biology 69:3–29.

Dhondt, A. A. 1989. Blue tit. Pages 15–33 *in* I. Newton, ed. Lifetime reproduction in birds. Academic Press, London.

Dobzhansky, T. 1968a. On some fundamental concepts of Darwinian biology. Evolutionary Biology 2:1–34.

———. 1968b. Adaptedness and fitness. Pages 109–121 *in* R. C. Lewontin, ed. Population biology and evolution. Syracuse University Press, Syracuse, N.Y.

Ehrlich, P. R., and J. Roughgarden. 1987. The science of ecology. Macmillan, New York.

Endler, J. A. 1986. Natural selection in the wild. Princeton University Press, Princeton, N.J.

Futuyma, D. J. 1986. Evolutionary biology. Sinauer, Sunderland, Mass.

Gillespie, J. H. 1977. Natural selection for variances in offspring numbers: a new evolutionary principle. American Naturalist 111:1010–1014.

Grafen, A. 1988. On the uses of data on lifetime reproductive success. Pages 454–471 in T. H. Clutton-Brock, ed. Reproductive success. University of Chicago Press, Chicago.

Gregorius, H. 1984. Fractional fitnesses in exclusively sexually reproducing populations. Journal of Theoretical Biology 111:205–229.

Hamilton, W. D. 1964. The genetical evolution of social behavior. Journal of Theoretical Biology 7:1–52.

Hedrick, P. W. 1984. Population biology. Jones & Bartlett, Boston.

Hougen-Eitzman, D., and M. D. Rausher. 1994. Interactions between herbivorous insects and plant-insect coevolution. American Naturalist 143:677–697.

Houston, A. I., and J. M. McNamara. 1992. Phenotypic plasticity as a state-dependent life-history decision. Evolutionary Biology 6:243–253.

Janzen, D. H. 1977. What are dandelions and aphids? American Naturalist 111:586–589.

Kalisz, S. 1986. Variable selection on the timing of germination in Collinsia verna (Scrophulariaceae). Evolution 40:479–491.

Kawecki, T. J., and S. C. Stearns. 1993. The evolution of life histories in spatially heterogeneous environments: optimal reaction norms revisited. Evolutionary Ecology 7:155–174.

Kingsolver, J. G., and D. W. Schemske. 1991. Path analysis of selection. Trends in Ecology & Evolution 6:276–280.

Kozłowski, J. 1993. Measuring fitness in life-history studies. Trends in Ecology & Evolution 8:84–85.

Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. Evolution 37:1210–1226.

Lenski, R. E., and P. M. Service. 1982. The statistical analysis of population growth rates calculated from schedules of survivorship and fecundity. Ecology 63:655–662.

Leslie, P. H. 1945. On the use of matrices in certain population mathematics. Biometrika 33:183–212.

———. 1948. Some further notes on the use of matrices in population mathematics. Biometrika 35:213–245.

Levitan, M., and A. Montagu. 1971. Textbook of human genetics. Oxford University Press, New York.

Lewontin, R. C. 1965. Selection for colonizing ability. Pages 77–91 in H. G. Baker and G. L. Stebbins, eds. The genetics of colonizing species. Academic Press, New York.

Meagher, T. R. 1986. Analysis of paternity within a natural population of Chamaelirium luteum. I. Identification of most-likely parents. American Naturalist 128:199–215.

Meagher, T. R., and E. Thompson. 1987. Analysis of parentage for naturally established seedlings of Chamaelirium luteum (Liliaceae). Ecology 68:803–812.

Metz, J. A. J., R. M. Nisbet, and S. A. H. Geritz. 1992. How should we define "fitness" for general ecological scenarios? Trends in Ecology & Evolution 7:198–202.

Mills, S. K., and J. H. Beatty. 1979. The propensity interpretation of fitness. Philosophy of Science 46:263–286.

Mitchell-Olds, T., and R. G. Shaw. 1987. Regression analysis of natural selection: statistical inference and biological interpretation. Evolution 29:533–544.

Newton, I., ed. 1989. Lifetime reproduction in birds. Academic Press, London.

Popper, K. R. 1959. The propensity interpretation of probability. British Journal for the Philosophy of Science 10:25–42.

———. 1983. Realism and the aim of science. Rowman & Littlefield, Totowa, N.J.

———. 1990. A world of propensities. Thoemmes, Bristol.

Price, D. K., and N. T. Burley. 1994. Constraints on the evolution of attractive traits: selection in male and female zebra finches. American Naturalist 144:908–934.

Primack, R. B., and H. Kang. 1989. Measuring fitness and natural selection in wild plant populations. Annual Review of Ecology and Systematics 20:367–396.

Rausher, M. D. 1992. The measurement of selection on quantitative traits: biases due to environmental covariances between traits and fitness. Evolution 46:616–626.

Ricklefs, R. E. 1990. Ecology. Freeman, New York.

Schluter, D., and D. Nychka. 1994. Exploring fitness surfaces. American Naturalist 143:597–616.
Service, P. M., and R. E. Lenski. 1982. Aphid genotypes, plant phenotypes, and genetic diversity: a demographic analysis of experimental data. Evolution 36:1276–1282.
Sober, E. 1984. The nature of selection. MIT Press, Cambridge, Mass.
Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford.
Stearns, S. C., and R. E. Crandall. 1981. Quantitative predictions of delayed maturity. Evolution 35:455–463.
Thoday, J. M. 1953. Components of fitness. Evolution: Symposia of the Society for Experimental Biology 7:96–113.
———. 1958. Natural selection and biological progress. Pages 313–333 in S. A. Barnett, ed. A century of Darwin. Harvard University Press, Cambridge, Mass.
Tuljapurkar, S. D. 1990. Population dynamics in variable environments. Springer, New York.
Wade, M. J., and S. Kalisz. 1990. The causes of natural selection. Evolution 44:1947–1955.

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