Article ID: 1001-0742(2002)03-0333-06 **CLC number**: X820.3;X21 **Document code**: A

On the minimum cost of an evolutionary strategy response to environment stress

LIN Zhen-shan[1,2], LI Bai-lian[2]

(1. Department of Geography, Nanjing Normal University, Nanjing 210097, China. E-mail: zslin@email.njnu.edu.cn; 2 Department of Biology, the University of New Mexico, Albuquerque, NM 87131-1091, USA)

Abstract: Two revised drafts about a simple evolution trade-off function studied by Mitchell (Mitchell, 2000) were put up first. Considering the complex of the environment, or the nonlinear interaction of the environment and species, we put up two new cost functions: $c(u,z) = c_0 + c_1 u + \frac{k(z + az^2)}{u}, u > 0; c(u,z) = c_0 + c_1 u + \frac{kz^d}{u}, u > 0, d > 0$.

In the first case, if the environment is adverse to species ($a > 0$), the region of low-stress which is more suitable for the intolerant species is very small, and at the same environment stress z, the tolerant species will pay the more cost than it will paid in the normal environment. However the tolerant species will pay more cost but low strategies in the environment of $a < 0$ than that it will paid in the environment of $a = 0$ or $a > 0$.

In the second case, the results showed that the greater the stress of the environment is, or the more complex the environment is, the lower cost the intolerant species will pay in the region of $z < 1$. In order to exist or to evolve from an environment of high-stress, the organisms must possess a higher u, or a better means of mitigating of the stress of environment. Meanwhile in the region $d > 1$, when d decrease, the intolerant species will pays more lower cost of exploiting a habitat in the low-stress environment while the tolerant one will pays more lower cost in the high-stress environment. This means that scale d describes the selection character of the species system in the evolution process, the smaller the d ($d < 1$) is, the better the selection or the mitigation the system will possesses.

Keywords: evolutionary strategy response; environment stress

Introduction

To predict species richness and how it is expected to change with environmental conditions requires an understanding of the travel cost, strategy and the environment stress. Brown *et al*. (Brown, 1994) hypothesized that body size represents a trade-off between more efficient energy harvest by larger species and more efficient energy conversion for reproduction by smaller species. They also suggested that the evolution of body size is the result of competition for limited resources generating frequency-dependent fitnesses. The low travel cost or low maintenance and replacement costs caused species in isolation to evolve to a strategy that resided to perturbations in the strategy used by the species as a whole. Mitchell (Mitchell, 2000) considered that travel cost should also be important for species that "travel" through time to select profitable periods for activity, germination, flowering, and so on. He also noted that because of the trade-off, each species is guaranteed level below that which can be exploited by competing species. While Rosenzweig (Rosenzweig, 1981; 1987) suggested that the habitat selection is a source of biological diversity.

As is known to all, if habitat heterogeneity is continuous, then there is no apparent limit to the number of ways that species could divide it up, allowing each species to be superior over some range of habitat. That means that such an environmental continuum could allow an almost unlimited number of species to coexist on a single resource. Huisman and Weissing (Huisman, 1999) present away to reconcile the persistence of diversity with competitive exclusion in undisturbed ecosystems with few limiting resources.

Many theoretical and empirical studies of the species richness and the evolution stability have also accumulated. Eshel (Eshel, 1983) noted that a strategy in a population game is evolutionarily stable, Holt

Foundation item: part by Ministry of Science and Technology of China under grant NKPDBS G1998040900 – part 1, and U. S. National Science Foundation under grant DEB – 94 – 11976

(Holt, 1985) explored the effect of dispersal on population size and stability between two discrete habitat patches while Abrams *et al*. (Abrams, 1993) studied the evolutionarity unstable fitness maximum and stable fitness minima of continuous traits and Brown(Brown, 1990; 1996) studied the habitat selection as an evolutionary game.

Mitchell(Mitchell, 2000) used a co-evolutionary model to investigate the co-existence of species in ecological and evolutionary time in an environment that comprises a continuum of habitat heterogeneity. His study showed that the intolerant species pays a high cost in high-stress environments, but a relatively lower cost in low-stress environments, and the tolerant species still prefers low-stress environments but this species finds its relative advantage in high-stress environments. However the minimum z of the point of tangency of the cost line with the curve of u_m in Milchell's work is 3.9 not 0, the value of c_m may be negative in the region of low stress. On the other hand, because of the environment is very complex, and the interaction between the species and environment maybe a nonlinear one, it is necessary for us to consider the nonlinear effect of environmental stress.

