

EFFECTS OF MORTALITY RISK AND GROWTH ON A MODEL OF REPRODUCTIVE EFFORT:  
WHY THE SHINE AND SCHWARZKOPF MODEL IS NOT GENERALPETER H. NIEWIAROWSKI<sup>1</sup> AND ARTHUR E. DUNHAM<sup>2</sup><sup>1</sup>*Department of Biology, University of Akron, Akron, Ohio 44325-3908**E-mail: phn@uakron.edu*<sup>2</sup>*Department of Biology, Leidy Labs, University of Pennsylvania, Philadelphia, Pennsylvania 19104**E-mail: adunham@sas.upenn.edu*

**Abstract.**—Using data and reanalysis of a model published by Shine and Schwarzkopf (1992) we reject the two unsubstantiated assertions made by Shine et al. (1996) about modeling the evolution of reproductive effort in squamate reptiles: (1) mortality schedules do not affect predictions of the Shine and Schwarzkopf (1992) model; and (2) growth rates that would affect the predictions of the original model are biologically unreasonable. On the basis of these two points alone, we strongly reject Shine et al.'s (1996) claim that a critique by Niewiarowski and Dunham (1994) actually reinforces the original conclusions of Shine and Schwarzkopf (1992). Furthermore, results and data presented here are strong enough to severely circumscribe the generality of the Shine and Schwarzkopf (1992) model. Though we do not provide data or new analyses of the potential effects of offspring size variation, we reaffirm the position of Niewiarowski and Dunham (1994) that the sensitivity of the Shine and Schwarzkopf (1992) model to such effects should be explored before using it as a basis for structuring future research on the evolution of reproductive effort in squamate reptiles.

**Key words.**—Costs of reproduction, fecundity, lifetime reproductive success, lizards, offspring size, reproduction, reproductive effort, snakes, survival.

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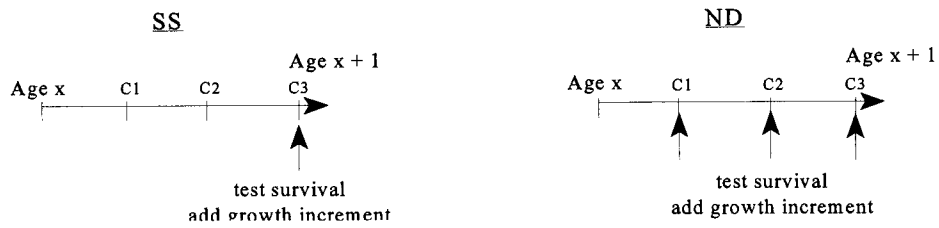
In a recent paper, Shine et al. (1996) reply to criticisms raised by Niewiarowski and Dunham (1994) of a model of the evolution of reproductive effort in squamate reptiles published earlier (Shine and Schwarzkopf 1992). In this paper, we demonstrate that the claims of Shine et al. (1996) are incorrect and that the original criticisms raised by Niewiarowski and Dunham (1994) have not been substantively addressed. We also assert that resolution of our debate has important implications for understanding the evolution of reproductive effort in squamates. Before evaluating Shine et al. (1996), we provide a very brief review of the debate between Shine and Schwarzkopf (1992) and Niewiarowski and Dunham (1994).

Costs of reproduction are typically identified as trade-offs between a current reproductive bout and either future *survival* or *fecundity* (Bell 1980; Shine 1980). Survival costs in squamate reptiles are thought to arise primarily from risk of death associated with a reproductive event; for example, a gravid female may be more susceptible to capture by a predator because of reduced mobility or increased conspicuousness while carrying eggs or young (Shine 1980). However, fecundity costs arise because energy devoted to a current reproductive bout cannot be used for growth that would lead to increased body size and higher fecundity at a later time (Shine 1980). Shine and Schwarzkopf (1992) presented a simple mathematical model suggesting that survival costs of reproduction are much more important in the evolution of reproductive effort in squamate reptiles than fecundity costs. In fact, they argued that fecundity costs could be ignored in most squamate populations. Niewiarowski and Dunham (1994) criticized the conclusions of Shine and Schwarzkopf (1992) by showing that the disproportionate effect of survival costs they found derived from the particular way in which

growth and mortality were modeled. The main conclusion of Niewiarowski and Dunham (1994) was that the importance of survival costs depends completely upon how mortality is modeled. Finally, Niewiarowski and Dunham (1994) used a qualitative analysis to argue that the conclusion of Shine and Schwarzkopf (1992) was also limited by their assumption (for the sake of simplicity) that offspring size is constant.

