

Evolutionary branching/speciation: contrasting results from systems with explicit or emergent carrying capacities

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ABSTRACT

In this paper, we use the theory of adaptive dynamics to highlight the differences in evolutionary behaviour when contrasting formulations of the carrying capacity are used. We use two predator–prey systems, one with a fixed carrying capacity and one in which the carrying capacity is an emergent property compounded of an intrinsic growth rate and a susceptibility to crowding. We consider prey evolution in both systems and link the evolving parameters by a trade-off which requires that prey with higher per capita growth experience a greater risk of predation. We find that the two approaches for representing the carrying capacity can lead to markedly different evolutionary behaviour. In particular, the possibility of exhibiting evolutionary branching requires an emergent carrying capacity. This is significant, since evolutionary branching is regarded as a possible mechanism by which sympatric speciation may occur.

Keywords: adaptive dynamics, carrying capacity, evolutionary branching, speciation.

INTRODUCTION

The concept of the carrying capacity is central to population ecology. It is easy to interpret and often relatively straightforward to estimate from the field. However, there are important population dynamical implications to modelling intraspecific competition using a carrying capacity explicitly or using it implicitly as an emergent property compounded of an intrinsic growth rate and a susceptibility to crowding (Kuno, 1991). Furthermore, it has been argued that formulations that use an explicit carrying capacity can produce biologically counter-intuitive results (Fulda, 1981; Pollard, 1981; Kuno, 1991). In particular, in models with an explicit carrying capacity the intrinsic growth rate has no effect on competitive outcomes. The formulation of an explicit carrying capacity is also at the heart of classical ideas in

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evolutionary ecology (such as r and K selection; MacArthur and Wilson, 1967), where the intrinsic growth rate is not important in crowded situations. Also, rather alarmingly, models can predict an increase in population size when the intrinsic growth rate is negative (which occurs when deaths outweigh births) if the population size is above the (explicit) carrying capacity (Fulda, 1981; Kuno, 1991). These effects arise from the fact that the carrying capacity is assumed to be independent of birth and death rates, an assumption that is incorrect in most systems. Indeed, an explicit carrying capacity may only be appropriate for systems where the major limiting resource is rigidly externally fixed. This could occur in particular systems where, for example, the availability of space fixes the maximum population size, but in most ecological systems the carrying capacity emerges from the characteristics of the organisms. Despite this, by far the greater prevalence of formulations involve the carrying capacity explicitly.

Thus, there are good biological and analytical reasons why it may be preferable to use the alternative formulation involving an implicit carrying capacity that is an emergent property of the intrinsic growth rate and a susceptibility to crowding. This places individuals and populations in a more realistic biological perspective, since the individual properties relating to birth, death and susceptibility to crowding come first and population-level properties such as carrying capacities emerge. Furthermore, as Begon *et al.* (1996) argue, it is the individual properties which are acted on by natural selection and evolve and, therefore, this formulation is particularly appropriate for evolutionary models. In this study, we use the recent development of adaptive dynamics as a tool for evolutionary modelling (Metz *et al.*, 1996a; Geritz *et al.*, 1997, 1998) to highlight the differences in evolutionary behaviour when an explicit or implicit formulation of the carrying capacity is used. We find that the two approaches can lead to markedly different behaviour, especially in terms of the possibility of exhibiting evolutionary branching (Metz *et al.*, 1996a; Geritz *et al.*, 1997, 1998; Doebeli and Dieckmann, 2000).

MODELS AND ANALYSIS

We consider two predator–prey models differing only in how intraspecific competition is handled in the evolving species, which we take to be the prey. In one case, we have dynamics in which the carrying capacity is incorporated implicitly through a parameter h , the susceptibility to crowding:

$$\begin{aligned} dN/dt &= N(r - hN - cP) \\ dP/dt &= P(-d + ceN) \end{aligned} \quad (1)$$

The other case explicitly involves the carrying capacity K , so that:

$$\begin{aligned} dN/dt &= N(r(1 - N/K) - cP) \\ dP/dt &= P(-d + ceN) \end{aligned} \quad (2)$$

In both cases, N represents the density of the prey and P that of the predator. All parameters are positive; r is the intrinsic growth rate of prey, c is the rate of predation, d is the death rate of the predator and e is the rate of conversion of predation into predator births. (We could include a term in the predator dynamics relating to intraspecific competition for resources other than the prey we explicitly consider. This has no bearing on the results below and is, therefore, omitted.)

