

TO AGE, TO DIE: PARITY, EVOLUTIONARY TRACKING AND COLE'S PARADOX

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The existence of semelparity or “big bang” reproduction (reproducing only once in a lifetime) and iteroparity (reproducing more than once in a lifetime) has led to many questions investigating the evolution or persistence of these strategies. Here we investigate semelparity and iteroparity for their evolutionary importance. A mathematical model is used to illustrate how a population's ability to evolve depends on this life-history trait, and how this rate of evolution impacts the individual. We find that the ability of a trait to evolve is greater toward a semelparous strategy and this expresses a fitness advantage. This leads to an optimality between survival, population tracking ability, and lifetime fecundity.

KEY WORDS: Cole's paradox, evolution, fecundity, iteroparity, life-history, semelparity.

In this article we investigate the relationship between a life-history characteristic, parity, and the ability of a population to evolve to a changing environment. For many organisms, such as for many species of fish, insects, and plants, a single reproductive episode occurs before dying: this strategy is termed as “semelparity.” For others, such as almost all mammals (Smith and Charnov 2001), reproductive episodes are spread over the course of their lifetime: a strategy called “iteroparity.” Evolutionary ecologists have tried to find explanations for this difference in life-history (see Klinkhamer et al. 1997; Tesar 2000 for reviews). The first investigation into these strategies was by Lamont Cole who compared the intrinsic growth rates of semelparous and iteroparous species and concluded: “for an annual species, the absolute gain in intrinsic population growth which could be achieved by changing to the perennial reproductive habit would be exactly equal to adding one individual to the average litter size” (p. 118, Cole 1954). Considering the ease at which an organism could increase offspring number by one, Cole reasoned that se-

lection should favor semelparity. In nature, however, iteroparous species abound; this apparent contradiction between theoretical prediction and natural occurrence has been known as Cole's paradox.

The possible selective advantages of iteroparous strategies were addressed by Murdoch (1966). His study asserts that growth rate is not always the most important factor in the growth and maintenance of a population, and that selective pressure toward an iteroparous strategy would be generated when survival from zygote to first maturity became uncertain. This was also the conclusion of Murphy (1968) and Charnov and Schaffer (1973). Murphy (1968) determined the conditions for coexistence or dominance of either type based on a simple competition model.

Building on previous analytical studies (Cole 1954; Gadgil and Bossert 1970; Bryant 1971; Charnov and Schaffer 1973), Schaffer (1974) includes environmental variation in his model. He concludes that semelparity is favored in a fluctuating environment in which post reproductive survival was uncertain, whereas iteroparity is favored when fecundity became uncertain.

In a fluctuating environment, different strategies can evolve through the option of “bet-hedging” (Hogate 1967; Den Boer 1968; Schaffer 1974; Slatkin 1974; Stearns 1976; Seger and

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Brockmann 1987; Yoshimura and Jansen 1996; Stumpf et al. 2002). Bulmer (1985) studied the evolution of parity under density dependence by adapting Charnov and Schaffer's (1973) model. Compared to a semelparous strategy, the iteroparous strategy is able to spread reproductive effort over time. Thus, by increasing the probability of encountering reproductively favorable conditions, iteroparity is regarded as a bet-hedging strategy.

The evolution of parity has mainly been studied in either constant or highly variable environments. In this article we study the relationship between parity and the rate of evolutionary change in a slowly changing environment (for approaches to measuring microevolution see Hendry and Kinnison 1999; Kinnison and Hendry 2001). How a population tracks the environment through evolution is a subject that has received scarce attention (but see Pease et al. 1989; Lynch and Lande 1993). In these studies the emphasis is on how tracking, or the lack thereof, determines a population's survival.

Here we investigate how far a life-history, such as parity, can influence the evolutionary rate of change of traits and, in particular, what the consequences are for the individual. To do so we formulate a mathematical model, based on Bulmer's (1985) adaptation of Charnov and Schaffer (1973), and use it to compare the evolutionary tracking ability of populations of semelparous and iteroparous individuals. First, we investigate each strategy independently, in isolation, and derive results on evolutionary rates before putting the two types into competition. We explain how the fitness of a secondary trait depends on parity. We also explore how parity evolves, and analyze the importance for lifetime fecundity.

The Model

Following Cole's (1954), Gadgil and Bossert's (1970), and Bryant's (1971) works, Charnov and Schaffer (1973) proposed the following model investigating the question of why perennials (an iteroparous strategy) exist at all. For the annual (a semelparous strategy) species

$$n_a(t+1) = S_a P_s n_a(t); \quad (1)$$

and the perennial species

$$n_p(t+1) = (S_p P_s + P_A) n_p(t) \quad (2)$$

where $n_i(t)$ represents the number of plants of a certain type at time t , and S_i the number of seeds produced per individual. For simplicity we use "seeds" as a surrogate for offspring to maintain consistency with previous papers, and similarly, from hereon "annual" and "perennial" will be the terms representing the semelparous and iteroparous strategies, respectively. Subscripts a and p represent "annual" and "perennial" in the model. P_A is the

adult survival rate, and P_s is the competitive share of safe sites: thus symbolizing the seedling survival probability. Building on Charnov and Schaffer's model, Bulmer incorporates the effects of population dynamics and density dependence on strategy selection. In his model, all seeds compete for unoccupied safe sites through a lottery, thus

$$P_s = \frac{K - P_A n_p(t)}{S_a n_a(t) + S_p n_p(t)}; \quad (3)$$

K being the carrying capacity. The probability of survival depends on the number of spaces made available through adult mortality. This has an equilibrium in which the population is always maintained at carrying capacity (see Appendix A). This result is robust for all combinations of strategies, making the population dynamics entirely tractable.