Shine et al. (1996) focuses on three aspects of Niewiarowski and Dunham's (1994) analysis of the Shine and Schwarzkopf (1992) model: (1) effects of different mortality patterns, (2) effects of concurrent growth and reproduction, and (3) effects of allowing offspring size to vary and the meaning of reproductive effort (RE) and cost of reproduction (CR). Our response has three components. First, we reexamine the effects different mortality schedules have on the predictions of Shine and Schwarzkopf (1992) and quantitatively demonstrate why the model is, contrary to the claims of Shine et al. (1996), very sensitive to the distribution of mortality risk. Second, we present data showing concurrent growth and reproduction in four squamate species demonstrating that growth rate effects of the magnitude suggested by Niewiarowski and Dunham (1994) are observed in squamate populations. Third, we briefly examine the differences between Shine and Schwarzkopf (1992), Shine et al. (1996), and Niewiarowski and Dunham (1994) on the question of variable offspring size, and the meaning of RE and CR.

Our response addresses the debate both with new analysis and new data. With respect to the importance of mortality schedules, our purpose here is to demonstrate that the analyses of Shine and Schwarzkopf (1992) and Shine et al. (1996) are simply incorrect. With respect to differences we have with Shine and Schwarzkopf (1992) and Shine et al. (1996) on the relevance of growth rate, our main goal is to question



	$p_x$	$p_x$	$p_x$	$l_1$	$R_0$
3	1.0	0.8944	0.8944	0.8	11.155
ND	0.9283	0.9283	0.9283	0.8	11.139
SS	1.0			0.8	9.600

Age 0 C<sub>1</sub> C<sub>2</sub> C<sub>3</sub> → Age 1

Where  $R_0 = \sum l_x * m_x$

For example:

$$R_0(\text{"3"}) = (1*4) + (0.8944*4) + (0.8944*4) = 11.155$$

FIG. 1. Differences in the implementation of mortality risk between Niewiarowski and Dunham (1994) [ND] and Shine and Schwarzkopf (1992) [SS], along with their consequences for estimating fitness ( $R_0$ ). Note that the overall annual survival probability is equal among the three different schedules, and that the Shine and Schwarzkopf (1992) implementation defines the lower extreme, while the "3" implementation defines the upper extreme. Each calculation of  $R_0$  assumes a clutch size of four at each reproductive event.

the generality of the assumptions of Shine and Schwarzkopf and Shine et al. by providing counter-examples using data, rather than biologically reasonable arguments. Toward that end, this paper resolves differences between Shine and Schwarzkopf (1992), Shine et al. (1996) and Niewiarowski and Dunham (1994) with respect to issues of mortality and growth. We hope our discussion spurs the collection of data that might bear on the generality of the assumptions about offspring size variation made by Shine and Schwarzkopf (1992) and Shine et al. (1996).

EVALUATING THE RESPONSE OF SHINE ET AL. (1996)

*Mortality Schedule*

The Shine and Schwarzkopf (1992) model assessed mortality and allowed individuals to grow at the end of each reproductive season. Niewiarowski and Dunham (1994) recognized that, in species with multiple clutches, the net reproductive rate of a female who did not die until all clutches

had been produced would be greater than the net reproductive rate of a female with the same annual mortality but who died midyear (i.e., between clutches). Niewiarowski and Dunham (1994) preserved the original structure of the Shine and Schwarzkopf (1992) model (Fig. 1), but then allowed mortality to occur continuously rather than episodically (Shine and Schwarzkopf 1992; Fig. 1); mortality could accrue between clutches in the Niewiarowski and Dunham (1994) model. When mortality was assessed in the Shine and Schwarzkopf (1992) model, survivors grew and commenced another reproductive season. Similarly, growth was incremented directly after mortality was assessed in the Niewiarowski and Dunham (1994) implementation.

