A critique of directionality theory

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Directionality theory suggests that demographic entropy, defined in a way analogous to thermodynamic entropy, is as important as the Malthusian parameter in determining life history evolution in an age-structured population. In particular, it suggests that entropy should increase in equilibrium species and decrease in opportunistic species. This theory has been applied to explain the evolution of body size and of senescence. It has been claimed recently that this theory has been validated by a simulation study, but it is argued here that this study reveals substantial flaws in directionality theory and that the Malthusian parameter rather than entropy is the appropriate tool in the study of life history evolution.

Keywords: directionality theory; demographic entropy; Malthusian parameter; life history evolution

1. INTRODUCTION

Lloyd Demetrius and his collaborators have over the past 30 years developed the concept of the entropy of an age-structured population, defined as an analogue of thermodynamic entropy, and have argued that it is as important as the Malthusian parameter in understanding life history evolution (Demetrius 1974, 1975a,b, 1977a,b, 1978, 1989, 1992, 1997, 2000a,b, 2001; Demetrius & Gundlach 1999; Demetrius *et al.* 2004; Kowald & Demetrius 2005; Ziehe & Demetrius 2005). The earlier papers concentrate on the maximization of entropy, but since 1992 the idea has been refined in the assertion that entropy is maximized in equilibrium species and minimized in opportunistic species. This is called directionality theory and it has been used to explain the evolution of body size and of senescence (Demetrius 2000a, 2001). The purpose of this note is to examine the validity of this theory, with particular reference to the simulation study published recently in this journal (Kowald & Demetrius 2005).

The Leslie model of growth in age-structured populations in discrete time will be used; similar results hold in the corresponding continuous time model. Suppose that the maximum lifespan is ω , and that $n(x, t)$ is the number of individuals of age x in year t ($x = 1, \dots, \omega$), $P(x)$ is the probability that an individual aged x will survive for 1 year ($x = 0, \dots, \omega - 1$), and $m(x)$ is the average number of newborn individuals of age 0 produced by an individual of age x ($x = 1, \dots, \omega$). In a sexual population only females are counted on the assumption of female reproductive dominance. If $\mathbf{n}(t)$ is the vector of the numbers of individuals of different ages (from 1 to ω) in year t , it satisfies the recurrence

$$\mathbf{n}(t + 1) = \mathbf{L}\mathbf{n}(t), \quad (1.1)$$

where $\mathbf{L}$ is the Leslie matrix having $P(0)m(1)$, $P(0)m(2)$, ..., $P(0)m(\omega)$ in the first row, $P(1)$, $P(2)$, ..., $P(\omega - 1)$ immediately below the leading diagonal, and zero everywhere else. Hence

$$\mathbf{n}(t) = \mathbf{L}^t \mathbf{n}(0). \quad (1.2)$$

The Leslie matrix usually has a unique dominant eigenvalue λ satisfying

$$\sum_{x=1}^{\omega} \lambda^{-x} l(x) m(x) = 1, \quad (1.3)$$

where $l(x) = P(0)P(1) \cdots P(x-1)$ is the chance that a newborn survives to age x . After a sufficiently long time

$$n(x, t) = \text{const.} \quad \lambda^t [\lambda^{-x} l(x)]. \quad (1.4)$$

This says that the number of individuals in each age class increases geometrically each year at rate λ and that the stable age distribution, the frequency of individuals aged x , is proportional to $\lambda^{-x} l(x)$.

The theory of life history evolution in age-structured populations is usually considered in terms of the geometric rate of increase λ or of its natural logarithm, $r = \log \lambda$, the Malthusian parameter, on the assumption that this is the appropriate measure of the fitness of a genotype (Roff 1982; Stearns 1992; Charlesworth 1994). Demetrius (1974) introduced a new demographic parameter which he called entropy. Define

$$p(x) = \lambda^{-x} l(x) m(x). \quad (1.5)$$

From the stable age distribution this is the probability distribution of the parental age of a randomly chosen newborn individual; from equation (1.3) these probabilities sum to unity. The entropy is defined as

$$H = - \frac{\sum_{x=1}^{\omega} p(x) \log p(x)}{\sum_{x=1}^{\omega} x p(x)}. \quad (1.6)$$

This is an analogue of the Boltzmann–Gibbs definition of the entropy of a thermodynamic system. The numerator is analogous to the Shannon–Weaver measure of the amount of information in a message; it measures the variability of the contribution of different age classes to the stationary population. The denominator is the average maternal age, which is a natural measure of generation time.

