Reply

Critique of directionality theory

Bulmer's critique of directionality theory (Bulmer 2006) can be distilled in terms of two claims. (i) The characterization of equilibrium and opportunistic species in terms of bounded and unbounded growth constraints has little justification as an ecologically meaningful definition. (ii) The Malthusian parameter is the primary variable in the study of life-history evolution—natural selection maximizes the Malthusian parameter and drags the entropy along with it. This article contests and refutes these claims.

Specifically, we provide an analytical argument and give empirical evidence to justify the characterization of equilibrium and opportunistic species in terms of certain bounds on the population growth rate. We also show that the standard model of life-history evolution, based on the Malthusian parameter as the measure of Darwinian fitness, is a limiting case (as population size tends to infinity) of directionality theory. Accordingly, it represents an *approximation*—whose validity increases with population size—of directionality theory. We therefore reaffirm the significance of directionality theory as an evolutionary model of life-history variation and claim that entropy rather than the Malthusian parameter is the appropriate measure of Darwinian fitness, and hence the fundamental concept in the study of life-history evolution.

1. INTRODUCTION

Bulmer (2006), in his critique of directionality theory, writes

The mathematical results that underpin evolutionary entropy and directionality theory appear to be correct, but it is argued here that their biological interpretation is questionable.

(Bulmer 2006, p. 638)

The issues of biological interpretation which the 'critique' raises are embodied in the following two statements.

- (i) The characterization of equilibrium species as having $r < H$ and opportunistic species as having $r > H$ have little justification as an ecologically meaningful definition.
- (ii) The standard model based on the Malthusian parameter is sufficient to explain life-history evolution in large populations—natural selection maximizes the Malthusian parameter which drags the entropy along with it.

This article provides evidence based on analytical and empirical grounds to refute these two claims. We will address the first claim in terms of both an analytical

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argument and an empirical study. These studies show that the analytical bounds $r < H$ and $r > H$ provide a valid and meaningful description of the qualitative notions—equilibrium and opportunistic species, respectively.

We will address the second claim in terms of an analytic study which contrasts the standard model of life-history evolution based on the Malthusian parameter, r , with directionality theory based on evolutionary entropy, H . We will show that the standard model is a limiting case, as population size tends to infinity, of directionality theory. Accordingly, the standard model represents an *approximation*—whose validity increases with population size—to directionality theory. We therefore conclude that entropy rather than the Malthusian parameter is the appropriate measure of Darwinian fitness in structured populations, and hence the fundamental concept in the study of life-history evolution.

2. DIRECTIONALITY THEORY

The dynamics of structured populations can be described in terms of the age-specific fecundity and mortality variables: $\ell(x)$, the chance that a newborn survives to age x ; $m(x)$, the average number of newborn individuals of age 0 produced by an individual of age x (Leslie 1945). A fundamental parameter in this model is the quantity $p(x)$, the probability distribution of the parental age of a randomly chosen newborn individual. Here

$$p(x) = \lambda^{-x} \ell(x) m(x),$$

where λ denotes the dominant eigenvalue of the Leslie matrix.

Evolutionary entropy, H , and the reproductive potential, Φ , are functions of $p(x)$, and are given by (Demetrius 1974)

$$H = -\frac{\sum p(x) \log p(x)}{\sum x p(x)}, \quad \Phi = \frac{\sum p(x) \log \ell(x) m(x)}{\sum x p(x)}. \quad (2.1)$$

These two quantities are related to the population growth rate $r = \log \lambda$, by the identity

$$r = H + \Phi. \quad (2.2)$$

Directionality theory studies the long-term changes in entropy as one population type replaces another under the action of mutation and natural selection. The theory distinguishes between two classes of populations in terms of the intensity of fluctuation in population numbers. Equilibrium species, typically vertebrates and perennial plants, refer to populations which are either stationary or fluctuating around some constant size. Opportunistic species, typically insects and annual plants, describe populations which are subject to large, irregular fluctuations in numbers (e.g. Pianka 1994).