Substantial differences in the trade-off trajectories between the Niewiarowski and Dunham (1994) and Shine and Schwarzkopf (1992) model led Niewiarowski and Dunham to conclude that the way in which mortality was implemented had drastic effects on the conclusions drawn by Shine and Schwarzkopf. Shine et al. (1996) determined that the source

of the effect on the position of the trade-off trajectories shown by Niewiarowski and Dunham (1994) was in fact due to the accrual of growth between clutches, rather than by the change in the mortality schedule. We concur with their analysis; Niewiarowski and Dunham (1994) were in error in ascribing the effect on the positions of the trade-off trajectories to differences in the mortality schedule.

Shine et al. (1996) correctly identified our misinterpretation, however, they drew the incorrect conclusion that the way in which mortality is modeled is inconsequential to modeling the trade-off. The distribution of mortality must have an effect on the position of the trade-offs if mortality of a female can occur between breeding events within a single breeding season. A simple example clearly demonstrates this. Consider an organism that has an annual probability of survival of 0.8 and produces three clutches of four eggs, each year (Fig. 1). Three different schedules of the distribution of mortality within a year have different consequences for the annual contribution to *net* reproductive rate ( $R_0$ ). It is important to note that the overall annual survival probability is the same for each case (0.8), only the distribution of mortality risk changes. The range of  $R_0$  in this example is bounded by Shine and Schwarzkopf (1992) on the low side and "3" on the high side. In other words, for a squamate reptile that produces multiple clutches in a single season, *any* change in the distribution of mortality that results from reducing allocation to reproduction will be subject to selection.

If differences in the distribution of mortality risk can affect estimates of  $R_0$ , then why do the models of Shine et al. (1996) and Niewiarowski and Dunham (1994) produce identical results when the growth effect is removed from the Niewiarowski and Dunham implementation? It turns out that if the mortality schedules of the standard and mutant female are modeled identically, then there is no net effect on the position of the trade-off trajectories when modeling the fecundity trade-off. In other words, if you make the same error in calculating mortality risk for both the mutant and the standard female, the relative position of the fitness trajectories does not change. However, the magnitude of the error produced by modeling mortality as episodic (Shine and Schwarzkopf 1992) when it is continuous (Niewiarowski and Dunham 1994) becomes very evident by examining positions of the survival trade-off trajectories. Specifically, compare the position of the trajectories arising from a survival trade-off in Shine and Schwarzkopf (1992; episodic mortality) with those calculated using Niewiarowski and Dunham's (1994) continuous mortality risk (Fig. 2). Note that the effect on the position of the trade-off trajectories of changing survival rates (from 1.01 to 1.1 annually) is very slight when modeling mortality as a continuous risk (Niewiarowski and Dunham 1994), relative to the effect modeled in Shine and Schwarzkopf (1992; episodic mortality). What does this indicate about the Shine and Schwarzkopf (1992) model, and the importance of the distribution of mortality risk? Recall that Shine and Schwarzkopf (1992) concluded from the sensitivity of the position of the trajectories to varying mortality, that the survival trade-off is likely to be much more important than the fecundity trade-off. In effect, Shine and Schwarzkopf (1992) overemphasized the relative importance of the potential survival trade-off by modeling mortality risk episodically. It