In his earlier papers, Demetrius (1975b, 1977a,b) emphasized the maximization of entropy in life history evolution, but since 1992 he and his colleagues have developed directionality theory which argues that entropy

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Table 1. Age-specific survival rates and fecundities used for the four starting genotypes in the simulations of Kowald & Demetrius (2005).

age x	genotype 1		genotype 2		genotype 3		genotype 4	
	$P(x)$	$m(x)$	$P(x)$	$m(x)$	$P(x)$	$m(x)$	$P(x)$	$m(x)$
0	0.357 942	—	0.375 889	—	0.254 114	—	0.406 048	—
1	0.047 443	2.866 13	0.054 854	2.725 96	0.712 322	4.4472	0.730 378	0.001 394
2	0.926 569	0.313 614	0.929 94	0.331 418	0.199 784	4.633 79	0.422 079	4.865 05
3	0.813 835	0.084 323	0.821 858	0.094 862	0.854 797	2.296 88	0.891 402	3.543 16
4	0.007 943	0.080 553	0.01	0.090 818	0.01	1.364 95	0.003 981	0.710 871
5	0.000 708	0.007 943	0.001	0.01	0.001	0.01	0.000 251	0.003 981
6	—	0.000 708	—	0.001	—	0.001	—	0.000 251
r	0.0327		0.0337		0.5134		0.2984	
H	0.0475		0.0597		0.5367		0.2626	

is maximized in equilibrium species and minimized in opportunistic species. Ziehe & Demetrius (2005) write that this ‘theory predicts that in populations that spend the greater part of their evolutionary history in the stationary growth phase (equilibrium species), entropy will increase.... In populations that spend the greater part of their evolutionary history in the exponential growth phase (opportunistic species), entropy will decrease when population size is large, and will undergo random variation when population size is small.’ In evaluating this theory I shall concentrate on the recent simulation of Kowald & Demetrius (2005) since simulations can reveal explicitly assumptions which may not otherwise be obvious.

2. A SIMULATION STUDY OF DIRECTIONALITY THEORY

Kowald & Demetrius (2005) presented the results of a computer simulation to test the validity of directionality theory, which they encapsulated in the following principles:

- (i) equilibrium species: a unidirectional increase in entropy;
- (ii) opportunistic species, large population size: a unidirectional decrease in entropy;
- (iii) opportunistic species, small population size: random changes of entropy.

Starting from a genotype with age-specific survival rates and fecundities $P(x)$ and $m(x)$, they simulated rare mutations which changed these values to $P(x)^{1+\delta}$ and $m(x)^{1+\delta}$, where $\delta = \delta_1 + \delta_2 + \dots + \delta_m$ is the sum of the effects of the m mutations that have occurred up to that time at that gene, with δ_i being a random number between -0.1 and $+0.1$; Kowald & Demetrius discarded mutations that changed the sign of $r-H$ for reasons that will be discussed later but it is unlikely that this altered the results of their simulations. Note that δ cannot be less than -1 since the survival rates would then exceed unity. For simplicity Kowald & Demetrius simulated an asexual population. They used four starting genotypes shown in table 1.

According to Kowald & Demetrius, ‘principle (i) asserts that, in populations that spend the majority of their life history in a stationary growth phase, entropy increases under mutation and selection.’ To test this

prediction they simulated a population of 10 000 individuals, and at the end of each year they applied an extrinsic mortality which reduced the population size to this value by multiplying all the age classes of all the genotypes by $N(t)/10\,000$, where $N(t)$ is the population size before this extrinsic mortality. They did simulations for 100 000 years with starting genotypes 1, 2 and 3 in table 1 and presented a graph of the evolution of the entropy H (Kowald & Demetrius 2005, fig. 4). For this first set of simulations, the entropy increased from starting values of 0.05, 0.06 and 0.54 for the three genotypes to final values in the range of 0.65–0.68.

