AN EVOLUTIONARY ARGUMENT FOR EGG LIMITATION

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Insect parasitoids and insect herbivores with parasitoid-like biologies (e.g., some fruit flies and seed beetles) deposit eggs in or upon hosts that represent a discrete resource for the development of offspring. As a result, there is an unusually direct link between oviposition behavior and fitness gains for these insects, making them particularly suitable for the development and testing of theory for reproductive behavior, including clutch size (Godfray 1994), sex allocation (Charnov 1982; Wrensch and Ebbert 1993), and evolutionary conflicts between siblings or between parents and offspring (Godfray 1987a; Godfray and Parker 1992; Grbic et al. 1992; Rosenheim 1993; Ode and Strand 1995).

A central question that has arisen during the course of this work is: what is the nature of the trade-off between current and future reproduction? The existence of such a trade-off has been suggested by the observation of clutch sizes smaller than the "Lack clutch size," which is the optimal clutch size when there is no cost of reproduction (Godfray 1987b; Vet et al. 1994). Early theoretical work postulated that the realized lifetime reproductive success of parasitoids was limited by the time available to locate hosts and oviposit. Thus, the trade-off was mediated by the time required to deposit each additional egg within a clutch (Charnov and Skinner 1984, 1985; Skinner 1985). This approach was widely adopted, in large part because a rate-maximizing strategy is amenable to mathematically tractable analyses that yield simple analytical solutions. This approach also had the advantage of familiarity, as it was directly analogous to optimal foraging theory developed for predators (Stephens and Krebs 1986). For many parasitoids, however, the time required to deposit eggs is very small compared with the time required to locate hosts; thus, oviposition time can make only a small and often negligible contribution to the cost of reproduction (Godfray 1994). Other workers have argued, therefore, that the trade-off is unlikely to involve only time (Weis et al. 1983; Iwasa et al. 1984; Parker and Courtney 1984; Begon and Parker 1986; Parker and Begon 1986; Godfray 1987b; Mangel 1987, 1989; Charnov and Skinner 1988; Charnov and Stephens 1988).

An alternate factor that could mediate a cost of reproduction is the cost of the eggs themselves. This cost can take two forms. First, there may be a physiological cost if the energetic outlay required to mature oocytes accelerates senescence (Roitberg 1989; Kirkwood and Rose 1991; Lessells 1991; Tatar et al. 1993). Second, there may be an opportunity cost, because an egg laid on one host cannot be laid on a subsequently encountered (and potentially higher quality)

host. Empirical studies have shown that insect oviposition behavior may change in response to changing egg load, supporting the idea that eggs mediate at least part of the cost of reproduction (Rosenheim and Rosen 1991; Minkenberg et al. 1992; Fletcher et al. 1994; Prokopy et al. 1994; Heimpel and Rosenheim 1995). Nevertheless, many workers continue to argue that egg limitation (defined as the temporary or permanent exhaustion of the supply of mature oocytes) is either extremely rare or completely absent in some parasitoids (Godfray 1987b; Janssen 1989; van Dijken et al. 1991, 1993; Hardy et al. 1992; van Alphen et al. 1992; Visser et al. 1992), and the question has become the focus of debate (Driessen and Hemerik 1992).

One question that has not been posed, but which is central to understanding insect life histories, is whether egg limitation is a plausible outcome of the evolutionary process. Here I construct simple models that predict that egg limitation will be a common component of parasitoid life histories. The prediction of egg limitation is derived from simple assumptions of trade-offs between (1) egg size versus egg number; and (2) resource allocations to somatic maintenance versus reproduction.