We consider the case of prey evolution in which mutation only affects the parameters r and c , with these parameters being linked by a trade-off (Stearns, 1992; Boots and Haraguchi, 1999; Bowers and White, 2002), $r=f(c)$ (with $f'(c) > 0$), implying that an increased ability to 'resist' predation (lower c) results in a lower intrinsic growth rate r . Without the trade-off, it is easy to show that the prey would evolve to achieve its maximum value of r and minimum value of c . The focus here, therefore, is on the consequences for the evolution of the parameters r and c . We distinguish mutant parameters from their resident counterparts by the use of an overbar – that is, \bar{r} and \bar{c} versus r and c .

The model descriptions chosen in equations (1) and (2) reflect the most common formulations for representing the carrying capacity used in ecological modelling. For any fixed set of parameter values, these models are analogous. This is not the case when considering the evolution of parameters (r and c in this study). In model (1), as the parameters evolve the carrying capacity also changes (since it equals r/h). Thus here the cost of predator resistance is paid for both in terms of the intrinsic growth rate and the carrying capacity. In model (2), the carrying capacity remains fixed and, therefore, the cost of predator resistance is paid for only in terms of the intrinsic growth rate. We seek to explain how these different formulations affect the evolutionary outcomes.

We now start our investigation of the adaptive dynamics of our systems, beginning with equations (1). The key expression in the analysis of adaptive dynamics is the fitness function of the mutant strategy, which is calculated as the per capita growth rate of a mutant strategy, \bar{s} , in an environment determined by the resident population, c , and denoted \bar{s} . If \bar{s} is negative, the mutant dies out; if \bar{s} is positive, it may spread, increase in density and begin to reshape the environment. The mutant fitness can be written as follows (see Appendix, A1–A3):

$$\bar{s} = (f(\bar{c}) - f(c)) - (\bar{c} - c)P \quad (3)$$

Here, P now denotes the resident equilibrium population density and, therefore, depends only on resident parameters. (Note the criteria for positive resident predator and prey population densities are assumed to be satisfied.) Given that mutations are small, the population will evolve in the direction of the local fitness gradient, defined as

$$\partial \bar{s} / \partial \bar{c} = f'(\bar{c}) - P \quad (4)$$

until it reaches the neighbourhood of a 'singular strategy', c^* , for which the fitness gradient is zero (a prime on f denotes differentiation). Thus, c^* occurs when (see Appendix, A5)

$$f'(c^*) = P^* \quad (5)$$

[We use asterisks generally to denote evaluation at the singular parameter values. So, for instance, $P^* = (f(c^*)ec^* - hd)/(e(c^*)^2)$, the equilibrium value of P at the singular strategy, c^* .] The behaviour at the singular strategy is determined from combinations of the non-mixed second derivatives of \bar{s} evaluated at $c = \bar{c} = c^*$ and can be characterized by four properties (Table 1). For instance, if c^* is an evolutionarily unbeatable strategy (EUS) and convergence stable (CS), then it is necessarily an evolutionary attractor (Fig. 1a) [called a continuously stable strategy or CSS (Eshel, 1983)]; if it is not EUS and not CS, it is a (non-EUS) evolutionary repeller (Fig. 1b). The phenomenon of branching occurs when c^* is CS but not EUS. Here we evolve towards c^* but when close by undergo disruptive selection and two distinct strategies co-exist either side of c^* (Fig. 1c). Branching points are at the forefront of theoretical attempts to explain speciation [see Metz *et al.* (1996a) and Geritz *et al.* (1998) for

Table 1. Properties of singular points, c^* (see Geritz *et al.*, 1998)

Property	Characteristic
Evolutionarily unbeatable strategy (EUS)	$\partial^2 \bar{s} / \partial \bar{c}^2 \Big _* < 0$
Convergence stable (CS)	$\partial^2 \bar{s} / \partial c^2 \Big _* - \partial^2 \bar{s} / \partial \bar{c}^2 \Big _* > 0$
Singularity can spread (SPR)	$\partial^2 \bar{s} / \partial c^2 \Big _* > 0$
Mutually invadable (MI)	$\partial^2 \bar{s} / \partial c^2 \Big _* + \partial^2 \bar{s} / \partial \bar{c}^2 \Big _* > 0$

more details on the theory of adaptive dynamics]. For dynamics represented by equation (1) at the singular points $c = \bar{c} = c^*$, we find (see Appendix, A6–A9)

$$\partial^2 \bar{s} / \partial \bar{c}^2 \Big|_* = f''(c^*) \text{ and } \partial^2 \bar{s} / \partial c^2 \Big|_* = -f''(c^*) + 2hN^*/(c^*)^2 \tag{6}$$