We begin by studying evolutionary change in the annual and perennial types in isolation, that is without competition. To do so, we first consider evolutionary change in the number of seeds produced before allowing variation in P_A . We therefore subdivide a population that is homogeneous with respect to parity, but in which the population is structured with respect to its seed production: subclass n_i produces S_i seeds. In essence

$$P_s = \frac{K - P_A \sum n_i(t)}{\sum S_i n_i(t)}. \quad (4)$$

To calculate the rate of evolutionary change in this model we must first consider the fitness of a mutant (denoted by " $*$ ") when rare in a resident population. The mutant produces a different number of seeds but is otherwise identical to the resident population. Importantly, resident and mutant have the same parity. The parameter P_s is common to both types

$$P_s = \frac{K - P_A (\sum n_i(t) + n^*(t))}{\sum S_i n_i(t) + S^* n^*(t)}. \quad (5)$$

For a perennial species in isolation, the fitness, W , of a mutant producing S^* seeds in a population producing, on average, $\bar{S}$ seeds, can be found by considering the rate of invasion if the mutant is rare (Metz et al. 1992). This is given by $n^*(t+1) = W(S^*, \bar{S}) n^*(t)$ with

$$W_{(S^*, \bar{S})} = S^* P_s + P_A. \quad (6)$$

If n^* is small, then P_s is determined by the resident population only and is approximately

$$P_s \approx \frac{K - P_A \sum n_i(t)}{\sum S_i n_i(t)}.$$

The total equilibrium population size is $\sum n_i(t) = K$ irrespective of parity (see Appendix A), and hence $P_s \approx (1 - P_A)/\bar{S}$, where

$\bar{S} = \sum S_i n_i / K$ is the average number of seeds produced. Using this we find

$$W_{(S^*, \bar{S})} = \frac{S^*}{\bar{S}}(1 - P_A) + P_A \quad (7)$$

and the marginal fitness, resulting from a small change in the number of seeds produced, is

$$\frac{\partial W_{(S^*, \bar{S})}}{\partial S^*} = \frac{1 - P_A}{\bar{S}}. \quad (8)$$

Note that the marginal fitness for an annual species is also given by equation (8) with $P_A = 0$. This shows that an annual will always have a higher marginal fitness than a perennial producing the same number of seeds during a single reproductive bout. Lynch and Lande (1993) present the importance of additive genetic variance in tracking a changing environment. For now, we here adopt the derivation that evolutionary change is proportional to marginal fitness (Lande 1979; Dieckmann and Law 1996).

EVOLVING TO THE ENVIRONMENT

We determine the ability of a trait, μ , to evolve. To do so we assume fecundity (S) is dependent upon both the state of the environment (E) and maximum fecundity (S_{max}), in such a way that fecundity is maximal when μ matches the environment. We assume S_{max} depends on adult survival

$$S(P_A, \mu) = S_{max}(P_A)e^{-(E-\mu)^2}. \quad (9)$$

The closer μ matches the environment the larger S becomes; hence, a changing environment will cause μ to react and change. In what follows, we consider the evolution of μ and P_A in isolation and, therefore, suppress one of the arguments of $S(P_A, \mu)$.

We can now define fitness with respect to S using a mutant expressing a different trait value μ^* in a population with mean trait value μ . We assume that variance in μ is small such that $\bar{S} = S(\mu)$. Accordingly, the fitness and marginal fitness are, respectively

$$W_{(\mu^*, \mu)} = \frac{S(\mu^*)}{\bar{S}(\mu)}(1 - P_A) + P_A, \quad (10)$$

and

$$\left. \frac{\partial W_{(\mu^*, \mu)}}{\partial \mu^*} \right|_{\mu^* = \mu} = 2(E - \mu)(1 - P_A). \quad (11)$$

The marginal fitness is zero if the trait matches the environment. If the environment is changing, selection will favor variants that have a better match to the environment. Marginal fitness is proportional to $1 - P_A$, hence, an annual has the faster evolutionary response. This is confirmed by simulation in Figures 1 and 2. The reason for the increased tracking ability of a population with a smaller survivorship is that, in such populations, advantageous traits can be established faster than in a population in which individuals take up potential recruitment patches by surviving.

TRACKING LAG

From Figures 1 and 2 it can be seen that a population tracks a changing environment at distance from that environment: a "tracking lag." The rate of change is generally determined by the additive genetic variance (Lynch and Lande 1993). Here we expose the importance of parity in influencing the rate of evolution using the result that the rate of change is also proportional to the marginal fitness (Lande 1979; Dieckmann and Law 1996). This leads to

$$\frac{d\mu}{dt} = 2\lambda(E - \mu)(1 - P_A), \quad (12)$$

where λ is the genetic variance, which scales the rate of evolution of μ (Lande 1979). This parameter will incorporate the effects of population genetical phenomena such as mutation rate, population size, and ploidy on the evolutionary potential. If evolution is mutation limited, the parameter can be interpreted as the product of the mutation rate, the population size, and the width of the mutation kernel (Dieckmann and Law 1996).

If $\tau = dE/dt$, the tracking distance between trait and environment can be described simply

$$\frac{d(E - \mu)}{dt} = \tau - 2\lambda(E - \mu)(1 - P_A). \quad (13)$$

In a constantly changing environment, a tracking population will eventually maintain a constant lagging distance behind that environment (Lynch et al. 1991) (Fig. 2). Here the rate of change of both the environment and trait can be described as being equal. A population's equilibrium tracking lag can be found by setting equation (13) to zero and solving for $E - \mu$, and is given by $\tau/2\lambda(1 - P_A)$.