Stochasticity in Reproductive Opportunity, Allocation Trade-Offs, and Egg Limitation

Here I develop the logic underlying the thesis that evolution can produce egg limitation. Consider an insect parasitoid that has its full complement of oocytes fully matured upon or shortly after adult eclosion (i.e., a "proovigenic" parasitoid; proovigeny is one of the two major patterns of egg production among insect parasitoids). Reproductive opportunities for the adult parasitoid will vary as a function of host availability and the time available to search for hosts. Each of these factors will vary in time (within and across generations) and space. Almost all insect parasitoids attack other insect hosts, and insect population densities vary (Connell and Sousa 1983). In extreme cases, for parasitoids that attack hosts with "outbreak" dynamics, host density can vary across many orders of magnitude (Barbosa and Schultz 1987). The time available for foraging will also change as a function of weather conditions (e.g., Fink and Völkl 1995) and because of biotic agents that kill presenescent adult parasitoids (e.g., pathogens and predators; Rosenheim et al. 1995). Although rarely studied, predation on adult parasitoids can be intense (e.g., Rees and Onsager 1982). Even mortality in nonrepro-

ductive adults that is attributed to "old age" can occur across a broad range of age classes (e.g., Carey et al. 1995). All of these factors create stochastic variation in reproductive opportunity, making a precise evolutionary matching of egg production with realized reproductive opportunity virtually impossible at the individual level.

Assume, then, that we begin with a population whose members are never egg limited. To achieve this in the face of stochastic reproductive opportunity, virtually all members of the population must have "excess" oocytes; that is, parasitoids must die with mature oocytes remaining in their ovaries. Can this be an outcome favored by natural selection? Resources allocated to excess oocytes make no contribution to realized fitness. Thus, zero egg limitation can only represent an evolutionarily stable state if there is no alternate allocation of the resources present in excess oocytes that would contribute to fitness.

There are at least two widely available alternate allocations of resources that are likely to increase reproductive success. First, the nutrients in excess oocytes could be evolutionarily redirected to other oocytes to produce a smaller number of larger gametes (Berrigan 1991). Larger eggs provide a range of advantages for insects, including higher developmental success rates, more rapid development, and larger offspring size and fecundity (reviewed in Tauber et al. 1991; Fox 1993). Second, the nutrients in excess oocytes could be redirected to enhance somatic maintenance, leading to increased longevity and therefore increased time to locate hosts and oviposit. A large number of studies have demonstrated both phenotypic and genetic trade-offs between reproduction and longevity in insects (Roitberg 1989; Kirkwood and Rose 1991; Lessells 1991; Tatar et al. 1993).

There will therefore be directional selection for producing fewer oocytes. Assuming that the appropriate genetic variation is available, this selection will produce declining fecundity until the proportion of adults that are egg limited becomes sufficiently large to oppose further decreases in fecundity. An evolutionary equilibrium will then exist, with the benefits of larger eggs and/or enhanced somatic maintenance favoring the production of fewer eggs, and egg limitation favoring more eggs. Such a balance cannot exist without some fraction of the population being egg limited. Thus, egg limitation is a predictable outcome of the evolutionary optimization of resource allocations.

Egg Limitation as a Result of the Trade-Off between Oocyte Size and Number

The verbal arguments presented above can be translated into mathematical terms that allow us to explore quantitatively the predictions for egg limitation. In particular, the goal will be to contrast the expected incidence of egg limitation given variable opportunities to reproduce under the assumptions of (a) fixed oocyte size versus (b) oocyte size that is evolutionarily optimized under a trade-off between oocyte size and number.

Assume that a proovigenic insect parasitoid has a fixed total amount of resources to invest in egg production, R. Eggs of size s are produced, so that total fecundity is R/s. Thus, the production of larger eggs entails a reduction in the total number
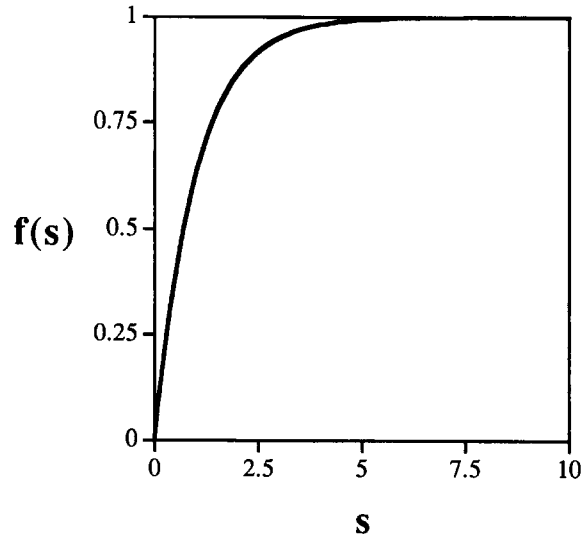