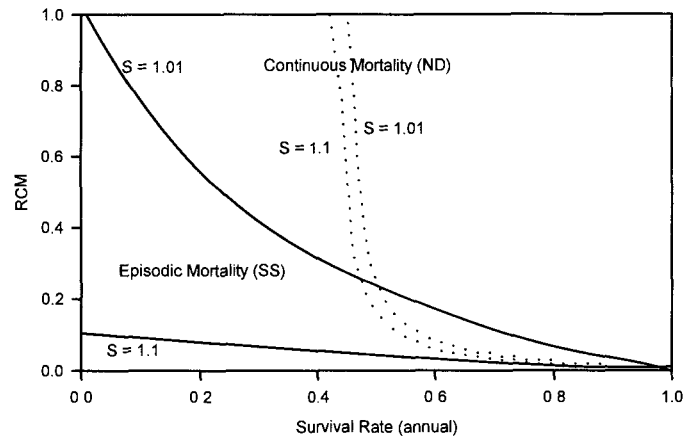


FIG. 2. Trajectories for the "survival trade-off" of Shine and Schwarzkopf under an assumption of episodic mortality (Shine and Schwarzkopf 1992) versus an assumption of continuous mortality (ND). Differences in the positions of the trade-off trajectories based on schedule of mortality risk demonstrate that the mortality schedule does matter.

remains to be seen how mortality risk is distributed in natural populations of squamates, but the effect still calls the generality of the Shine and Schwarzkopf (1992) model into serious question (Niewiarowski and Dunham 1994). We assert that the scrutiny of the Shine and Schwarzkopf (1992) model (and ongoing debate) by both Shine et al. (1996) and Niewiarowski and Dunham (1994) reveals how important it is to consider how assumptions affect inferences drawn from a model.

Ignoring consequences of shifts in the mortality schedule obscures an important aspect of the very trade-offs Shine and Schwarzkopf (1992) originally tried to model and that Shine (1980) has argued is important for many Scincid lizards. In that light, our original criticism about episodic mortality is not simply about mathematical correctness; shifts in the mortality schedule are biologically relevant (Fig. 2). For example, the distribution of mortality risk is critical if the mutant female in Shine and Schwarzkopf (1992), the one reducing relative clutch mass (RCM) has her schedule and/or annual level of mortality risk altered by virtue of reducing RCM, as may occur when episodes of mortality are associated with reproduction (e.g., the locomotor burden of carrying eggs; Shine 1980). The same argument would apply to conditions where mortality risk is positively related to the level of expenditure (RCM). Our illustration demonstrates that mortality schedules must be explicitly included in the estimation of the position of the trajectories in the Shine and Schwarzkopf (1992) model. To ignore this effect is to ignore some of the very patterns that ostensibly initiated the Shine and Schwarzkopf (1992) model.

#### Concurrent Growth and Reproduction

Shine et al. (1996) correctly identified that differences between the position of the trade-off trajectories in their original model (Shine and Schwarzkopf 1992; Fig. 2) and Niewiarowski and Dunham (1994, Fig. 2) were due to changes in body size (growth) that are possible. However, Shine et al.

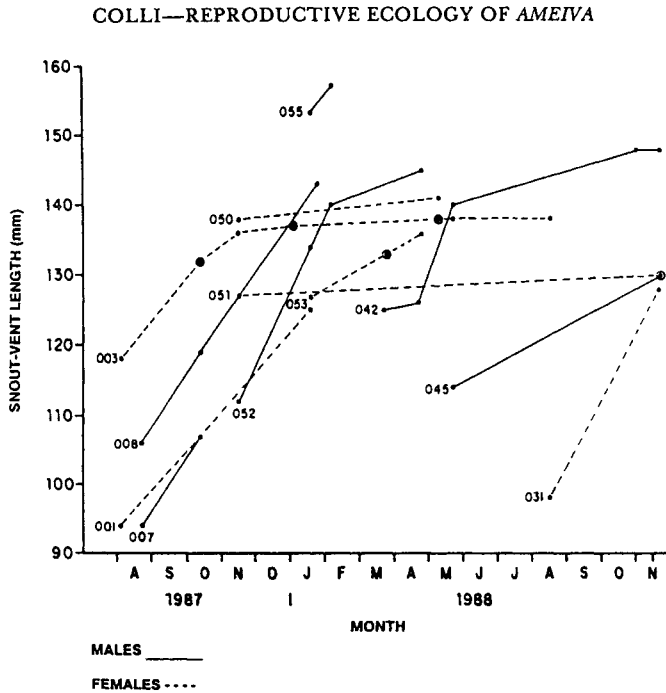
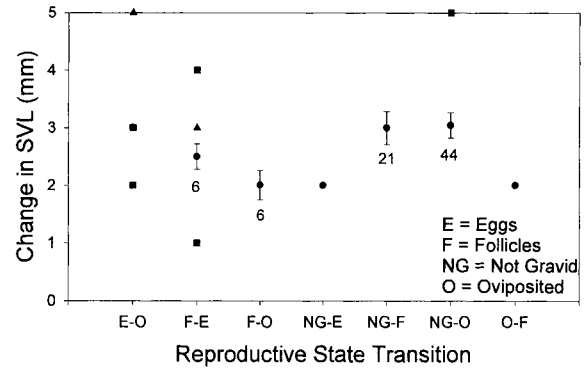


