

## AGE-SPECIFIC REPRODUCTIVE TACTICS

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Interest in ontogenetic changes in reproductive tactics, especially from a theoretical standpoint, has been intense during the last decade (for a sampling, see Williams 1966*a*, 1966*b*; Tinkle 1969; Emlen 1970; Gadgil and Bossert 1970; Fagen 1972; Gadgil and Solbrig 1972; Goodman 1974; Taylor et al. 1974; Schaffer 1974; Hirshfield and Tinkle 1975). Central concepts in this literature have been the notions of reproductive value and reproductive effort, both formulated first by R. A. Fisher (1930). Reproductive value is simply age-specific expectation of all present and future offspring (the latter discounted back to the present), while reproductive effort can be thought of as an organism's investment in any current act of reproduction.

In a population that is not changing in size, reproductive value,  $v_x$ , is readily calculated from the standard demographic schedules of age-specific survivorship ( $l_x$ ) and fecundity ( $m_x$ ):

$$v_x = \sum_{t=x}^{\omega} \frac{l_t}{l_x} m_t,$$

where  $x$  and  $t$  subscripts represent age and  $\omega$  is the age of last reproduction. The equation for a population changing in size is slightly more complicated with exponential terms to weight progeny by the intrinsic rate of increase (see Fisher 1930).

Reproductive effort is considerably more difficult to quantify but has been crudely approximated in organisms without parental care by various ratios of reproductive tissue to total somatic tissue (for discussion of the rationale and limitations of this procedure, see Tinkle 1969; Harper et al. 1970; Clark 1970; Gadgil and Solbrig 1972; Tinkle and Ballinger 1972; Ballinger and Clark 1973; Tinkle and Hadley 1973, 1975; Hirshfield and Tinkle 1975). None of the measures of reproductive effort used so far has adequately incorporated risk of mortality as a cost of reproduction.

Reproductive value is easily partitioned into its two components, namely, *present* progeny versus *future* progeny, as follows:

$$v_x = m_x + \sum_{t=x+1}^{\omega} \frac{l_t}{l_x} m_t.$$

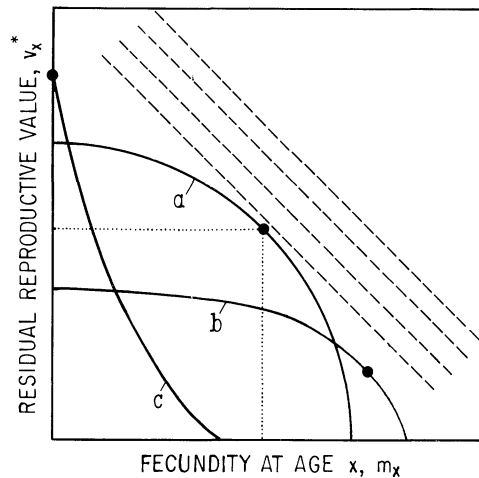


FIG. 1.—Expectation of future reproductive success, or residual reproductive value, is plotted against current reproductive effort as measured by current fecundity for three hypothetical cases (solid curves). Dashed lines represent a family of straight lines corresponding to equal lifetime production of offspring through both current and future reproduction. The reproductive tactic that maximizes total lifetime reproductive success for each case is indicated by a dot. This tactic maximizes reproductive value at age  $x$ . See text for further discussion and fig. 2 for a three-dimensional representation with an age axis.

The second term on the right-hand side represents the expectation of *future* offspring of an organism at age  $x$ , or the “residual reproductive value” at age  $x$  (Williams 1966b). Rearranging this equation shows that residual reproductive value (hereafter abbreviated  $v_x^*$ ) is equal to an organism’s reproductive value in the next age interval,  $v_{x+1}$ , multiplied by the probability of surviving from age  $x$  to age  $x + 1$ , or  $l_{x+1}/l_x$  (Williams 1966b; Taylor et al. 1974; Schaffer 1974):

$$v_x^* = \frac{l_{x+1}}{l_x} v_{x+1}.$$

A little reflection on residual reproductive value and reproductive effort suggests that these two parameters should generally vary inversely, due to feedback between them. Successful reproduction often involves taking risks such as exposing oneself to predators, which by reducing longevity decreases future reproductive success. Moreover, allocation of time and energy to reproduction in itself doubtlessly often decreases survivorship and hence expectation of future progeny. Thus, an organism with a high residual reproductive value would be expected to invest less in current reproduction than another organism with a lower expectation of future offspring.