And, therefore,

$$\partial^2 \bar{s} / \partial c^2 \Big|_* - \partial^2 \bar{s} / \partial \bar{c}^2 \Big|_* = -2f''(c^*) + 2hN^*/(c^*)^2 \tag{7}$$

This has the consequence that the singularity will be non-EUS [$f''(c^*) > 0$ from Table 1 and (6)] and CS [see Table 1 and (7)] if, and only if,

$$0 < f''(c^*) < hdl/e(c^*)^3 \tag{8}$$

Thus with susceptibility to crowding (rather than the carrying capacity) explicitly included, a weak convexity condition on the trade-off f is sufficient to guarantee branching/speciation. To summarize, if $f''(c^*) < 0$, c^* is an evolutionary attractor (Fig. 1a); if $f''(c^*) > 0$ but (8) is not satisfied, then c^* is an evolutionary repeller (Fig. 1b); and if the weak convexity condition in (8) is satisfied, then c^* is an evolutionary branching point (Fig. 1c).

What then of the alternative model of equations (2) which explicitly includes the carrying capacity? The fitness function satisfies

$$\bar{s} = (f(\bar{c}) - f(c))(1 - N/K) - (\bar{c} - c)P \tag{9}$$

where N and P now denote the resident equilibrium population densities (which are positive). Singular points are solutions of

$$\partial \bar{s} / \partial \bar{c} = f'(\bar{c})(1 - N/K) - P = 0 \tag{10}$$

Thus, c^* occurs when

$$f'(c^*) = f(c^*)/c^* \tag{11}$$

The second derivatives evaluated at c^* are

$$\partial^2 \bar{s} / \partial \bar{c}^2 \Big|_* = f''(c^*)(1 - N^*/K) \text{ and } \partial^2 \bar{s} / \partial c^2 \Big|_* = -f''(c^*)(1 - N^*/K) \tag{12}$$

Thus the two partial derivatives differ only in sign and

$$\partial^2 \bar{s} / \partial c^2 \Big|_* - \partial^2 \bar{s} / \partial \bar{c}^2 \Big|_* = -2\partial^2 \bar{s} / \partial \bar{c}^2 \Big|_* \tag{13}$$

Thus, according to Table 1, if the singular point is not evolutionarily unbeatable (not EUS), then it cannot be convergent stable (CS). Therefore, this model involving an explicit carrying capacity is incapable of supporting branching/speciation (and only evolutionary repeller or attractor dynamics can be exhibited). Moreover, we show that this model