At equilibrium lagging distance the fecundity is: $S_{max}(P_A) \exp[-(\tau/2\lambda(1 - P_A))^2]$. Adult survivorship constrains the ability to track nearer the environment and thus reduces number of seeds. In extreme cases this could lead to the extinction of the population. This subject has been expounded by Lynch and Lande (1993) using models of genetic variance. They explicitly derive the critical rates of environmental change that will lead to extinction and, as such, will not be discussed in detail here. In the case of a plant with a potentially large number of seeds we deem it unlikely that a tracking lag actually leads to extinction.

LIFETIME FECUNDITY

So far, we have contrasted an annual strategy with a perennial one. In reality, however, one would also expect various perennial strategies living and competing in the same space and selection to occur on the degree of iteroparity (quantified through adult survival, P_A). The model to describe this situation is analogous to equation (3). In Appendix B we give results for an invasion

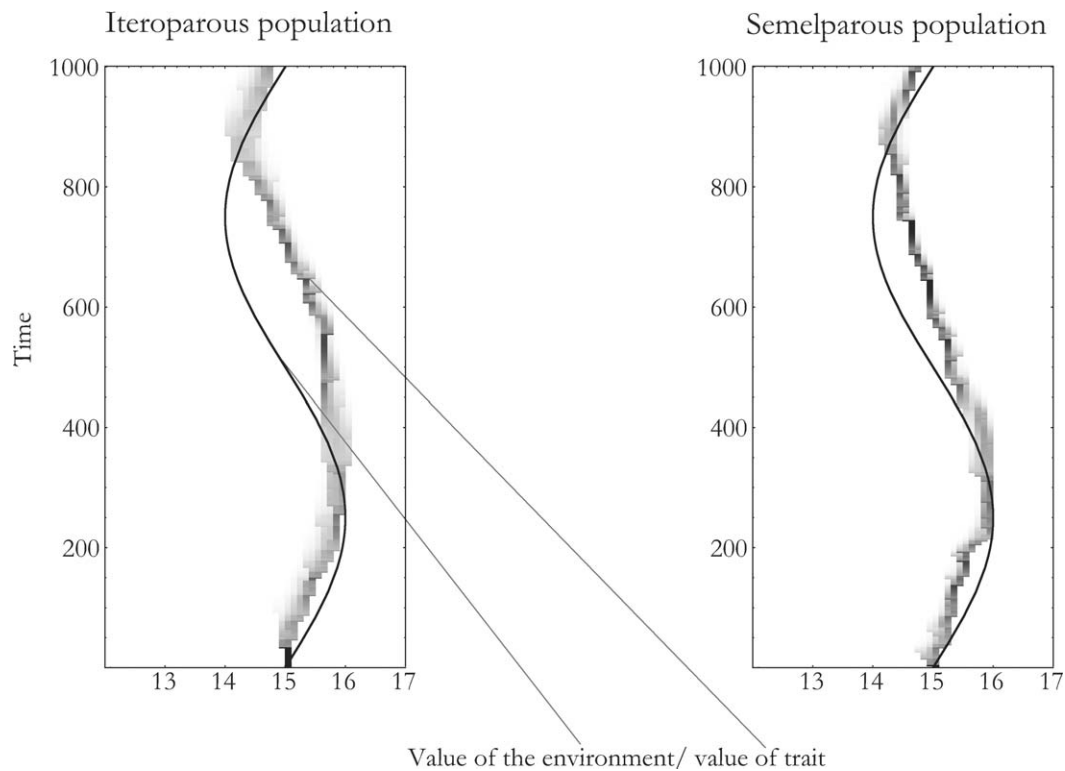


Figure 1. The respective abilities of annual and perennial organisms in tracking a slowly changing environment. An environment was generated and each population was allowed to reproduce over time. For this simulation the population was divided into subpopulations that differed in their value of μ . Subpopulations with a density below a set tolerance level were removed to avoid infinitely small populations. As can be seen, the annual population is better able to match the environment as it changes. This not only means that semelparity allows a greater evolutionary rate but also, by allowing a quicker adaptive rate in its traits, subsequent offspring gain a fitness advantage over their perennial counterparts. This effect is observed over a relatively short time scale. The environment was generated as a single sine wave to be run over the number of generations set. $K = 1000$, mutation rate = 10^{-4} , run over 1000 generations, $P_A = 0.6$ for perennial type only, otherwise $P_A = 0$, tolerance = 10^{-6} .

analysis of the two types in both a linearly and stochastically changing environment.

We now work out how degrees of parity evolve. To do so we must first consider what happens in a constant environment. We consider two types, which differ in their adult survival and their reproductive success, and determine which of these is the likely winner of competition. It is useful to first define lifetime fecundity, or the number of seeds per lifetime, R . To directly compare reproductive strategies we consider $t = 0$ as the first adult year. Thus, for established individuals in a constant environment

$$R = S(P_A) \sum_{t=0}^{\infty} P_A^t = \frac{S(P_A)}{1 - P_A}. \quad (14)$$

Note that species with the same number of seeds per lifetime have the same marginal fitness in equation (8). Also, note that extinction will occur if $R < 1$.