We will discuss a simple evolutionary trade-off function in Section 1, and two nonlinear functions of evolutionary trade-off in Section 2.

1 The discussion of a simple evolutionary trade-off function

In order to study the species richness in a continuum of habitat heterogeneity, Mitchell(Mitchell, 2000) chose a simple evolution trade-off function, the cost function $c(u,z)$ in which the cost paid by an individual of evolutionary strategy u per unit time while exploiting a habitat patch characterized by the environmental stress z:

$$c(u,z) = c_0 + c_1 u + \frac{zk}{1+u}. \tag{1}$$

Here k is a constant that transforms the environmental stress into energy cost per unit time, and the first term, c_0 is just a base cost that must be paid in any environment. The second term represents the energy cost of u, where the constant, c_1 is the unit energy cost. The third term represents the effect of environmental stress, z. As an evolutionary strategy u, its dynamics depend on the selection pressure imposed by a combination of the environment, population densities and strategy frequencies. In Eq. (1) the strategy u enters in the denominator so that it mitigates the effect of z, i.e., the effect of increasing environmental stress is less when an organism possesses a higher value of u. In Eq.(1) the cost increases with z, but may increases or decreases with u.

If

$$\frac{\partial c(u,z)}{\partial u} = 0, \tag{2}$$

that is if

$$\frac{\partial^2 c}{\partial u^2} = 2zk(zk/c_1)^{-3/2}, u_m = (zk/c_1)^{1/2} - 1, \tag{3}$$

there is a extreme value of the cost $c(u, z)$

$$c_m = c(u_m, z) = c_0 - c_1 + 2(zkc_1)^{1/2}. \tag{4}$$

Because

$$\frac{\partial^2 c}{\partial u^2} = 2zk(zk/c_1)^{-3/2} > 0, \tag{5}$$

so c_m is the minimizes cost, and describes the minimum cost envelope which is illustrated in Fig. 1.

Fig.1 shows how the cost of exploiting a habitat increase with environmental stress for each different species that differ in their tolerance to the environmental stress. The line c_5 represents the cost of tolerant species and the line c_3 represents the cost of intolerant ones for the reason that the z value of the point of tangency of line c_5 with curve $u_1(z)(u_m)$ is greater than that of line c_3 with curve $u_1(z)$. Because the resource density in each habit z will affected mainly by the species that pays the lowest cost in the habitat, the tolerant species will exclude intolerant species from high-stress habitats while the intolerant species will reduce resource density in low-stress habitat to a level that is unprofitable for the tolerant species. This means that many species can coexist globally in a system by having competitive advantages in different types of habitat which is consistent with Abramsky's view (Abramsky, 1988).

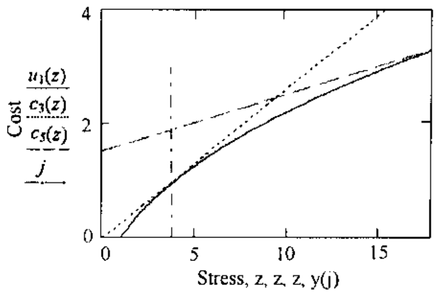

Fig.1 The relation between the cost function with the environment stress z (c_3 and c_5), and u_m curve ($u_1(z)$) or the envelope of the cost curves (dashed line) which generated by a range of tolerant-to-intolerant species, here $k = 1$, $c_0 = 0.1$, $c_1 = 1$

However on the other hand, because: (1) the minimum z of the point of tangency of the cost line with the curve of $u_1(z)(u_m)$ is 3.9, not 0 (showed in line c_4); (2) according to Eq.(4) if $c_1 < c_0$, for example which is set by Mitchell in his Fig.1, the value of may be negative in the region of low stress. We consider that it is necessary to improve the Eq.(1). Following are two the most simplest plans:

$$\text{(a)} \quad c(u,z) = c_0 + c_1 u + \frac{zk}{u}, \quad u > 0, \tag{6}$$

$$u_m = (zk/c_1)^{1/2}, \quad c_m = c(u_m, z) = c_0 + 2(zkc_1)^{1/2}. \tag{7}$$

$$\text{(b)} \quad c(u,z) = c_0 + c_1 u + \frac{zk}{(c_0/c_1) + u}, \quad c_0 \sim (10)^{-1} c_1, \tag{8}$$

$$u_m = (zk/c_1)^{1/2} - c_0/c_1, \quad c_m = c(u_m, z) = 2(zkc_1)^{1/2}. \tag{9}$$