Table 1. Demographic variables for equilibrium and opportunistic species.

taxon	species	r	H	Φ	reference
mammal	<i>Homo sapiens</i> Sweden (1965)	0.024	0.264	-0.240	Keyfitz & Flieger (1968)
mammal	<i>Cervus elaphus</i>	0.058	0.44	-0.38	Lowe (1969)
perennial plant	<i>Pinus palustris</i>	-0.0047	0.037	-0.041	Franco & Silvertown (1996)
insect	<i>Calandra oryzae</i>	0.843	0.23	0.61	Birch (1948)
insect	<i>Tribolium castaneum</i>	1.26	0.27	0.99	Leslie & Park (1949)
annual plant	<i>Poa annua</i>	5.54	0.035	5.5	Begon & Mortimer (1981)

The main tenets of the theory can be qualitatively annotated as follows (Demetrius 1997):

- (I) *equilibrium species*: a unidirectional increase in entropy;
- (II) *opportunistic species (large size)*: a unidirectional decrease in entropy;
- (III) *opportunistic species (small size)*: random, non-directional change in entropy.

The mathematical analysis which underpins the directionality principles revolves around the study of the following three elements:

- (i) *an invasion process*. Conditions for the invasion of a mutant allele in a resident population can be expressed in terms of $\Delta H = H^* - H$, where H^* and H denote the entropy of the mutant and resident, respectively. The invasion criteria are contingent on the ecological constraints as defined by the conditions bounded growth $\Phi < 0$, and unbounded growth $\Phi > 0$ (Demetrius & Gundlach 2000; Demetrius 2001);
- (ii) *the establishment process*. This process models the competitive interaction between the array of genotypes generated by random mating between the invading type and the resident genotype. The central parameter in this class of models is $\tilde{\Delta}H = \tilde{H} - H$, where $\tilde{H}$ is the entropy of the composite population when the system has achieved a new steady state defined by ecological constraints. Analysis of this process shows that (Demetrius 1992)

$$\Delta H \tilde{\Delta} H > 0. \quad (2.3)$$

This equation asserts that *local* changes in entropy ΔH , induced by invasion of new mutants and the *global* changes $\tilde{\Delta}H$, as the population evolves from one steady state to the next are positively correlated;

- (iii) *equilibrium and opportunistic species: a characterization*. Equilibrium and opportunistic species are depicted in terms of the constraints $\Phi < 0$, which implies $r < H$, and $\Phi > 0$, which entails $r > H$, respectively.

3. EQUILIBRIUM AND OPPORTUNISTIC SPECIES

A central feature of Bulmer's critique Bulmer (2006), is directed at the characterization given in item (iii). It is claimed that the representation of equilibrium and opportunistic species in terms of the conditions $\Phi < 0$ and $\Phi > 0$, respectively, has little ecological justification. We now provide an analytical argument and empirical evidence in support of item (iii).

(a) The analytical argument

The analytical argument rests on equation (2.2) and the mathematical fact that evolutionary entropy, H , characterizes demographic stability, and hence constitutes a measure of the intensity of fluctuations in population numbers (Demetrius *et al.* 2004).

Now equilibrium species, we recall, are defined as populations which maintain approximately a constant size ($r \sim 0$), with attendant small fluctuations (H large). Accordingly, the equilibrium condition will be described by $\Phi < 0$.

Opportunistic species, by contrast, are defined as populations which are subject to episodes of rapid population growth (r large), and, concomitantly, large irregular fluctuations in size (H small). Consequently, the opportunistic condition will be described by $\Phi > 0$.

(b) The empirical study

We give in table 1 values for r , H and Φ for selected examples of equilibrium species—two large mammals and a perennial plant, and opportunistic species—two insects and an annual plant. The absolute values of the demographic variables will depend on the scaling—weeks, years or decades—which is used to generate the various life tables. We observe, however, that equilibrium species are all described by $\Phi < 0$, the opportunistic by $\Phi > 0$.