FIG. 1. Relationship between egg size, s, and the fitness of the resulting offspring, f(s).

of eggs that can be produced. Assume further that the fitness of offspring developing from each egg of size s is:

$$f(s) = (1 - e^{-s}). \tag{1}$$

Thus offspring fitness increases with increasing egg size, but at a decelerating rate (Fig. 1). This equation has been used previously to investigate the evolution of gamete size (Bulmer 1994). Stochasticity in reproductive opportunities (i.e., number of ovipositions), which is a key element of the verbal argument presented above, can be introduced most easily by assuming probabilistic (stochastic) mortality during the adult stage. Host availability may then be assumed to be fixed (deterministic). Thus, let parasitoids encounter a constant number of hosts per day, k, and deposit one egg per host. Again to retain the maximum simplicity in the model, assume that adult parasitoids experience a constant daily mortality rate, μ. Thus, the proportion of adult parasitoids surviving to age x is:

$$p(x) = e^{-\mu x}. \tag{2}$$

Fitness can only be accrued by adult parasitoids prior to exhausting their egg supply, which occurs at age R/sk. We can then express the expected lifetime reproductive success, LRS, of each adult parasitoid as:

$$LRS = \int_0^{R/s \cdot k} e^{-\mu \cdot x} \cdot k \cdot (1 - e^{-s}) \, dx. \tag{3}$$

$$LRS = (k/\mu)(1 - e^{-s})[1 - e^{-(\mu R/sk)}]. \tag{4}$$

Equation (4) can be solved numerically for the egg size, s^*, that maximizes lifetime reproductive success (see also Begon and Parker [1986] who analyzed a similar model to investigate optimal age-dependent changes in egg size). Assuming that parasitoids produce this optimal egg size, the proportion of adult parasitoids that are expected to become egg limited is then simply the proportion living to reach age R/s^*k:

$$p(R/s^*k) = e^{-\mu R/s^* k}. \tag{5}$$

The predictions of this model can be explored readily with

an example (Fig. 2). The qualitative results of the model are the same as long as values for R and μ are chosen such that s^* falls in a range where $f(s)$ is still sensitive to s (i.e., $s <$ 5); that is, we must retain a real fitness benefit for offspring developing from larger eggs. Figure 2 plots predictions for R = 10 and μ = 0.1 (such that half of all adults die within the first 6.9 days of their adult lives). Optimal oocyte size declines as host availability, and thus lifetime opportunities to oviposit, increase (Fig. 2a, b). As a result, even as host availability varies over two orders of magnitude (k ranges from 0.2 to 20), the proportion of parasitoids predicted to be egg limited never declines below 0.1 and never exceeds 0.8 (Fig. 2c). This can be contrasted with the proportion of individuals predicted to experience egg limitation when adopting a fixed oocyte size, rather than allowing oocyte size to be evolutionarily adjusted. If parasitoids adopt a fixed oocyte size of s = 2.23 (the large oocyte size that is optimal when k = 0.2) across all values of host availability, rates of egg limitation are quite high, reaching 0.98 when k = 20. Conversely, if parasitoids adopt a fixed oocyte size of s = 0.22 (the small oocyte size that is optimal when k = 20), rates of egg limitation are extremely low (0.0000–0.0001) when host availability is low to moderate (0.2 $\leq k \leq$ 0.6); these are the low rates of egg limitation that have been argued for previously. In this model of constant rates of host contact, low rates of egg limitation are produced only when parasitoids do not adjust their oocyte size upward in the face of limited host availability.

My conclusion that optimal shifts in egg size will produce intermediate levels of egg limitation appears at first to conflict with results presented by Begon and Parker (1986), who concluded from their analysis of optimal age-dependent shifts in egg size that the probability of butterflies living to lay all possible eggs might be quite small. However, they obtained this result only when fitness increments from additional increases in egg size were almost zero.