FIG. 3. Figure 6 of Colli (1991) showing concurrent growth and reproduction in *Ameiva ameiva*. The larger circles indicate presence of oviductal eggs or enlarged vitellogenic follicles identifying individuals with concurrent growth and reproduction.

(1996) did not provide data with which to evaluate the likelihood of such an effect. Instead, they merely asserted that concurrent growth and reproduction of the magnitude modeled by Niewiarowski and Dunham (1994) was unlikely and not biologically realistic. Below, we present data to the contrary.

Putting the concurrent growth and reproduction problem into perspective, a 10-g female with an RCM of 0.33 (the mean RCM of lizards presented in Shine and Schwarzkopf, 1992) would reduce her clutch mass by 1% and divert it to growth ( $0.01 \times 10 \times 2.3 = 0.23$  g-mass increment). The growth increment represents a 2.3% change in mass between clutches. Explicit analysis of interclutch growth is unfortunately lacking from the literature (at least among studies published since 1975 and listed in BIOSYS). Nevertheless, some published studies on growth and reproduction and some of our own data allow us to evaluate if concurrent growth and reproduction is possible. For example, Colli (1991) showed that female *Ameiva ameiva* do indeed grow during the production of a clutch of eggs (his fig. 6; reproduced here as Fig. 3). Note that interclutch growth as well as growth during the production of a first clutch is indicated by several females in his sample. In a different study of the same species at a different locale (Vitt 1982), fat bodies in females were observed to be continuously large throughout the year, suggesting that simultaneous growth and reproduction would at least not be limited by energy reserves. Simultaneous investment in growth and reproduction (including interclutch growth) is also apparent in data we have analyzed for *Sceloporus undulatus*, *Uta stansburiana*, and *Sceloporus merriami* (Fig. 4). Most importantly, note that change in snout-vent



*Sceloporus undulatus*:  $mass[g] = -6.96 + 0.25(SVL[mm])$  (40-75 mm)  
*Uta stansburiana*:  $mass[g] = -2.92 + 0.14(SVL[mm])$  (40-55 mm)  
*Sceloporus merriami*:  $mass[g] = -5.64 + 0.19(SVL[mm])$  (40-55 mm)

FIG. 4. Concurrent growth and reproduction in three *Sceloporine* lizards. Average change in SVL in *Uta stansburiana* is shown by solid circles, with error bars representing 95% CIs and numbers below symbols giving sample sizes. Solid triangles and solid squares show changes in SVL for *Sceloporus merriami* and *Sceloporus undulatus*, respectively. Species-specific regressions of body mass on SVL (the range of reproductive adult body sizes in parentheses) translate length change into mass change (the variable modeled in Shine and Schwarzkopf 1992). Note that changes in length greater than 1 mm represent mass changes greater than the mass changes modeled by Niewiarowski and Dunham (1994). Each single transition in reproductive status (values on the x-axis) represents a period when reproduction is concurrent with growth.

lengths (SVLs) entail growth in mass roughly twice the growth simulated in the Niewiarowski and Dunham (1994) implementation (Fig. 4).