Kowald & Demetrius then wrote: ‘principle (ii) asserts that in large populations described by episodes of rapid population growth and decline (unbounded growth), entropy decreases over evolutionary time.’ To test this prediction they simulated a population of 200 individuals which was allowed to grow geometrically for 15 generations before an extrinsic factor reduced it as before to 200 individuals. Ten repetitions of this simulation were continued for 200 000 years with starting genotype 4. The results of this second set of simulations (Kowald & Demetrius 2005, fig. 5) showed that the entropy declined from an initial value of 0.26 to nearly zero.

Finally Kowald & Demetrius wrote: ‘principle (iii) asserts that in small populations described by recurring episodes of rapid population growth and decline (unbounded growth), the long-term change in entropy is random.’ To test this prediction they repeated the above simulation with a population of 50 individuals growing geometrically for 5 years before being reduced to 50 individuals. Ten repetitions over 1 million years in this third set of simulations showed little change in entropy (Kowald & Demetrius 2005, fig. 6).

Kowald & Demetrius conclude that their simulations provide strong support for the three principles embodied in directionality theory, but closer analysis leads to some questions. First, the difference between applying an extrinsic mortality factor every year or every 15 years cannot explain the increase in entropy in the first case and its decrease in the second in a large population. An extrinsic mortality factor which acts in the same way on *all* year classes and genotypes has *no* effect on the *relative* frequencies of the year classes or the genotypes, whether it is applied every year, every 5 years or every 15 years.

Figure 1. The Malthusian parameter r (solid line) and the entropy H (dashed line) as functions of the mutational effect δ for the four genotypes in table 1.

Thus, the distinction between the increase in the entropy in the first set of simulations and its decrease in the second set cannot be due to the difference in the ecological constraints, and it can only be due to the difference in the starting genotypes. To investigate this, the Malthusian parameter r and the entropy H have been calculated as functions of the mutational effect δ for the four starting genotypes. The results are shown in figure 1. When δ takes its minimum value of -1 so that $P(x) = m(x) = 1$ for all x , $r = H = 0.68$. The entropy H decreases to zero with increasing δ , but the Malthusian parameter r declines at first but then increases, having its minimum value where the two curves intersect. This point is at a small positive value of δ for genotypes 1, 2 and 3, but at a small negative value of δ for genotype 4. This corresponds with the fact that $r < H$ for genotypes 1, 2 and 3 but that $r > H$ for genotype 4 when $\delta = 0$ (see table 1).

Under the conventional idea that selection will maximize r , it is predicted that δ will climb the slope to its left towards zero if it starts to the left of its minimum value (genotypes 1, 2 and 3) while it will climb the slope to its right towards infinity if it starts to the right of its minimum value (genotype 4). Thus, H will increase towards 0.68 in the first case while it will decrease towards zero in the second case. This is the behaviour observed by Kowald & Demetrius in their first two sets of simulations. But if they had used genotype 4 in their first set of simulations and genotypes 1, 2 and 3 in the second set, they would have found the opposite result. Thus, Kowald & Demetrius obtained results consistent with directionality theory by using the three genotypes with $r < H$ for the first set of simulations and the genotype with $r > H$ for the second. Their reason for doing this will be discussed below.

The third set of simulations was designed to test the principle that in opportunistic species with small