In summary, this model predicts that parasitoids adopting a fixed egg size may experience extremely low (indeed, near zero) probabilities of egg limitation, but that parasitoids that optimize the trade-off between egg size and egg number will experience intermediate levels of egg limitation. This result is consistent with the verbal model developed above.

Egg Limitation as a Result of the Trade-Off between Reproduction and Somatic Maintenance

The model can be modified to incorporate a trade-off between reproduction and somatic maintenance. For simplicity, assume that offspring fitness is independent of oocyte size, and let s = 1 so that R can be thought of as the total number of oocytes produced. Assume that the mortality rate is a linear function of the total investment in reproduction:

$$\mu = aR, \tag{6}$$

where a is some constant. Equation (3) can then be rewritten:

$$LRS = \int_0^{R/k} e^{-a \cdot R \cdot x} \cdot k \, dx \tag{7}$$

$$LRS = (k/aR)[1 - e^{-(aR^2/k)}]. \tag{8}$$

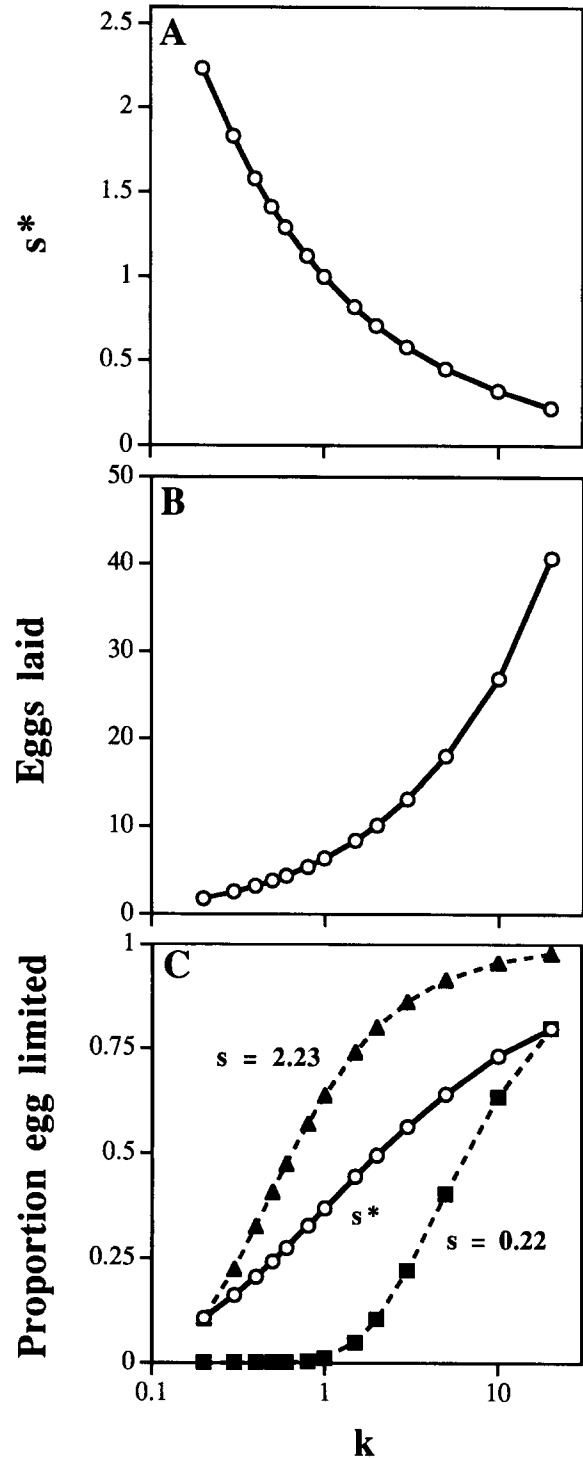Equation (8) can be solved numerically for the investment