The trade-off between present progeny versus expectation of future offspring can be depicted graphically by plotting residual reproductive value against current fecundity, as measured by  $m_x$  (fig. 1). All-out or so-called big-bang (semelparous) reproduction maximizes current fecundity but drives future reproductive success to zero; conversely, failure to reproduce at some particular

age leads to a current  $m_x$  of zero but maximizes residual reproductive value at that age. Several different logically possible forms for the interaction between  $m_x$  and  $v_x^*$  are shown in figure 1; these curves relate profits in present offspring to costs in future offspring (see Williams 1966b) and are analogous to fitness sets of Levins (1962, 1968). Families of straight lines representing equal lifetime production of offspring are the corresponding "adaptive functions," depicted as dashed lines in the figure. In a stable population with present and future offspring of equivalent value, these lines have slopes of  $-1$ . (In an expanding population, current progeny gain a greater contribution to the gene pool [and are therefore worth more than future ones] and slopes are steeper; in contrast, in a declining population with future offspring more valuable than present ones, slopes would be gentler than 45 degrees.) The point of intersection of the "fitness set" curves with the "adaptive function" line that is farthest from the origin (shown as dots in the figure) marks the optimal reproductive tactic that maximizes reproductive value and lifetime production of offspring. When these "fitness set" curves are convex, fitness is maximized by allocating only part of the available resources to current reproduction and the remainder to somatic tissues and activities; thus, reproductive effort is not maximized and repeated reproduction (iteroparity) is optimal as shown by the dotted lines for curve *a*. As an iteroparous organism ages, the curve relating its present reproductive effort to its future reproductive success might change from a form like curve *a* to one somewhat like that labeled *b*, resulting in an increased reproductive effort (see also fig. 2). Note, however, that concave  $m_x$  versus  $v_x^*$  curves can lead to "big-bang" reproduction; should maximal residual reproductive value be greater than maximal current fecundity (curve *c*), the optimal tactic is to withhold from reproducing and to invest all available resources in somatic tissues and activities and ultimately to produce offspring at some time in the future.

In figure 2, we attempt to depict the probable trade-offs between current reproduction and future reproductive success during the lifetime of an organism that reproduces repeatedly (an organism with "big-bang" reproduction would have a similar plot with current fecundity increasing as residual reproductive value falls, but the three-dimensional surface would be everywhere concave). The age-specific sections through this three-dimensional solid marked *a*, *b*, and *c* identify the corresponding two-dimensional curves in figure 1. The dark line connecting the dots in figure 2 traces the organism's optimal reproductive tactic during ontogeny. The projection of the shadow of this line on the age versus  $m_x$  plane represents the expected  $m_x$  schedule that maximizes lifetime reproductive success (presumably this will be the  $m_x$  schedule observed in a demographic study). The surface of this three-dimensional solid shows the effects of various nonoptimal levels of current fecundity on the organism's future reproductive success, as measured by its residual reproductive value. The *cost* of any particular intensity of current reproduction (either suboptimal or superoptimal) is simply the decrease in lifetime reproductive success resulting from that level of current fecundity.

In practice, testing such models of age-specific reproductive tactics is extremely difficult. For example, to test the formulation of an optimal reproductive