population size there will be a random change in entropy. This reflects the conclusion under standard population genetic theory that drift will dominate selection in sufficiently small populations. The conventional wisdom is that selection will be effective when $N_e s \gg 1$ and ineffective when $N_e s \ll 1$, where N_e is the effective population size and s is the selective advantage of a mutant (Crow & Kimura 1970; Hartl & Clark 1989). The problem of calculating the effective population size in an age-structured population is complicated (Charlesworth 1994), and the harmonic mean of the population sizes appropriate to a discrete generation model will be used here. The population size for genotype 4 at $\delta = 0$ increases at a rate of $\exp r = 1.348$ each year, and the harmonic mean of the population sizes over 15 years starting with 200 individuals is $N_e = 783$; the harmonic mean of the population sizes over 5 years starting with 50 individuals is $N_e = 83$. The selective advantage of a mutant with $\delta = 0.1$ (the largest mutation permitted) over the wild type with $\delta = 0$ is 0.0045. To a first approximation $N_e s$ is about 3.5 for the second set of simulations and about 0.4 for the third set. Thus, standard theory suggests that selection should be effective in the second set, leading to an increase in δ and a decrease in H , and ineffective in the third set, leading to little or no change in either δ or H , as observed by Kowald & Demetrius. The population size used in the first set of simulations was so large that selection was bound to be effective, but if it had been much smaller standard theory would predict that it would become ineffective; directionality theory does not seem to encompass this possibility.

3. DISCUSSION

Some ambiguity has arisen from Kowald & Demetrius's failure to distinguish between two different definitions of equilibrium and opportunistic species. The first definition

corresponds with a simple ecological model of r and K selection. Kowald & Demetrius write:

To test the predictions for equilibrium and opportunistic species, additional (although different) growth constraints have to be imposed. Equilibrium species are defined as populations with a roughly constant size. If the actual population size... exceeds the maximum population size (carrying capacity), an extrinsic mortality... is applied in every iteration (year) to each individual, such that the population is reduced to the carrying capacity....

Opportunistic species are defined by a different life history. They expand in population size, until resources become depleted and the population collapses abruptly. The simulation mimics this behaviour. The population begins with an initial size... and grows exponentially for a certain period of time. After that an extrinsic mortality... is applied equally to all individuals to reduce the population to [the initial size].

(Kowald & Demetrius 2005, p. 744)

The problem is that equilibrium and opportunistic species thus defined would behave in exactly the same way (see above). 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 first three genotypes, the entropy would have increased to 0.68. The model might be made more realistic by supposing that different genotypes have different carrying capacities, which would certainly affect the outcome, or that density dependence affects a critical age group (Charlesworth 1994), but this has no connection with entropy.

Kowald & Demetrius started the first set of simulations from the first three genotypes and the second set from the fourth genotype because they adopted an ancillary definition that equilibrium species have $r < H$ and opportunistic species have $r > H$. They define a parameter $\Phi = r - H$ and they write:

Bounded growth corresponds to the condition $\Phi < 0$. This characterizes a population with a stationary growth rate, $r = 0$, or a growth rate which is exponentially increasing ($r > 0$), but bounded by entropy ($r < H$) [misprint corrected]. The bounded growth condition is typical of what we have called equilibrium species, a species that spends the greater part of its evolutionary history in the stationary growth phase or with a population size that fluctuates around some constant value.

Unbounded growth corresponds to the condition $\Phi > 0$. This situation represents a population that is exponentially increasing with a population growth rate that exceeds entropy. The unbounded growth condition is typical of certain growth phases of opportunistic species that are subject to episodes of rapid exponential growth followed by brief periods of decline in population numbers.

(Kowald & Demetrius 2005, p. 745)

The logic of this argument raises some questions. If the difference between an equilibrium species and an opportunistic species is that the former is reduced to its carrying capacity by extrinsic mortality every year while

the latter is so reduced every 5 or 15 years, why should the intrinsic rate of increase in the absence of density dependence affect the definition of a species as equilibrium or opportunistic? Even if it did, why should genotype 3 with $r = 0.51$ be classed as equilibrium while genotype 4 with $r = 0.30$ is classed as opportunistic? Yet the validity of directionality theory, as defined in terms of the distinction between equilibrium and opportunistic species, depends on the definition of such species as having $r < H$ or $r > H$.

Another problem is that the simulation was done with a model of mutational effects which has little biological realism. Figure 1 shows that the system may tend to one of two endpoints. The first is at $\delta = -1$, at which point $l(x) = m(x) = 1$ ($x = 1, \dots, 6$); every individual lives for exactly 6 years and has one offspring each year. (δ cannot be less than -1 because survival rates cannot exceed unity.) At this point $r = H = 0.68$.