FIG. 2. The evolution of egg limitation when oocyte size influences the fitness of offspring and there is a trade-off between oocyte size and oocyte number. Influence of host availability (k, the number of hosts encountered per day) on: (A) the optimal oocyte size (s^*); (B) the mean lifetime number of eggs laid per female that produces oocytes of optimal size; and (C) the proportion of females that become egg limited (i.e., deposit all of their eggs before dying). In panel (C) levels of egg limitation are plotted for females that produce the optimal oocyte size (circles), a fixed oocyte size of 2.23 units (triangles), and a fixed oocyte size of 0.22 units (squares).

in reproduction, R^*, that maximizes lifetime reproductive success. Assuming that parasitoids make this investment, the proportion of adult parasitoids that are expected to become egg limited is the proportion living to reach age R^*/K:

$$p(R^*/k) = e^{-aR^{*2}/k}. \qquad (9)$$

It can be shown that the solution to Equation (9) is independent of k (Appendix A). A representative solution is presented in Figure 3 for a = 0.01 and for k ranging from 0.2 to 20. The optimal investment in reproduction, R^*, increases with increasing host availability (Fig. 3a). Despite the fact that increasing R is associated with greater mortality rates, lifetime reproductive success also increases as host availability and R increase (Fig. 3b). The proportion of adults predicted to experience egg limitation is constant (at a value of 0.285). As in the earlier model, this outcome can be contrasted with the proportion of individuals predicted to experience egg limitation when adopting a fixed investment in reproduction, rather than allowing R to be evolutionarily adjusted. If parasitoids adopt $R = 5.01$ (the small investment in reproduction that is optimal when $k = 0.2$) across all values of host availability, levels of egg limitation are high, reaching 0.99 when $k = 20$. Conversely, if parasitoids adopt a fixed reproductive investment of $R = 50.13$ (the large investment that is optimal when $k = 20$), rates of egg limitation are very low (0.000–0.007) over most of the range of host availability considered (0.2 ≤ k ≤ 5). Again, these are the low rates of egg limitation that have been argued for by previous authors. Under this model, they are only predicted to occur when parasitoids do not allocate excess resources away from reproduction and to somatic maintenance.

In summary, this model predicts that parasitoids adopting a fixed investment in reproduction may experience near zero probabilities of egg limitation, but that parasitoids that optimize the trade-off between allocation to reproduction versus somatic maintenance will experience intermediate levels of egg limitation. This result is again consistent with the logic developed in the purely verbal model.

DISCUSSION

If parasitoid life histories are shaped by natural selection, then egg limitation appears to be a plausible result. Natural selection cannot produce a perfect matching of oocyte production with realized oviposition because of stochastic variation in reproductive opportunity. Given competing demands for nutrients allocated to oocytes (under a trade-off between the number and size of oocytes or between reproduction and somatic maintenance), the optimal compromise is one in which members of the population face an intermediate risk of exhausting their oocyte supply.

The logical structure of the model developed here is directly analogous to that developed for the evolution of senescence by Kirkwood and Rose (1991). Senescence may occur because of stochastic variability in age-independent mortality factors, coupled with competing demands for resources allocated to somatic maintenance.