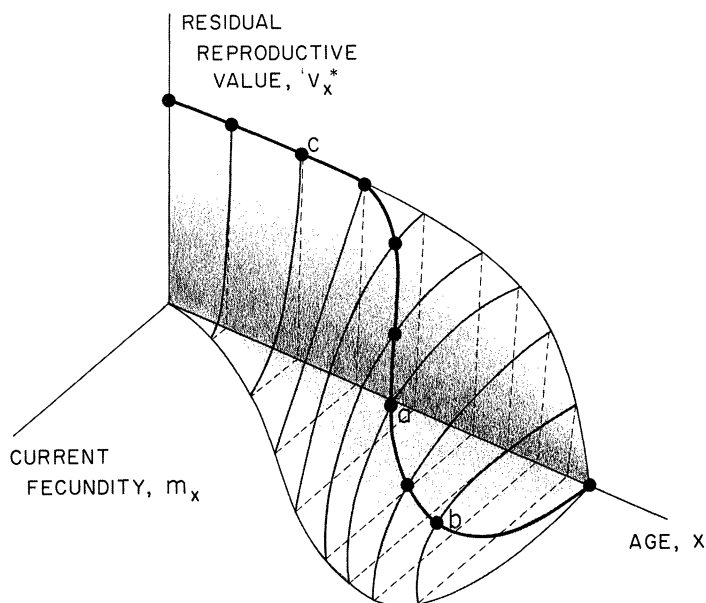


FIG. 2.—Plot showing the probable trade-offs between current reproduction and future reproductive success during the ontogeny of an iteroparous organism. The dark line traces the reproductive tactic that maximizes lifetime reproductive success, which corresponds to maximizing reproductive value at each age. The curved surface of this three-dimensional solid shows the effects of various non-optimal levels of current fecundity on the organism's future reproductive success as measured by its residual reproductive value. Slices through this solid at particular ages corresponding to the respective curves shown in fig. 1 are marked with an *a*, *b*, and *c*. In a real organism, the shape and intercepts of this surface would vary with immediate environmental conditions for foraging, survival, and reproduction (see text), as well as with the actual reproductive tactic taken.

tactic depicted in figure 2, an organism must somehow either be tricked or manipulated into taking a nonoptimal tactic, thereby lowering its lifetime reproductive success. Moreover, after getting the organism to expend either more or less than the appropriate optimal amount of effort on current reproduction, one must thereafter monitor the organism's future reproductive performance against that of a control to measure a corresponding decrease or increase, respectively. Indeed, mere demonstration of a convex or concave relationship between  $m_x$  and  $v_x^*$  would be exceedingly difficult or impossible for most organisms.

Such an oversimplified demographic approach to optimal reproductive tactics has conspicuous limitations. All individuals are assumed equivalent, and mortality and fecundity are presumed to be constant at any given age. Clearly, real survivorship and fecundity schedules must vary in time and space and among individuals. Animals at the same age doubtlessly differ in their expectation of further life and reproductive success. An individual with higher than average reproductive effort that therefore suffered above-average mortality

might still produce as many progeny during its short lifetime as another longer-lived individual with lower than average reproductive effort but above-average survivorship. Variation among individuals of this sort could result in seemingly inexplicable variability in reproductive effort within an age class. Immediate environmental conditions for survivorship, foraging, and reproduction (particularly resource availability) must often alter the shape of the surface depicted in figure 2. Nevertheless, despite these plaguing problems, an individual's age-specific expectation of future offspring is probably best estimated operationally by its residual reproductive value.

Relatively few data exist on age specificity in reproductive tactics (but see Clark 1970; Tinkle and Ballinger 1972; Neill 1972; Tinkle and Hadley 1973, 1975; Ballinger 1973; Constantz 1974). We now examine such data for several species of lizards and snakes using published information from the literature as well as some new data from our own studies. Tinkle et al. (1970) recognized two distinct lizard reproductive tactics, namely, species with a single clutch or litter each reproductive season versus those with multiple reproduction. In the former group (fig. 3), reproductive value and residual reproductive value vary relatively gradually with age, whereas in the latter group (multiple-clutched species)  $v_x$  and  $v_x^*$  are pronounced sawtooth functions of age (actually, single-brooded species would also have sawtoothed plots if finer, say monthly, age intervals were used, but the *proportional* annual variation in residual reproductive value would be much less than in multiple-clutched species). In species that reproduce more than once per reproductive season, expectation of future progeny is very high early in each season due to the high probability of laying subsequent clutches. However,  $v_x$  drops precipitously as the season progresses, and the possibility of subsequent clutches decreases. Provided that such an animal survives the next winter, its reproductive value rises again to a very high value the following spring, when prospects of producing several more clutches are again good. In such multiple-clutched species, both reproductive value and residual reproductive value vary more within each reproductive season than between year classes. We might therefore expect concomitant variation in reproductive effort to be rather great within the season in these sorts of species. In contrast to the situation in multiple-brooded species as just described, residual reproductive value ( $v_x^*$ ) is fairly flat with age in species that produce only a single clutch or litter per season (fig. 3). In such species, reproductive effort should not vary greatly with age alone but may be more sensitive to other factors, such as resource availability.