The second endpoint is at $\delta \rightarrow \infty$, in which case the terms $[l(x)m(x)]^{\delta+1}$ ($x = 1, \dots, 6$) are dominated by the age class, say $x = \xi$, with the largest value of $l(x)m(x)$. In table 1, $\xi = 1$ for genotypes 1, 2 and 3, while $\xi = 2$ for genotype 4. $H \rightarrow 0$ since the life history is effectively semelparous. A newborn individual has a vanishingly small chance $l(\xi)^{\delta+1}$ of surviving to the critical age ξ , but has an effectively infinite number of offspring $m(\xi)^{\delta+1}$ if it does so. (Note that $m(\xi) > 1$ for all four genotypes.) For large δ the Malthusian parameter is

$$r \cong \frac{\delta + 1}{\xi} \log l(\xi)m(\xi). \quad (3.1)$$

Thus, the model considered by Kowald & Demetrius is biologically unrealistic and does not incorporate the constraints and tradeoffs usually thought to be important in life history evolution. But a general result applicable to any model of life history evolution throws light on what is happening. In a sympathetic account of Demetrius's earlier work, Emlen (1984, p. 352) has extended his argument to obtain the conclusion that

$$\Delta H = \text{cov}(H, r), \quad (3.2)$$

which states that the change in the entropy is equal to the covariance between the entropy and the Malthusian parameter. In particular, if natural selection acts to maximize r , then H should increase or decrease according as it is positively or negatively correlated with r . This is exemplified in the simulations of Kowald & Demetrius. In figure 1, H declines with δ , while r declines at first and then increases, with a minimum value where the two curves intersect. If the starting genotype with $\delta = 0$ is to the left of the minimum value so that $r < H$ (genotypes 1, 2 and 3) then, for small values of δ , r and H will be positively correlated and H will increase; if it is to the right of the minimum value so that $r > H$ (genotype 4) then r and H will be negatively correlated and H will decrease. Emlen's result is consistent with the view that natural selection maximizes the Malthusian parameter, which drags the entropy along with it.

The mathematical results which underpin evolutionary entropy and directionality theory appear to be correct, but it is argued here that their biological interpretation by Demetrius and his colleagues is questionable. Demetrius (2001) has summarized the mathematical argument underlying directionality theory in an appendix. Write

r and H for the Malthusian parameter and the entropy of a wild type genotype and consider whether a mutant with parameters $r + \Delta r$ and $H + \Delta H$ will invade. This is determined by the sign of the selective advantage of the mutant (Demetrius 2001, eqn. (A4))

$$s = \Delta r - \frac{1}{N} \Delta \sigma^2, \quad (3.3)$$

where N is the population size and σ^2 is a measure of the demographic variance. Demetrius also observes that

$$\left. \begin{array}{l} \text{when } r < H, \quad \Delta r \Delta H > 0, \\ \text{when } r > H, \quad \Delta r \Delta H < 0, \end{array} \right\} \quad (3.4)$$

and he shows that in large populations H will increase when $r < H$ and will decrease when $r > H$. This conclusion follows immediately from equations (3.3) and (3.4) if the population size is large enough to ignore the second term on the right hand side of equation (3.3), and states no more than the fact that r always tends to increase. (Compare Emlen's theorem in equation (3.2).) Finally, Demetrius derives the first two principles of directionality theory, that entropy will increase in equilibrium species and decrease in opportunistic species by defining the former as having $r < H$ and the latter as having $r > H$; but as discussed above there seems little justification for adopting this as an ecologically meaningful definition. This casts doubt on directionality theory and its application to the evolution of body size and ageing (Demetrius 2000a, 2001).

Demetrius and his colleagues accept that natural selection maximizes the Malthusian parameter in a very large population (Demetrius 2000a, 2001; Kowald & Demetrius 2005; Ziehe & Demetrius 2005), from which it seems to follow that there is no additional role for entropy in deterministic models of life history evolution. I conclude that 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 (Roff 1982; Stearns 1992; Charlesworth 1994).

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