How broad is the applicability of the argument for egg limitation? Although the arguments are (perhaps) most transparent for proovigenic parasitoids, the thesis was originally
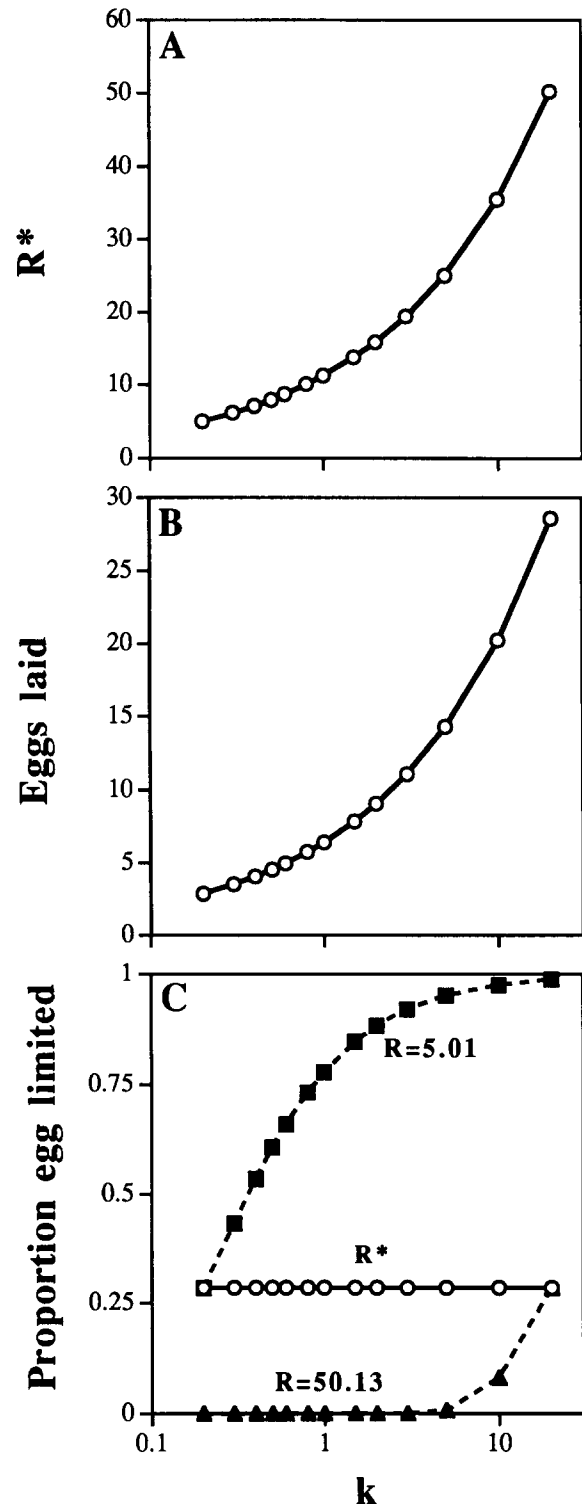

Fig. 3. The evolution of egg limitation when there is a trade-off between reproduction and somatic maintenance (oocyte size is assumed to be fixed). Influence of host availability (k, the number of hosts encountered per day) on: (A) the optimal investment of resources in reproduction (R^*); (B) the mean lifetime number of eggs laid per female that makes the optimal investment in reproduction; and (C) the proportion of females that become egg limited (i.e., deposit all of their eggs before dying). In panel (C) levels of egg limitation are plotted for females that make the optimal investment in reproduction (circles), a fixed investment in reproduction of 5.01 units (squares), and a fixed investment in reproduction of 50.13 units (triangles).

developed through a consideration of parental investment by nest-building wasps, bees, and ants (Rosenheim et al. 1996). Empirical studies of reproduction by parasitoids and the closely related nest-building Hymenoptera have produced evidence for egg limitation in natural populations (reviewed by Rosenheim et al. 1996). Furthermore, there is abundant comparative evidence for large shifts in egg size as a function of reproductive opportunity: species that may have opportunities to oviposit in rapid succession (e.g., parasitic forms) have a larger number of ovarioles and produce a larger number of smaller eggs (Price 1973), whereas species that oviposit only at widely spaced intervals (e.g., because of the need to build and provision nest cells) produce a small number of potentially quite large oocytes (Iwata 1964; Michener 1971; Maeta 1978; Alexander and Rozen 1987; Sugiura and Maeta 1989). Evolutionary trends towards the production of larger eggs has proceeded to quite spectacular extents in some groups, such as the carpenter bees in the genus *Xylocopa*, which may produce eggs that are 12.5–16.5 mm long, more than 50% of their body length (Iwata 1964).

The nest-building Hymenoptera and many parasitoids are synovigenic; that is, they continue to mature oocytes as adults. Synovigenic species may experience transient periods of egg limitation, when oviposition rates temporarily outstrip egg maturation rates. For these species, the evolutionary problem is not to adjust total fecundity (as was the case for proovigenic species), but rather to adjust the maximum rate of egg production (Charnov and Skinner 1988). As long as there is some trade-off between the maximum attainable oocyte maturation rate and other fitness components (such as oocyte size or allocations to somatic maintenance), the argument developed here remains essentially the same.