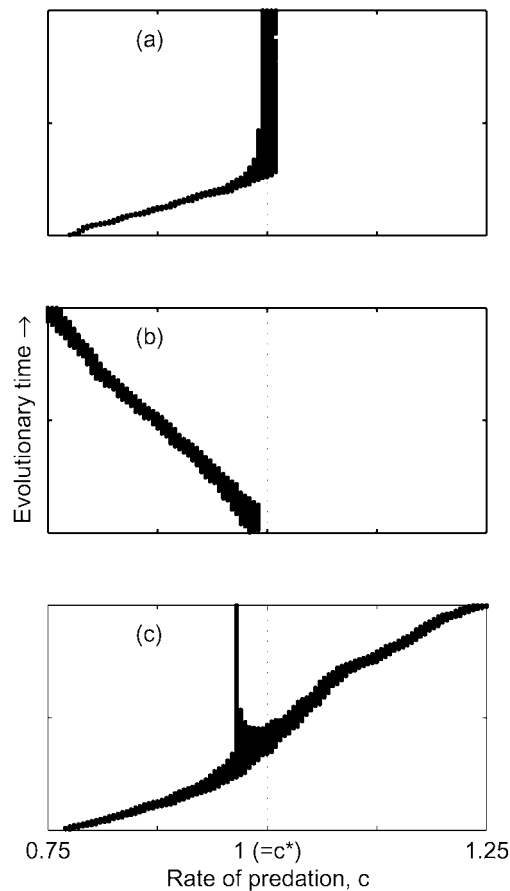


Fig. 1. Simulations of equations (1) showing how the rate of predation, c , evolves over time. Parameters are $h = 1$, $d = 1$ and $e = 1$ and the trade-off $r = f(c) = ac^2 + 2c + \alpha + 1$, which fixes a singularity $c^* = 1$. In (a) $\alpha = -0.5$ and, therefore, $f''(c^*) < 0$ and c^* is an evolutionary attractor; in (b) $\alpha = 0.8$ and, therefore, $f''(c^*) > 0$ but equation (8) is not satisfied and c^* is an evolutionary repeller; in (c) $\alpha = 0.3$ and equation (8) is satisfied and c^* is an evolutionary branching point. In the simulations, the population dynamics were numerically solved for a fixed time (t) according to equations (1) starting with a monomorphic population. Mutant strategies were generated by small deviations around the current strategies and introduced at low density. Then the population dynamics were solved for a further time t with strategies whose population density fell below a low threshold considered extinct and removed before considering new mutations. In this way, the parameter c could evolve. Note the simulations are not mutant-limited (i.e. new mutants could evolve before previous mutants had reached equilibrium or gone extinct), which accounts for the thickness of the lines in these figures. This, however, did not confound the model predictions.

supports an optimization principle. This is similar to the maximization of population density in many simple life-history models (Metz *et al.*, 1996b; see also Mylius and Diekmann, 1995; Kisdi, 1998; Meszena *et al.*, 2001) and indicates that branching is not possible. In the Appendix (see A10–A12), we show that a strategy can invade and replace the current resident whenever the quantity $E = P/(1 - N/K)$ in the current population is

lower than it would be in the invader's population. It follows that strategies cannot co-exist and the strategy with highest E is globally optimal (it invades and outcompetes any other strategy).

DISCUSSION

By applying the methods of adaptive dynamics, we have demonstrated quantitatively that branching/speciation is not possible for the formulation with an explicit (fixed) carrying capacity but is possible when the carrying capacity emerges from the interplay between an intrinsic growth rate and a susceptibility to crowding. Central to this result is that once the carrying capacity is formulated as an emergent property from individual-level processes, it is clear that the carrying capacity changes as a consequence of evolution. The population size is affected by growth rate and this, in turn, evolves as a cost of resistance to, or avoidance of, predation. Thus, there are costs of predator resistance associated with two characteristics of the population dynamics – the intrinsic growth rate and the carrying capacity (as opposed to just the first of these in the explicit carrying capacity formulation). It is this important process that allows the more complex and, we would argue, more biologically realistic evolutionary dynamics that are seen here. This emerges directly from the underlying biological processes in the implicit formulation of carrying capacities but not from the explicit form.

Our results can also be interpreted in terms of the correlation between the parameters r and h . In model 1 there is no correlation, whereas in model 2 there is a linear correlation (with the coefficient of correlation equal to $1/K$). The difference in evolutionary outcomes, therefore, also corresponds to different assumptions about this correlation. An interpretation in terms of parameter correlations is not, however, independent of the interpretation in terms of carrying capacity properties, since the particular correlation chosen determines whether the carrying capacity is fixed or evolving. In addition, our work also emphasizes that trade-offs between parameters can lead to sympatric speciation through evolutionary branching. In this study, branching occurs if there is a weak convexity condition on the trade-off between intrinsic growth rate and predation avoidance in which costs associated with the intrinsic growth rate additionally lead to costs associated with the population carrying capacity. As such, we have demonstrated another example where the intrinsic properties of the ecological interaction and evolutionary cost structure alone can lead to speciation. It is an intrinsic process that produces the disruptive selection required for speciation rather than an externally imposed assumption such as a habitat difference (see Doebeli and Dieckmann, 2000, for further discussion). Although our model only strictly applies to a haploid population, it has been shown (Dieckmann and Doebeli, 1999; Doebeli and Dieckmann, 2000) that this form of evolutionary process can also give rise to branching and speciation in sexual populations where there is assortative mating. As such, our work emphasizes that speciation may occur in species due to extremely simple cost–benefit structures, such as in this case a straightforward trade-off in which improved predator avoidance (lower c) results in a decreased growth rate (lower r). The weak convexity trade-off condition for branching was also found in related work on the evolution of resistance to parasites (Boots and Haraguchi, 1999) and the evolution of polymorphism in Levene-type models (Kisdi, 2001). Biologically this corresponds to a trade-off structure such that costs to a given improvement in a particular trait become slightly less severe as the improvements get more pronounced. Many cost–benefit relationships may in fact be such that a given

benefit is bought at an increasingly higher price and, therefore, does not lead to speciation in this context. However, it should be emphasized that the weak convexity is only required for part of the trade-off curve – the immediate neighbourhood of the singular point – and therefore general functions (such as a sigmoidal relationship) may allow speciation. In any case, the fact remains that relatively simple processes with particular basic underlying cost structures can lead to the intrinsic generation of disruptive selection leading to sympatric speciation. The fact that we find this process in a basic model of predators and prey emphasizes the importance and robustness of the results of adaptive dynamical theory to the understanding of speciation.