As in many fish (Williams 1966a; Constantz 1974), clutch or litter size is directly correlated with body size in many reptiles (Tinkle et al. 1970; Fitch 1970). Because the animals grow as they age, fecundity often increases with age. However, increased clutch sizes of larger older individuals need not be accompanied by heightened reproductive effort.

Constantz (1974) showed that various operational estimates of reproductive effort in the fish *Poeciliopsis* increased with size and presumably with age; moreover, his results also indicate that reproductive effort increased with greater availability of resources. Clark (1970) demonstrated that the ratio of clutch

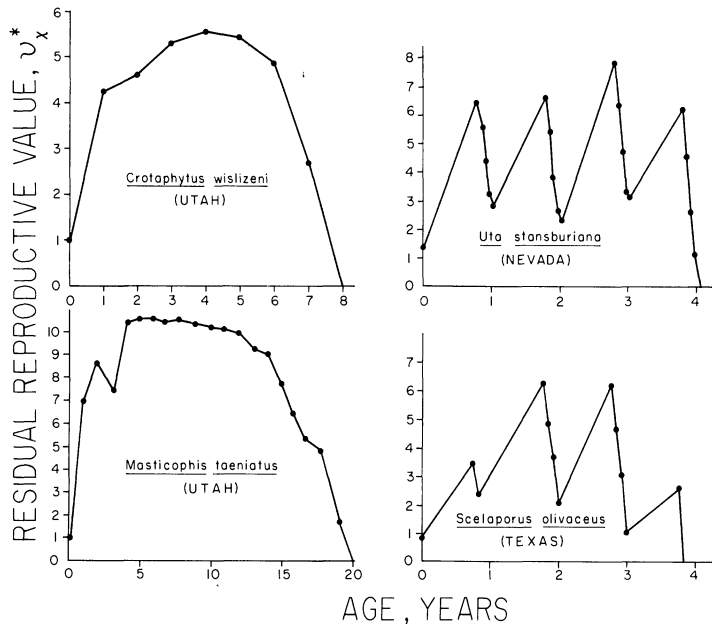


FIG. 3.—Residual reproductive value plotted against age for four species of reptiles. The two species on the left, the leopard lizard *Crotaphytus wislizeni* and the striped whipsnake *Masticophis taeniatus*, lay a single clutch each reproductive season, whereas the two species on the right, the side-blotched lizard *Uta stansburiana* and the rusty lizard *Sceloporus olivaceus*, lay multiple clutches each year. Both reproductive value and residual reproductive value rise and fall relatively smoothly with age in the single-clutched species but vary in a markedly sawtoothed manner in the species with multiple clutches each season (use of finer age intervals would produce sawtooth curves in single-clutched species, but the proportional annual variation in residual reproductive value would still be much less than in species with multiple clutches). Demographic data for *Crotaphytus* are from Parker and Pianka (1975), those for *Masticophis* from Parker (1974), those for *Uta* from Turner et al. (1970), and those for *Sceloporus* from Blair (1960) as reported in Turner et al. (1970).

weight to total female body weight increases with size (and, by inference, with age) in the worm snake *Carphophis vermis*.

In the viviparous montane lizard *Sceloporus jarrovi*, Tinkle and Hadley (1973) found that both litter size and calories invested in eggs increased significantly with both size and age. However, these workers reported that neither size nor age was significantly correlated with two perhaps more appropriate estimators of reproductive effort, namely, the ratio of litter weight over female weight and the ratio of egg calories to total body calories. A stronger statistical analysis of these data (generously provided by Dr. Tinkle) shows that ratios of total calories in eggs to total body calories are significantly greater ( $t$ -test,  $P < .025$ ) among larger females (probably about 32 months old) than these same calorific ratios are in smaller females estimated to be about 20 months old (table 1). Interestingly enough, demographic data of Ballinger (1973) indicate that, after reproduction begins, residual reproductive value of *S. jarrovi* decreases steadily

TABLE 1

STATISTICS ON EGG YOLK CALORIES EXPRESSED AS A PERCENTAGE OF TOTAL BODY CALORIES IN *Sceloporus jarrovi* FEMALES OF DIFFERENT SIZES AND PRESUMED AGE\*

Statistic	69-76-mm Snout-Vent Length (Probably 20 Months Old)	81-90-mm Snout-Vent Length (Probably 32 Months Old)
Mean .....	28.25	31.74
Standard deviation .....	2.81	1.47
Standard error of mean .....	0.94	0.66
Sample size .....	9	5

NOTE.— $t = 2.586$  with 12 degrees of freedom ( $P < .025$ ).