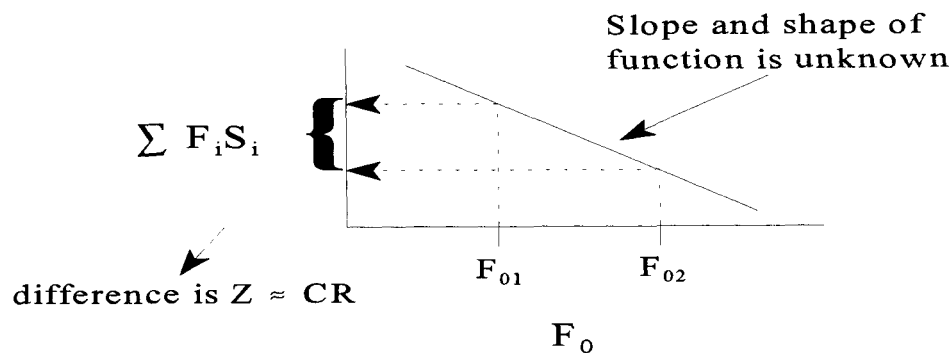
Overall, data we have presented demonstrate that some lizards are capable of concurrent growth and reproduction of a magnitude that would drastically change the predictions of the Shine and Schwarzkopf (1992) model. Unfortunately, our data do not allow us to infer the generality of the pattern. Nevertheless, although the species considered here certainly represent a limited sample, we would not characterize any as being highly unusual lizards in other respects. In the absence of contradictory data, we reject the assertion of Shine et al. (1996) that squamates are unlikely to be capable of such growth.

#### Constant Offspring Size

Niewiarowski and Dunham (1994) drew on three sources of evidence suggesting that Shine and Schwarzkopf (1992) should explicitly examine the sensitivity of their model to offspring size variation and size-number trade-offs. The first source is empirical: Offspring size may be variable within and among females of a population (see Kaplan and Cooper 1984). The second source is a body of theoretical work that questions classical optimal offspring size-number models that assume optimal offspring size is independent of total investment made by a female to reproduction. Models like those of Parker and Begon (1986) and McGinley (1989) show that optimal offspring size is not necessarily independent of the total level of parental investment if the assumption of temporal and spatial constancy of offspring size-fitness functions

$$E = \frac{F_0}{\sum_{i=1}^{\infty} F_i S_i} \quad \text{Williams (1966)}$$

effort ( $E$ ) is a measure of current reproduction ( $F_0$ ) relative to expected future reproduction. The change in future reproduction  $\sum F_i S_i$  given by the change in current effort  $F_0$ , shown below:



$$\Delta F_0 = F_{02} - F_{01}$$

$Z$  is the cost of reproduction (CR)

$$\therefore Z(\Delta F_0 = CR)$$

FIG. 5. Reproductive effort (RE) as defined by Williams (1966), and an expression for cost of reproduction (CR) derived from the concept of CR described by Williams. Note that CR and RE are not equivalent.

is relaxed. The implication of these models is that if there is a correlation between clutch size and offspring survival that is independent of offspring size, per se, then maternal investment and the offspring size-number trade-off may not be independent. Shine et al. (1996) refer to the mechanisms incorporated into the models by McGinley (1989) and Parker and Begon (1986) as "restrictive." Two points are important. First, if Shine et al. (1996) reject the specific mechanisms as not applying to squamates in general, then they should present data to justify it. Second, scrutiny by Shine et al. (1996) of the specific mechanisms is misplaced because, as argued by Niewiarowski and Dunham (1994), it is the effect the mechanisms achieve that is important (Roff 1992).