We have shown that branching is not possible when the intrinsic growth rate can evolve independently of carrying capacity even when there is a trade-off with predation avoidance. The particular formulation of the carrying capacity can, therefore, change the interpretation of even basic models. Our conclusions can therefore be seen as supporting the view that it is preferable to take the route via the individual-based property ‘susceptibility to crowding’ in which the carrying capacity is properly seen as an emergent population-level property.

ACKNOWLEDGEMENTS

S.A.H. Geritz and E. Kisdi are currently supported by the Finnish Academy of Sciences and by the European Research Training Network ‘Modern Life-History Theory and its Application to the Management of Natural Resources’, funded through the Human Potential Programme of the European Commission (HPRN-CT-2000-00051).

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APPENDIX

The fitness or per capita growth rate of a rare mutant in an environment determined by the resident population at equilibrium for the dynamics represented by equation (1) is:

$$\bar{s} = \bar{r} - hN - \bar{c}P \quad (\text{A1})$$

The fitness of the resident prey is by definition at equilibrium and so

$$s = r - hN - cP = 0 \quad (\text{A2})$$

We can combine these equations and introduce the trade-off giving the result shown in (3):

$$\bar{s} = (f(\bar{c}) - f(c)) - (\bar{c} - c)P \quad (\text{A3})$$

Evolutionarily singular points c^* are determined by setting the fitness gradient

$$\partial\bar{s}/\partial\bar{c} = f'(\bar{c}) - P \quad (\text{A4})$$

at $c = \bar{c}$ equal to zero. Using (A4), this yields the result in (5):

$$f'(c^*) = P^* \quad (\text{A5})$$

The non-mixed second derivatives of \bar{s} evaluated at $c = \bar{c} = c^*$ are

$$\partial^2\bar{s}/\partial\bar{c}^2|_* = f''(c^*) \quad (\text{A6})$$

as in equation (6) and

$$\partial^2\bar{s}/\partial c^2|_* = -f''(c^*) + 2\partial P/\partial c|_* \quad (\text{A7})$$

If we now set the terms in brackets in (1) equal to zero, use $r = f(c)$ and differentiate, it follows using (A5) that at a singularity

$$\begin{aligned} -h\partial N/\partial c|_* - c^*\partial P/\partial c|_* &= 0 \\ eN^* + c^*e\partial N/\partial c|_* &= 0 \end{aligned} \quad (\text{A8})$$

so that

$$\partial P / \partial c \big|_* = hN^*/(c^*)^2 \quad (\text{A9})$$

and the result in (6) follows by combining equations (A7) and (A9).

The adaptive dynamics results shown in the main text for equations (2), which involve the carrying capacity explicitly, follows using the same methodology as above. They are not detailed here, as a stronger result holds, determined from a global analysis in parameter space based directly on the population dynamics of (2). The prey dynamics for equation (2), with the trade-off incorporated, can be re-written as

$$dN/dt = Nf(c)(1 - N/K) \left\{ 1 - \frac{c}{f(c)} \frac{P}{(1 - N/K)} \right\} \quad \text{for } N < K \quad (\text{A10})$$

For a mutant to invade, we require that $\bar{s} > 0$, which is equivalent to

$$\rho(\bar{c}, E) = 1 - \frac{\bar{c}}{f(\bar{c})} E > 0 \quad (\text{A11})$$

where (A11) defines ρ and $E = P/(1 - N/K)$ is the environmental feedback variable and is set by the resident. Since the resident is in equilibrium, we know that $\rho(c, E) = 0$ and so $E = f(c)/c$. Thus, using (A11), the mutant can invade if, and only if,

$$\frac{f(\bar{c})}{\bar{c}} > \frac{f(c)}{c} \quad (\text{A12})$$

Mutual invasibility (and, therefore, branching) cannot occur. Therefore, any invading mutant that satisfies (A12) will replace the resident. The population evolves to the type that maximizes $f(c)/c$ and the unique global maximum of $f(c)/c$ (provided it exists) is the globally optimal strategy, regardless of mutation size.