\* Computed from unpublished data of Tinkle and Hadley (1973).

TABLE 2

ESTIMATED VALUES OF DEMOGRAPHIC PARAMETERS FOR *Sceloporus jarrovi*\*

Age (Years)	Survivorship ( $l_x$ )	Fecundity ( $m_x$ )	Reproductive Value ( $v_x$ )	Residual Reproductive Value ( $v_x^*$ )
0 .....	1.000	0.00	1.00	0.96
1 .....	0.180	1.20	5.35	4.00
2 .....	0.086	5.25	8.37	3.10
3 .....	0.032	5.75	8.09	2.25
4 .....	0.012	6.00	6.00	0.00

\* From data of Ballinger (1973).

TABLE 3

STATISTICS ON WEIGHT OF FULL-TERM EMBRYOS EXPRESSED AS A PERCENTAGE OF TOTAL BODY WEIGHT OF GRAVID FEMALE *Sceloporus jarrovi* OF DIFFERENT SIZES AND PRESUMED AGE\*

Statistic	Snout-Vent Length Under 68 mm (First-Year Animals)	Snout-Vent Length 69 mm and Over (Second- and Third-Year Animals)
Mean .....	29.62	33.36
Standard deviation .....	5.95	5.27
Standard error of mean .....	1.24	1.15
Sample size .....	23	21

NOTE.— $t = 2.199$  with 42 degrees of freedom ( $P < .05$ ).

\* Computed from unpublished data of R. E. Ballinger.

with age (table 2). Total weight of full-term embryos expressed as a percentage of female weight also increases significantly with size in *S. jarrovi* (table 3). Tinkle and Hadley (1975) later demonstrated a similar increase in reproductive effort with age in *S. jarrovi* but found that reproductive effort did not increase conspicuously with age in *Sceloporus graciosus* or *Uta stansburiana*.

TABLE 4

STATISTICS ON CLUTCH SIZE AND CLUTCH VOLUME/BODY WEIGHT PERCENTAGES  
IN THE AUSTRALIAN AGAMID LIZARD *Amphibolurus isolepis*\*

	Clutch Size	$\frac{\text{Clutch Volume}}{\text{Body Weight}} \times 100$
Early clutches		
(September–December):		
N . . . . .	67	25
Means . . . . .	3.01	11.23
95% confidence limits . . . . .	2.7–3.3	10.25–12.20
Late clutches		
(January–February):		
N . . . . .	41	15
Means . . . . .	3.88	15.12
95% confidence limits . . . . .	3.5–4.3	13.38–16.85

\* Partially adapted from Pianka (1971).

Although his data were limited, Vitt (1974) reported that calorimetric estimates of reproductive effort did not increase with size in the anguid lizard *Gerrhonotus coeruleus principis*. This result either could be due to small sample size or could arise from a long-lived iteroparous existence leading to a rather constant residual reproductive value. Unfortunately, no demographic data are available for this species. Vitt (1975) did demonstrate that total clutch calories increase significantly with size, and thus presumably with age, in two species of horned lizards (*Phrynosoma*).

Clutch size increases significantly with both female size and age in both the leopard lizard *Crotaphytus wislizeni* and the striped whipsnake *Masticophis taeniatus* in northern Utah (Parker and Pianka 1976, Parker 1974, 1975). However, in neither species does the ratio of clutch weight over total body weight vary significantly either with residual reproductive value or with age (fig. 4). In these two species and perhaps many others, reproductive effort is probably more sensitive to immediate environmental conditions for feeding and reproduction, such as food availability, than it is to residual reproductive value, which varies relatively little with age during peak years of reproduction (fig. 3).

Recall that species which reproduce more than once each reproductive season have much greater proportional variation in residual reproductive value during their ontogeny than do single-clutched species (fig. 3). Other things being equal, correlations between reproductive effort and residual reproductive value might therefore be expected to be stronger in multiple-clutched species.