It is important to note that the examples given in table 1 are generic. For example, studies of the French population (1851–1965) and the Swedish population (1778–1965) (Demetrius & Ziehe 1984) show that Φ has remained negative throughout these periods, although both r and H have been subject to significant variations.

4. THE SIMULATION STUDY

The simulations described in Kowald & Demetrius (2005) were intended to illustrate a particular feature of the analytical model, namely, the effects of population size and the conditions—equilibrium and opportunistic—on the long-term changes in entropy. These directional changes will not be highly sensitive to whether the population is haploid or diploid, nor on the demographic dependence of the mutation function. Consequently, the simulation studies assumed an asexual population and a mutation process that affects the life-history schedule in an age-independent way. This is a strong simplification of biological reality. However, the good agreement between the predictions of the analytical model (based on diploid populations and mutations with age-dependent effects) and the simulation study shows that the underlying theory is robust with respect to the effect of the equilibrium and opportunistic conditions on long-term changes in entropy.

Figure 1. Computer simulation showing the change of entropy over evolutionary time. The simulation was started with a large population (10 000 individuals) that consisted of the unbounded genotype 4 and was then performed under constraints of bounded growth. In this simulation the possible mutation step size is substantially larger ($\delta = \pm 0.3$) than in the simulations shown in the original paper.

The simulations were based on four genotypes. Genotypes 1–3 are described by the condition $\Phi < 0$. These genotypes represent equilibrium species. Genotype 4 is described by $\Phi > 0$. It represents an opportunistic species. The mutations imposed have a small step size, in the range of $\delta = \pm 0.1$. This small step size was implemented to take into account that in biological reality a single mutation is unlikely to cause large changes to the genotype. Genotypes 1–3 (equilibrium species) were subject to an evolutionary process under ecological constraints which maintains a constant size or small fluctuations. Genotype 4 (opportunistic species) was subject to evolution under constraints, which induce large fluctuations in size. The outcome of the simulation, an increase in entropy for genotypes 1–3, and a decrease or random, non-directional change for genotype 4, provides strong support for the three principles articulated in directionality theory.

Bulmer does not contest this observation. He asserts, however, that ‘a closer analysis leads to some questions’. He writes:

If the first set of simulations (mimicking an equilibrium species) had been started from genotype 4, the entropy would have decreased to zero, if the second set of simulations (mimicking an opportunistic species) had been started from one of the three genotypes, the entropy would have increased to 0.68.

(Bulmer 2006, p. 638)

The above scenario is of a different character from that which was carried out in the original simulation. However, it is of interest, since if the outcome were inconsistent with the predictions of the theory, this would be cause for concern.

We have carried out the simulation as suggested. The model distinguishes between mutations with small effects, assumed typical, and mutations with large effects, assumed rare and atypical. The results we obtain are given in figures 1 and 2.

Figure 2. Computer simulation showing the change of entropy over evolutionary time. The simulation was started with a large population (10 000 individuals) that consisted of the bounded genotype 1 and was then performed under constraints of unbounded growth. For this simulation a mutation step size of $\delta = \pm 0.2$ was used.

The long-term behaviour of a population depends both on the genotype as well as on the constraints that are used to mimic certain environmental conditions. One of the constraints that is imposed by bounded growth conditions is that new mutants have to be of the bounded genotype (to prevent switching between genotype classes during our simulation run). However, with a small mutation step size of $\delta = \pm 0.1$ (the typical situation), which we used to run our simulations, it is impossible to generate mutants with bounded genotype from the unbounded genotype 4. However, for mutations with a larger step size of $\delta = \pm 0.3$ (the atypical condition), switching of genotypes may occur. Accordingly, mutants with bounded genotypes can now originate from genotype 4. The simulation then proceeds with mutations of small step size under bounded growth conditions. As figure 1 shows, entropy increases. *It does not drop to zero as claimed.*

Similarly, if genotype 1 (equilibrium species) is now used as the starting genotype in a simulation mimicking unbounded growth constraints, the simulation procedure stops if mutation step size is in the range $\delta = \pm 0.1$. However, for mutants with large step size, say in the range ± 0.2 , switching will occur. The simulation then proceeds with mutations of small step size. As figure 2 shows, entropy decreases. *It does not increase as claimed.*

The trends in entropy for the opportunistic and equilibrium species, as described in figures 1 and 2, are consistent with the principles established by the analytical theory.