Finally, using the basic structure of the Shine and Schwarzkopf (1992) model, Niewiarowski and Dunham (1994) demonstrated that different optimal combinations of clutch size, offspring size, and RCM result from different functions relating offspring size to offspring survival. The goal of the Niewiarowski and Dunham (1994) analysis was to explore the consequences for combinations of offspring size, clutch size and RCM under different regimes relating offspring size variation to offspring survival. Niewiarowski and Dunham's

(1994) two conclusions were that (1) the shapes of the surfaces were different among different functions relating offspring size to survival (i.e., combinations of RCM, offspring size, and clutch size result in different estimates of lifetime reproductive success); and (2) the optimal or maximal combination of the three variables considered jointly was different, again depending upon the function relating offspring size to survival. Niewiarowski and Dunham (1994) suggested that the calculation of the trade-off trajectories might depend on the difference in shapes of the surfaces, as well as the differences in the optimal combination of RCM, clutch size, and offspring size (as well as their consequences for fitness). Niewiarowski and Dunham's (1994) analysis, along with results from models like those of McGinley (1989) and Parker and Begon (1986) that attempt to explain the ubiquity of offspring size variation, argues that the predictions of the Shine and Schwarzkopf (1992) (1992) model should not be considered robust without analysis of the effects of including offspring size. Resolution of this issue will only come from a demonstration that relaxing the assumption that offspring size is constant has no effect on the position of the trajectories.

## DEFINITIONS OF REPRODUCTIVE EFFORT AND COSTS OF REPRODUCTION

Shine et al. (1996) argue that the Shine and Schwarzkopf (1992) model demonstrates that energy allocation measures will provide little insight into evolution of RE in squamate reptiles. Our analysis shows why that interpretation is premature if not incorrect. But the claim that energy allocation measures should be abandoned also stems from confusion about the meaning of CR and RE. Contrary to what Shine and Schwarzkopf (1992) and Shine et al. (1996) state, CR is not the same as RE. In fact, CR is a function of RE. CR is measured in units of fitness and RE is measured in units of energy. The relationship between CR and RE can be derived from Williams (1966): E (reproductive effort), is the ratio of current reproduction to expected future reproduction (Fig. 5). A quantitative expression for CR involves an assumption and a mathematical expression, neither of which were provided by Williams. In the context of Williams's construct, an expression for CR must specify the relationship between the expected future reproduction and current reproduction. For example, we could specify an expression for CR as the magnitude of reduced future expectation of reproduction, Z, attendant upon changing current reproduction ( $F_0$ ) from  $F_{01}$  to  $F_{02}$  (Fig. 5). From this formalism, it is clear that CR and RE are not the same, and that the assertion that the Shine and Schwarzkopf (1992) model demonstrates that energy allocation measures will provide little insight into the evolution of RE is unfounded.

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## AN EVOLUTIONARY ARGUMENT FOR TIME LIMITATION

JAN G. SEVENSTER,<sup>1</sup> JACINTHA ELLERS, AND GERARD DRIESSEN

*Institute of Evolutionary and Ecological Sciences, P.O. Box 9516, NL-2300 RA Leiden, The Netherlands*

<sup>1</sup>E-mail: sevenster@rulsfb.leidenuniv.nl

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Rosenheim (1996) argued that egg limitation is a plausible outcome of the evolutionary process in insects, such as parasitoids, that oviposit on discrete resources. We extend his discussion on egg limitation (exhaustion of the egg supply before death) versus time limitation (death before exhaustion of the egg supply) by assessing their relative incidence. We argue that, in general, natural selection should lead to parasitoids that are predominantly time limited. Hence, parasitoid behavior should usually evolve to maximize the rate of offspring gain. We support our points with a modified version of one of Rosenheim's models.

## COMMENTS ON ROSENHEIM

Rosenheim's (1996) models suggest that a certain fraction of individuals spend their entire egg load before they die and, therefore, that egg limitation is a plausible outcome of evolution. He also suggests that time limitation is the most frequent outcome of evolution. His first model optimizes egg size versus egg number while keeping the total investment in eggs  $R$  and mortality  $\mu$  fixed. This approach has the drawback that a fixed investment into survival *must* be too low for a very poor environment and too high for a very rich