In at least one multiple-clutched species, the Australian agamid *Amphibolurus isolepis* (Pianka 1971), both clutch size and reproductive effort as measured by clutch weight/body weight ratios increase significantly (*t*-tests, *P*'s < .05) from early to late clutches (table 4), as expected from theoretical considerations. In both the rusty lizard *Sceloporus olivaceus* and the side-blotched lizard *U. stansburiana* (see fig. 3), however, clutch size actually *decreases* as the season progresses (Blair 1960; Tinkle 1967; Turner et al. 1970; Parker and Pianka



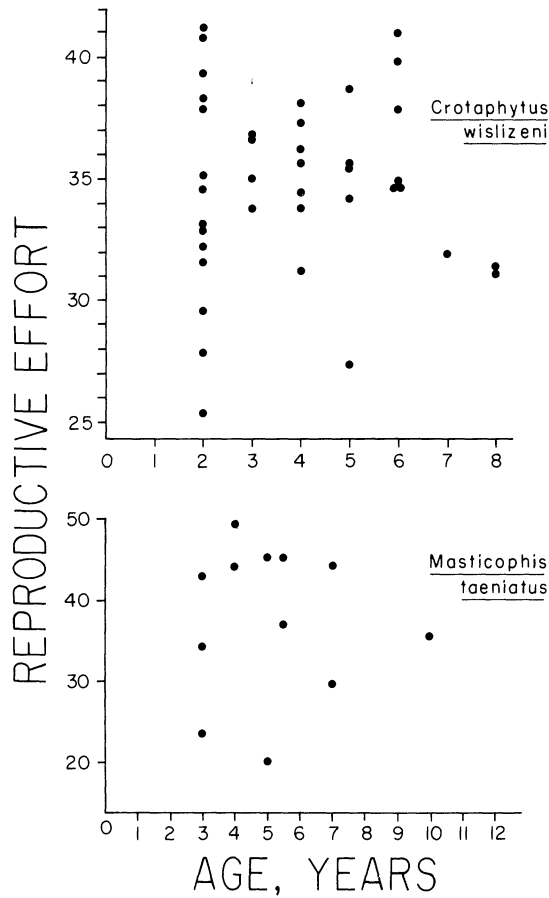


FIG. 4.—Clutch weight/body weight ratios plotted against age for the two single-clutched species of fig. 3 (data from the same sources). This operational estimator of reproductive effort does not vary consistently with age (residual reproductive values are relatively constant during the peak period of reproduction in these two species). See text.

1975). At first glance, this result seems to refute theoretical expectations, which of course predict an increased reproductive effort as residual reproductive value declines with age. At least three factors could contribute to this apparent anomaly: (1) A small clutch need *not* imply a low reproductive effort. Early in the season, females have large fat reserves that were accumulated during the previous winter; most of these stored lipids are rapidly mobilized and used in the first clutch. In contrast, most materials and energy devoted to subsequent clutches must be gathered during the reproductive season by the foraging female lizard. A female could thus actually be allocating a greater proportion of her available resources to reproduction and yet, because of a reduced supply of resources, she might still produce a smaller clutch. (2) Prey density doubtlessly varies seasonally, as is known for many insectivorous birds. Decreasing food

supplies as the season progresses could contribute to observed reduced clutch sizes later in the season. (3) Finally, lowered probabilities of survival of offspring born later in the season could in itself favor reduced reproductive effort.

Further, more detailed, energetic studies of multiple-clutched species with a time dimension and more sophisticated measures of reproductive effort will be of great interest. Fitzpatrick (1973) and Derickson (1975) have begun such studies, and L. C. Fitzpatrick (personal communication) is currently measuring seasonal changes in food availability and the energy budget of *S. olivaceus* with the intent of testing the hypothesis that females are actually allocating *more* of the energy available to them to their later smaller clutches than they are to the earlier larger ones. K. A. Nagy (personal communication) is undertaking a similar study on *Uta stansburiana* females using a powerful new technique involving doubly labeled water. Results of such studies will clearly be very informative.

#### SUMMARY

A simple graphical model for maximization of total lifetime reproductive success is developed using the demographic parameters of current fecundity and residual reproductive value. Trade-offs between present progeny and expectation of future offspring are treated in terms of costs and profits to lifetime reproductive success. Various limitations of the model and some relevant data are presented and discussed. Single-clutched species are distinguished from those that lay multiple clutches each reproductive season, because residual reproductive value in the latter group varies proportionally much more during ontogeny than in the former group. Some difficulties in measuring reproductive effort in a changing environment are pointed out.

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