To investigate the significance of lifetime fecundity on competitive ability, consider a rare mutant that differs in its survival

probability (P_A^*), the number of seeds it produces ($S(P_A^*)$), and its lifetime fecundity $R^* = S(P_A^*)/(1 - P_A^*)$:

$$n^*(t + 1) = (S(P_A^*)P_s + P_A^*) n^*(t). \quad (15)$$

Substituting equations (14) and (5) into equation (15) gives the fitness of this mutant: $(1 - P_A^*)R^*/R + P_A^* = 1 + (R^* - R)(1 - P_A^*)/R$. If $R^* > R$ the fitness exceeds unity. From this it is clear that, regardless of parity, whomever possesses the largest R is the dominant competitor. Additionally, it can be seen that any mutation in P_A , which would not lead to a change in R , does not carry any advantage as the term it is contained within would cancel if R and R^* are the same. It shows that, in a constant environment, Cole's paradox boils down to a question of lifetime reproductive success; the type producing most offspring over a lifetime will come to dominate (see Mylius and Diekmann (1995) for how this maximization applies to an invader in a constant environment set by the resident).

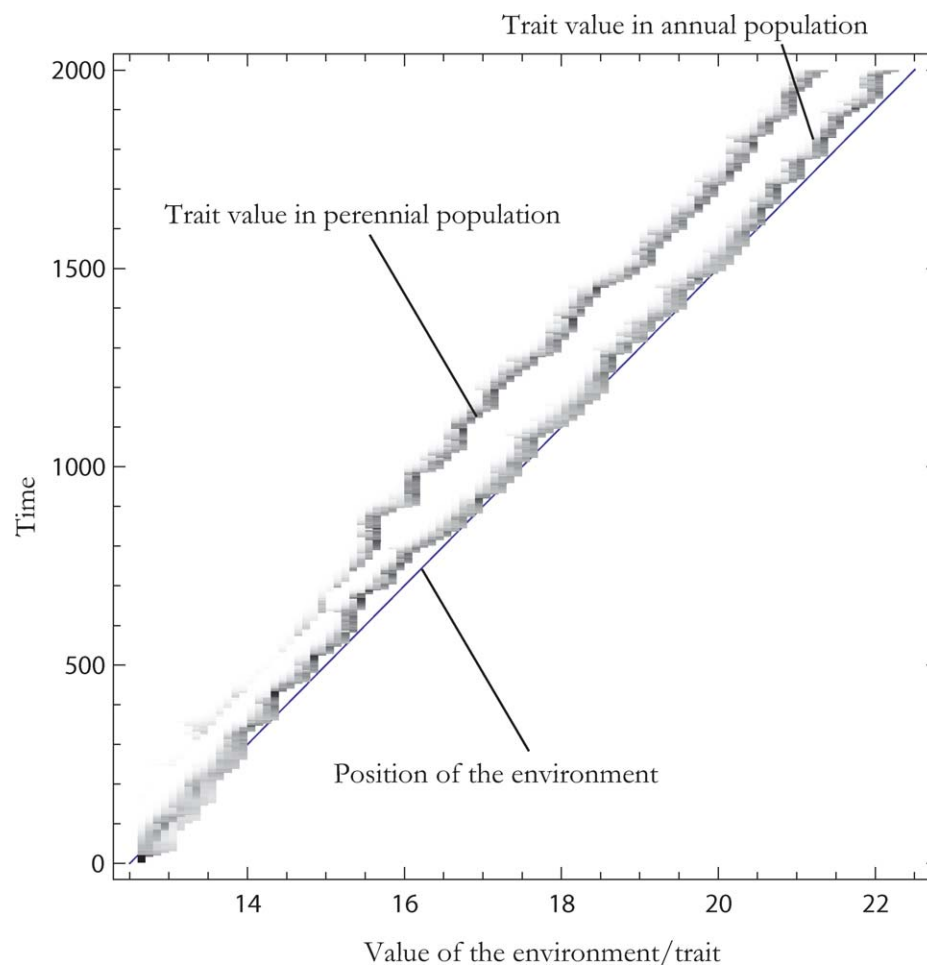


Figure 2. Differences in tracking abilities in a linearly changing environment. After a transient both types track the environmental parameter and maintain an equilibrium distance from the environment. The annual type shows its superior ability to track the environment over the perennial type, and has a bigger reproductive capacity. $K = 20,000$, mutation rate $= 10^{-5}$, run over 2000 generations, $P_A = 0.7$ for perennial type only, otherwise $P_A = 0$, tolerance $= 10^{-6}$.

Having established that the type with the most seeds per lifetime is most competitive, we can now investigate the importance of a slowly changing environment, and thus evolutionary tracking, on lifetime fecundity. Assuming that a species tracks at its equilibrium lag, but otherwise is in equilibrium, the lifetime fecundity is

$$R = \frac{S_{\max}(P_A)e^{-\left(\frac{\tau}{2\lambda(1-P_A)}\right)^2}}{1 - P_A}. \quad (16)$$

This clarifies the nature of adult survival on lifetime fecundity; hindering tracking, yet augmenting lifetime fecundity through survivorship.

If the maximum number of seeds is independent of adult survivorship a trade-off is present, which can result in an optimal survivorship (Fig. 3). In this case, as τ increases, the optimality will shift to decrease adult survivorship, and, thus, toward the annual strategy. If $S_{\max}$ is independent of P_A and if $\tau < \lambda\sqrt{2}$ the

optimal P_A is $1 - \frac{1}{\sqrt{2}} \frac{\tau}{\lambda}$. Even if $S_{\max}$ is dependent on P_A , this optimality argument still holds; provided the dependence is not too strong.