Thus, nontrivial levels of egg limitation appear to be a predictable aspect of animal life histories when the following conditions are met: (1) oocytes are sufficiently large that their cost of production is not negligible; (2) opportunities to deploy the eggs are shaped by stochastic factors, preventing a precise matching of oocyte production with realized lifetime oviposition; and (3) trade-offs exist between the allocation of resources to egg production and other allocations that contribute to fitness. These conditions appear likely to be met by a broad array of animal groups. Thus, a constraint on realized lifetime reproductive success by either a temporary or permanent exhaustion of mature oocytes may be widespread, and the risk of egg limitation may be expected to influence reproductive behavior in these animal groups even when a finite store of oocytes remains (e.g., Iwasa et al. 1984; Mangel 1987; Heimpel and Collier in press).

ACKNOWLEDGMENTS

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Corresponding Editor: J. Curtsinger

APPENDIX A

In this Appendix, I demonstrate that the incidence of egg limitation predicted by equation (9) is independent of host availability, k. The value of reproductive investment that maximizes lifetime reproductive success (R^*) is obtained by differentiating equation (8) with respect to R, setting the result equal to zero, and solving for R:

$$d(\text{LRS})/dR = 2e^{-(aR^2/k)} + (k/aR^2)[e^{-(aR^2/k)} - 1] = 0. \qquad (A1)$$

Equation (A1) cannot be solved for R in closed form. Note, however, that the parameters a, R, and k do not independently determine the optimal life history. Rather, they always appear together as aR^2K (or its inverse) in equation (A1) and equation (9). Letting $y = aR^2K$ and substituting into equation (A1) gives

$$2e^{-y} + 1/y(e^{-y} - 1) = 0 \qquad (A2)$$

Simplifying yields

$$e^y = 2y + 1. \qquad (A3)$$

Equation (A3) cannot be solved for y in closed form (neither Mathcad nor Mathematica could produce a symbolic solution). It can be shown graphically that equation (A3) has a two solutions, one that minimizes LRS (at y = 0) and one that maximizes LRS (at $y^* = 1.26$; Fig. A1). Thus, parasitoid lifetime reproductive success is maximized when $aR^2K = y^*$ assumes a single, fixed value. Equation (9) must, therefore, also have a single, constant solution. For any value of the constant a in equation (9), changes in k are balanced by changes in R such that a constant proportion of parasitoids is expected to become egg limited.
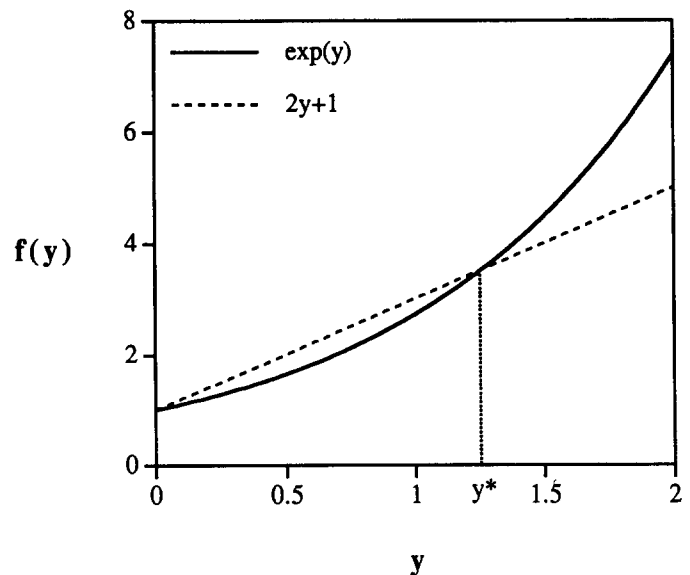

FIG. A1. Graphical solution for equation (A3). The left- and right-hand sides of the equation are both plotted; their intersection (at $y^* = 1.26$) identifies the unique solution that maximizes LRS.