5. DARWINIAN FITNESS: ENTROPY OR THE MALTHUSIAN PARAMETER?

As a conclusion to his critique, Bulmer writes:

The theory of life-history evolution, at least in a deterministic context, should continue to be studied in the traditional way by maximizing the Malthusian parameter in models taking biological constraints and tradeoffs into account.

(Bulmer 2006, p. 639)

We will assess the validity of this assertion by contrasting the standard model of life-history evolution with directionality theory. The standard model rests on the claim that the invasion dynamics of a mutant allele is

a *deterministic* process regulated by the Malthusian parameter, r . Selective advantage in this model is given by

$$s = \Delta r. \quad (5.1)$$

Directionality theory rests on the mathematical fact that the invasion dynamics of a mutant allele is a *stochastic* process which is regulated by evolutionary entropy. Selective advantage in this context can be expressed in terms of the Malthusian parameter, r , the demographic variance, σ^2 , and the population size, N . According to Demetrius & Gundlach (2000) it holds that

$$s = \Delta r - \frac{1}{N} \Delta \sigma^2. \quad (5.2)$$

Now when $s > 0$, invasion occurs; and when $s < 0$, extinction prevails. Accordingly, equation (5.2) can be invoked to derive invasion–extinction criteria in terms of the demographic variables Δr , $\Delta \sigma^2$ and N . Invasion criteria expressed in terms of the change in entropy ΔH , and the demographic constraints defined by the conditions $\Phi < 0$, $\Phi > 0$, can be inferred from equation (5.2). The entropic criteria derive from the following set of correlations between Δr , ΔH and $\Delta \sigma^2$ (Demetrius 2001):

$$\Phi < 0 \Rightarrow \Delta r \Delta H > 0; \quad \Phi > 0 \Rightarrow \Delta r \Delta H < 0; \quad \Delta H \Delta \sigma^2 < 0.$$

Now from equation (5.2), we observe that as $N \rightarrow \infty$, the selective advantage, given in terms of r , N and σ^2 , reduces to equation (5.1). This implies, as stated in Demetrius (2001), that the invasion criteria based on the Malthusian parameter are the limit ($N \rightarrow \infty$, N being population size) of the invasion criteria that describes the entropic model.

These observations indicate that the standard model is an *approximation* to directionality theory. The validity of the approximation increases with population size. *All* populations have finite size. We therefore conclude that the directionality theory and not the standard model is the appropriate system for the study of evolutionary processes in structured populations.

6. CONCLUSION

Directionality theory integrates population genetics, demography and ecology to give an analytical model of the evolutionary process by mutation and natural selection. The theory is structured around a mathematical fact: the rate at which a population returns to its original size after a perturbation—its demographic stability—predicts the outcome of competition between a rare mutant and the resident type. Demographic stability is analytically characterized by evolutionary entropy, hence entropy describes Darwinian fitness.

Support for the validity of the analytical theory has come from both computational (Kowald & Demetrius 2005) and empirical studies (Ziehe & Demetrius 2005). Bulmer's critique has invoked the computational study to question the biological interpretation of the tenets of the theory and to argue for the primacy of the standard model based on the Malthusian parameter. Our rebuttal of Bulmer's critique rests on the analytical fact that the standard model represents an approximation—whose validity increases with population size—of directionality

theory. We therefore refute the alleged primacy of the standard model and contend that directionality theory is the more general model for the study of life-history evolution.

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