INVASION ANALYSIS

We have demonstrated how survivorship, or parity, affects selection. To demonstrate that the ability of a population to track an environment is important in the evolution of parity, we have simulated a population in which types which differ in parity appear infrequently through mutation (Fig. 4). The maximum number of seeds was chosen to be $S_{\max}(P_A) = 1 - P_A$ so that in a constant environment both types would have identical fecundity. We find in simulations, an annual, which has superior tracking abilities, can invade and dominate a perennial population, whereas the reverse is seldom true. This may be explained by observations of the annual population tracking the environment closer than the outgoing perennial. This demonstrates that tracking ability, although a phenomenon that only manifests itself at the population level,

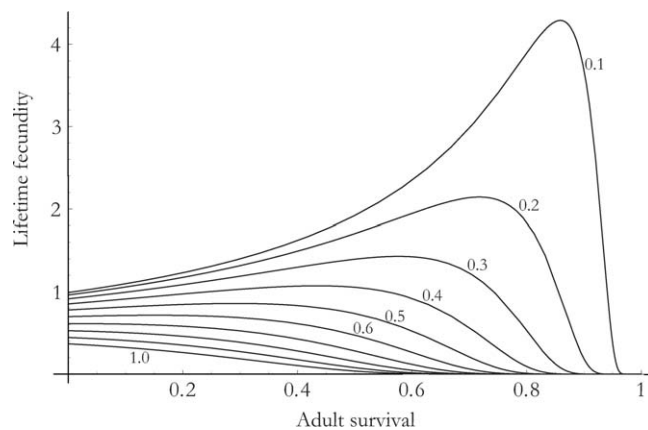


Figure 3. From equation (16) the optimal reproductive strategy in response to the rate of change of the environment, τ , can be deduced. $\lambda = 0.5$.

is a factor of importance in the evolution of parity. At the individual level it appears that this evolutionary ability translates into competitive ability and augments the resident resisting invasion by other types.

The conditions for invasion are given in Appendix B. By combining B3 and B4 (see Fig. 5) we study conditions for mutual invasion. If the environment is constant ($\tau = 0$) the invasion

boundaries coincide. With an increase in τ the distance between the invasion boundaries increases and the area distance between the boundaries increases. For nonzero τ a large area of parameter space is observed where mutual invasion and, thus, coexistence is possible. An annual mutant is able to invade in a larger proportion of parameter space compared to the invasion conditions available for a perennial mutant. This too is one conclusion of Ranta et al. (2000) who also observe mutual invasion and long-term persistence of both types under conditions of periodic and chaotic dynamics. Note that the invasion criteria represent the worst-case scenario for the resident population. If, however, the mutant has the same value for μ as the resident then both invasion boundaries coincide with the invasion criterion for a constant environment ($S_{max}(P_A)/S_{max}(0) = 1 - P_A$). Therefore, in order for a mutation to be beneficial in this scenario a change of μ toward the value of the environment is essential.

Discussion

The evolution of parity has provided much debate since its classification into semel- and iteroparity by Cole (1954). Much of the debate focuses on the maximization of fecundity through risk-benefit arguments, based in essence on the ratios of adult and

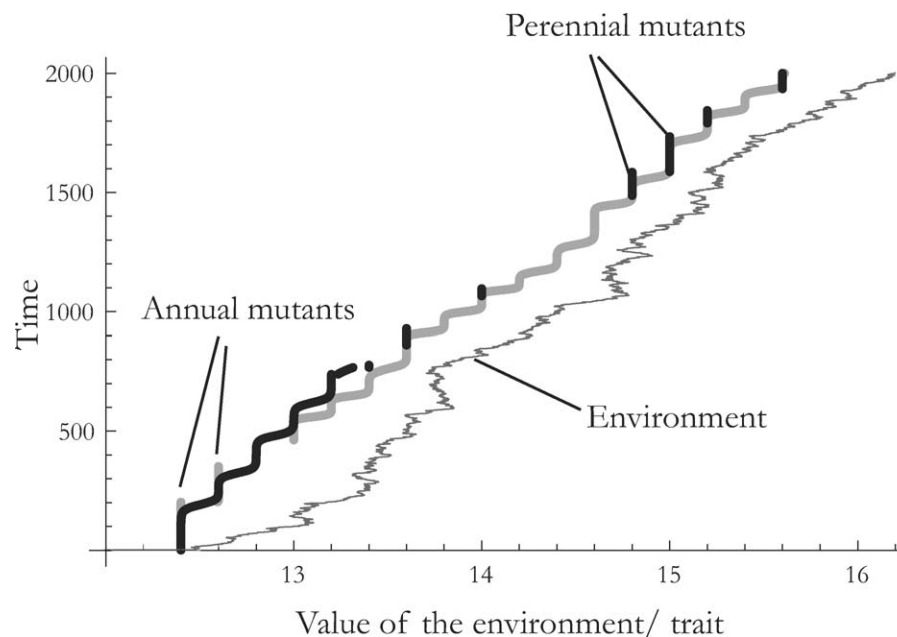


Figure 4. The invasion of a perennial population by an annual mutant. Here a stochastic environment is generated and a perennial (black line) population is resident and tracking the environment. Every time step there is a small probability (10^{-5}) that a perennial individual will give rise to an annual (gray line) mutant or any present annual individual may give rise to a perennial mutant. From this illustration, for $P_A = 0.6$, annual mutants are able to invade a perennial resident populations but not vice versa. In this particular environment the high adult survival of the perennial obviously hinders its ability to track and thus makes it vulnerable to invasion. Conversely, the annuals' tracking ability tracks the environment closely minimizing the risk of perennial invasion for the rest of the simulation. The difference in mutation rate is due to the otherwise too high success of the annual; note, tracking ability nevertheless exceeds that of the perennial. $K = 1000$, run over 2000 generations, mutation rate in μ : 10^{-4} for perennial and 10^{-5} for annual.

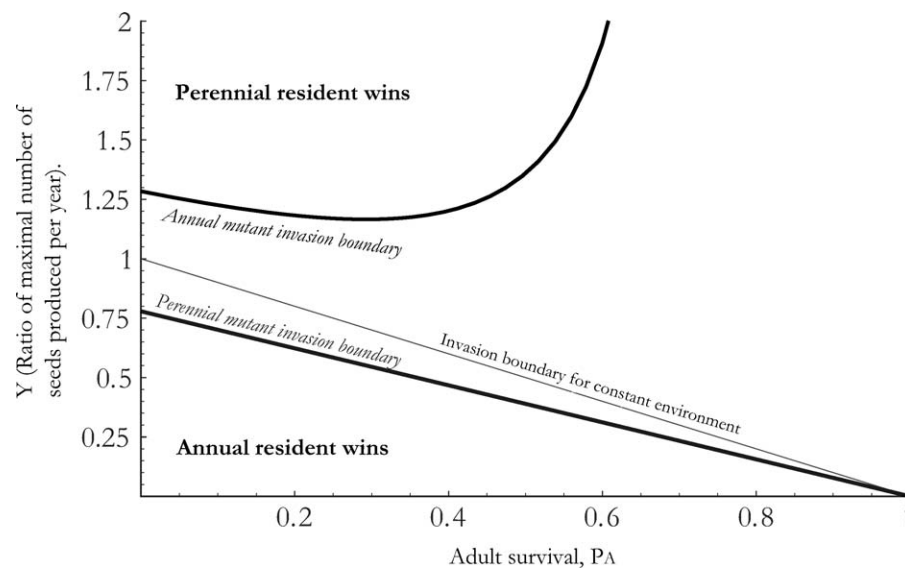


Figure 5. Invasion boundaries for annual and perennial mutants invading a perennial and annual resident population, respectively. The invasion boundary is determined by comparing the maximum number of seeds produced per year, S_{max} , of perennial and annual types using the ratio $Y = S_{max}(P_A)/S_{max}(0)$ (please refer to Appendix B for derivation). A linearly changing environment is assumed in which the resident is at its tracking equilibrium and in which the mutant appears at the worst-case scenario for the resident, that is at the environment. Below the annual mutant invasion boundary an annual mutant can invade a perennial resident and, similarly, above the perennial mutant invasion boundary a mutant perennial can invade an annual resident. Consequently, between both of these boundaries coexistence of both mutant strategies is possible. $\tau = 1$; $\lambda = 1$.

juvenile survival, and resource economics (Iwasa 2000). In this article we take another perspective on the issue of parity with the introduction of evolutionary tracking and lifetime fecundity. We show that tracking the environment is associated with the reproductive success of the individual, and that populations of annual and perennial individuals differ in their ability to evolve a trait. Both analytical derivation and simulations show the annual strategy has the higher rate of change of trait value and, thus, superior tracking abilities.

The evolution of parity is dominated by a single factor: the number of seeds produced per lifetime. The type that has the highest lifetime reproductive success will dominate any population. This result resolves Cole's paradox that emerges under a constant environment in the absence of outside interferences. However, conditions influencing lifetime fecundity, such as those explored in the Introduction, have been put forward as explanations for the success of iteroparous types. Here we have shown that reproductive success is dependent upon the evolutionary properties of a population. A population that tracks a constantly changing environment maintains a constant lagging distance between the state of the environment and the trait value in the population. The higher the adult survivorship, the bigger the tracking lag and the lower the overall fecundity. On the other hand, increased adult survival will generally increase the lifetime reproductive success. Adaptation will tend to lead to a compromise between the ability to track the environment and surviving to reproduce again.

In our model, tracking the environment, a characteristic of the population, expresses a fitness advantage: a characteristic of the individual. We find that in a gradually changing environment there exist perennial strategies that maximize lifetime fecundity through striking a balance between tracking ability and survival. It can be said that in a slowly changing environment iteroparous strategies become more optimal, whereas an environment that changes quickly with respect to the evolution of traits favors strategies toward the semelparous end of the spectrum. How one categorizes a changing environment will, however, be dependent upon the timescale in question; especially at the evolutionary level where short-term fluctuations can effectively be ignored. Within a slowly changing stochastic environment the advantages of tracking become more obvious (Fig. 4).

BET-HEDGING

If annual and perennial types compete in a steadily changing environment, we find that the fitness advantages of tracking the environment shift the invasion boundaries in favor of the annual strategy (Fig. 4). This result differs with those found in an environment that changes unpredictably and rapidly, in which one can expect the effects of bet-hedging to become more prominent. The perennial strategy is able to bet-hedge by surviving to reproduce more than once and thus increasing its chances of encountering a favorable season in which to reproduce. The annual strategy, however, does not bet-hedge, unless one incorporates a seed bank.

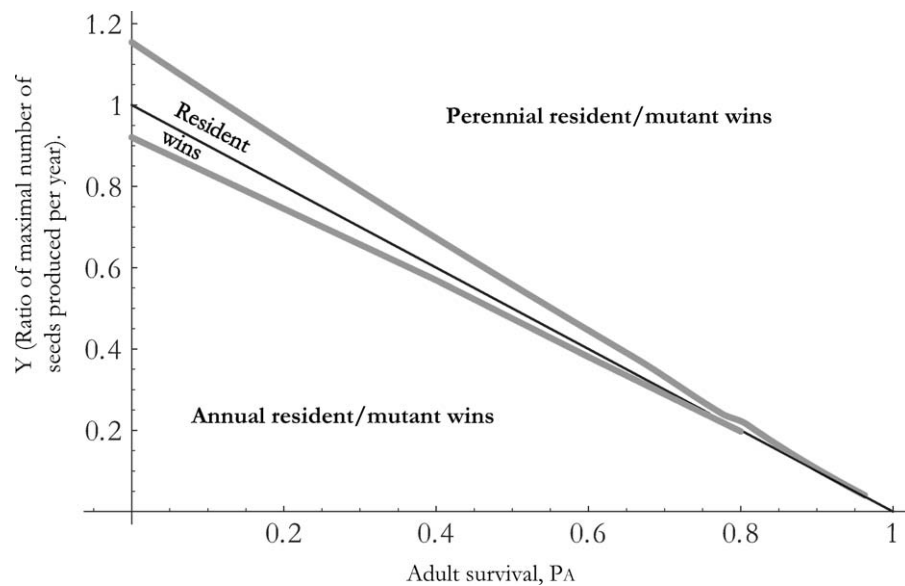


Figure 6. The invasion boundaries for annual and perennial mutants invading a perennial and annual resident population, respectively, in a stochastic environment, and thus, simulating the influence of bet-hedging. Fitness for both types was generated using an identical environment. Y being the ratio of maximal number of seeds produced per year (see figure 5). Thin black line is the invasion boundary in a constant environment. Stochastic environment generated as per Ranta et al. (2000) where $\beta = 0.999$. $K = 1000$, mutation rate = 10^{-5} , run over 7500 generations.

In a fast and randomly changing environment perennials can allow for bet-hedging: a population in which some individuals remain that are not well adapted to the current environment, but in the long run can potentially outgrow a population in which all individuals that are not optimally adapted are culled immediately. For this reason, it is argued that perennial populations potentially can outcompete an annual population in a rapidly and randomly changing environment (Murphy 1968; Schaffer 1974; Bulmer 1985). However, for bet-hedging to occur, the trait values present in surviving members of the perennial population must reside within the range of variation of the changing environment. In rapid, stochastically changing environments we find that the resident, regardless of parity, resists invasion (Fig. 6). An environment in which bet-hedging becomes favorable therefore appears to lead to a situation of bistability. The scenario of competition favoring the more common form can be found in Bulmer's (1985) lottery model. This result is in agreement with the theoretical results derived by Schaffer (1974) and indicates that in a rapidly changing environment bet-hedging prevents coexistence and will favor whichever type is predominant.

The invasion boundaries in a fast-changing stochastic environment are determined. The advantages of tracking, as observed in Figure 5, become less obvious and both parities seem to do well in a rapidly changing, unpredictable environment (Fig. 6). Note that coexistence is not possible, but that annual mutants cannot invade a perennial resident population, and vice versa, leading to a bistable situation. Simulations of the type in Figure 4 move to support this conclusion.

EMPIRICAL EVIDENCE

Experimental evidence to such theoretical conclusions are assumed difficult to obtain considering the probability of finding similar organisms with a suitable short generation time with which to study and compare. The evolution of senescence provides one such example. Why should something that detracts from the fitness of the individual not be selected against (Weissman 1889)? This question stimulates a few theories and Monaghan et al. (2008) give a good broad introduction of this phenomenon. However, this should not detract from efforts to obtain evidence from established wild situations.

Examples of semelparity and iteroparity residing within closely related species (Young 1984; see also Young 1990 for review) and within the same species (Maltby and Calow 1986; Baird et al. 1986) do occur in nature. Young (1990) places the evolution of semelparity, and the demographic divergence of the strategies, on adult mortality rates and time between reproductive efforts; the less hospitable, dry rocky slopes of alpine Mount Kenya supporting the semelparous *Lobelia telekii* compared to *L. keniensis* which tends more to inhabit the moist valleys of lower altitudes with varying degrees of iteroparity. The comparative environmental parameter, E in our model, would be soil moisture in Young's study; varying along a gradient down the mountain and separating the two strategies. μ in such an example would take the form of response to soil moisture content as here the number of seeds per pod for both plants depend on soil moisture content. Both the inflorescence size of *L. telekii* and the number of rosettes per plant of *L. keniensis* positively

correlate with this parameter (Young 1990). The relationship between phenotype and environment appears direct at a nonevolutionary timescale, nevertheless Young (1984) concludes by questioning the involvement of other factors in the evolution of the life-histories of these plants. However, to distinguish between these factors would necessitate a study of evolutionary rates in both populations in response to an environmental parameter, and how fitness and invasion boundaries, according to Y , change in response.

Semelparity and iteroparity existing within the same species has been observed in separate populations of the leech *Erpobdella octoculata* (Maltby and Calow 1986) residing in two Scottish lakes. After suspecting organic pollution to be the cause, Maltby and Calow suggest a genetic basis for the variation in fecundity and post reproduction mortality, and thus investment in reproduction, after this variation persisted in laboratory cultures of the wild populations.

The comparison of closely related organisms with different reproductive strategies can provide empirical evidence to test the hypothesis that parity can evolve to facilitate different tracking abilities. The above studies distinguish the trade-off between reproductive effort and postreproductive survival, a trade-off that is implicit in our model, and detailed as such in the invasion analysis and Appendix B. Semelparity is common when postreproductive survival is low, or time between reproduction is high, thus, reproductive effort is maximized to compensate for lack of future reproduction. In Maltby and Calow (1986) an environmental pressure forces the optimality toward the semelparous strategy in some bodies of water in comparison to others. This could be through simple competition of types (eq. 15) or evolution to an environmental parameter (eq. 16) or a combination of both. This is not to discount, of course, the various intrinsic and extrinsic factors skewing mortality rates. However, Maltby and Calow (1986) conclude a genetic basis to the disparity between their study populations. In our model the parameters affecting lifetime fecundity is the speed of environmental change and extent of adult survival (Fig. 3). This affects the fitness of the individual by determining the phenotypic correlation of offspring to the state of the environment, as well as the number of offspring produced at any one time. Although we should not discount the effects of environmentally induced phenotypic variability (Baird et al. 1986), it is helpful to keep in mind that the ranges of this plasticity must themselves be subject to selection. The degree of parity and plasticity will no doubt be shaped by the stochasticity of fluctuations of the environmental parameters linked to fitness. In our model Figures 5 and 6 show the effects of this stochasticity on invasion boundaries.

We need to further understand the dynamics of environmental parameters and their effects on life-history evolution: what types of environments necessitate the potential for rapid evolu-

tion? Thus, separating mortality rates between the evolution of parity and the effects of demographic pressures would be the critical issue here.

We have shown how parity alters the ability of a population to evolve and how this population level phenomena is intimately linked with the fitness of the individual. We also take another viewpoint on the argument of senescence. We expect many other life-history traits to have a bearing on evolutionary tracking ability and it would be complimentary to concurrently investigate the counterpart view: to what extent the evolution of life-histories depend on evolutionary tracking itself.

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Appendix A

In its most general form, the model of Bulmer (1985) allows for different survival probabilities and fecundities. Assume that there are m different survival probabilities $P_{A,j}$ with $1 < j < m$ and l different fecundities that we will denote S_i with $1 < i < l$. Let the fraction of the population that has survival probabilities $P_{A,j}$ and fecundity S_i be given by $n_{i,j}$, with dynamics $n_{i,j}(t + 1) = (S_i P_s + P_{A,j}) n_{i,j}$ where

$$P_s = \frac{K - \sum_{\forall i} \sum_{\forall j} P_{A,j} n_{i,j}(t)}{\sum_{\forall i} \sum_{\forall j} S_i n_{i,j}(t)}.$$

The population dynamics of this model are simple: the population has a single equilibrium at which the total population size is K irrespective of the choice of fecundity and survival probabilities (provided at least one subpopulation $n_{i,j}$ persists, which requires that $R > 1$).

This can be shown as follows. At equilibrium we find for each persisting subpopulation $\bar{n}_{i,j} = (S_i P_s + P_{A,j}) \bar{n}_{i,j}$. By adding the terms for all persisting subpopulations (using $\bar{n} = \sum_{\forall i} \sum_{\forall j} \bar{n}_{i,j}$) we find

$$\begin{aligned} \bar{n} &= \sum_{\forall i} \sum_{\forall j} (S_i P_s + P_{A,j}) \bar{n}_{i,j} \\ \bar{n} &= P_s \sum_{\forall i} \sum_{\forall j} S_i \bar{n}_{i,j} + \sum_{\forall i} \sum_{\forall j} P_{A,j} \bar{n}_{i,j} \\ \bar{n} &= K - \sum_{\forall i} \sum_{\forall j} P_{A,j} \bar{n}_{i,j} + \sum_{\forall i} \sum_{\forall j} P_{A,j} \bar{n}_{i,j} \\ \bar{n} &= K. \end{aligned} \quad (A1)$$

Appendix B

INVASION ANALYSIS

Here the conditions for invasion of an annual strategy in a population dominated by a perennial type (and vice versa) are analyzed. To do so, first study the worst-case scenario for a resident at its equilibrium tracking lag by introducing a mutant type differing in parity (the mutant is again denoted by “*”) which matches the state of the environment exactly, i.e. $\mu^* = E$. To derive Figure 5 first the invasion boundary for a perennial mutant invading an annual resident is found. With the annual resident at equilibrium $P_s = \frac{1}{S_a} = \frac{e^{(\frac{\tau}{2\lambda})^2}}{S_{max}(0)}$. The fitness of the mutant is:

$$W_{(P_A^*, 0)} = \frac{S_{max}(P_A^*)}{S_{max}(0)} e^{(\frac{\tau}{2\lambda})^2} + P_A^*, \quad (B1)$$

and a perennial mutant population will invade if

$$\frac{S_{max}(P_A^*)}{S_{max}(0)} > (1 - P_A^*) e^{-(\frac{\tau}{2\lambda})^2}. \quad (B2)$$

In a similar way the fitness of an annual mutant in a population dominated by a perennial resident tracking a slowly changing environment at its equilibrium lag is determined. Assuming, once again, the resident perennial population is at equilibrium, and therefore $P_s = \frac{1 - P_A}{S_p} = \frac{1 - P_A}{S_{max}(P_A)} e^{(\frac{\tau}{2\lambda(1 - P_A)})^2}$, the fitness of an annual mutant in a perennial population is

$$W_{0, P_A} = \frac{S_{max}(0)(1 - P_A)}{S_{max}(P_A)} e^{(\frac{\tau}{2\lambda(1 - P_A)})^2} \quad (B3)$$

and, hence,

$$\frac{S_{max}(P_A)}{S_{max}(0)} = (1 - P_A) e^{(\frac{\tau}{2\lambda(1 - P_A)})^2} \quad (B4)$$

is the invasion boundary.