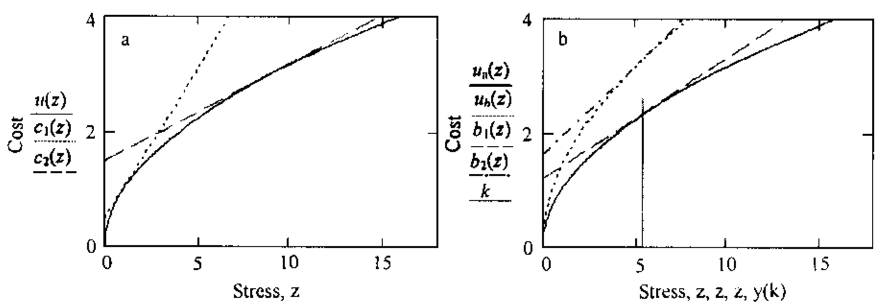

Fig.2 a. The cost line $c_1(z)$, $c_2(z)$ and the envelope of cost curve $u(z)$ on the Eq.(6) - (7). It is the same as Mitchell's Fig.1, here $k = 1$, $c_0 = 0.1$, $c_1 = 1$; b. the change of u_m and cost c with the parameter c_1, here $u_a(z)$ corresponding to $c_1 = 1$ and $u_b(z)$ corresponding to $c_1 = 0.5$.

From Fig.2 we can find that under the same environment stress, the less c_1 is, the bigger the cost and the evolutionary strategy u will paid.

Fig.3 shows the curves of c-u based on the Eq.(8) in which $k = 1$, $c = 1$, $c_0 = 0.1$, and $z = 8$ in c_8 curve, $z = 4$ in c_4 curve.

Fig.4 shows the curve c_m and curve u_m based on the Eq.(9) in which $k = 1$, $c_0 = 0.2$, $c_1 = 0.8$.

From Fig.3 we find that the bigger the strategy is, the less different will be in the costs of different stresses.

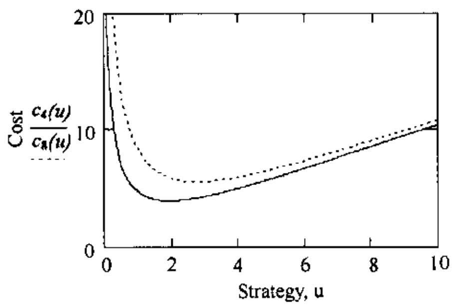

Fig.3 The change of u_m and cost c with the parameter c_1, here $u_2(z)$ corresponding to $c_1 = 1$ and $u_1(z)$ corresponding to $c_1 = 0.5$

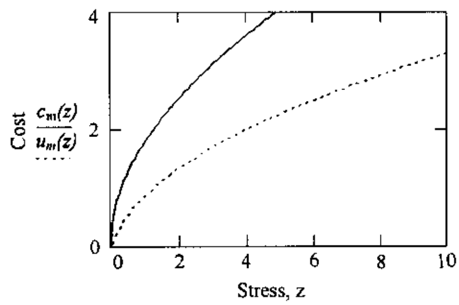

Fig.4 The curve of c_m and u_m based on the Eq.(9) in which $k = 1$, $c_0 = 0.2$, $c_1 = 0.8$

2 Some nonlinear function of evolutionary trade-off

2.1 A function about the second power of press

Considering the complex of the environment, or the nonlinear interaction of the environment and species, we will study the following nonlinear equation which is improved from the Eq.(1):

$$c(u,z) = c_0 + c_1 u + \frac{k(z + az^2)}{u}, \quad u > 0. \tag{10}$$

The third term represents the two powers nonlinear effect of environmental stress. Here a is a parameter which describes the intensity of the nonlinear effect.

From Eq. (10), we have

$$u_m = [(z + az^2)k/c_1]^{1/2}, \tag{11}$$

$$c_m = c(u_m, z) = c_0 + 2[(z + az^2)kc_1]^{1/2} = c_0 + 2c_1 u_m. \tag{12}$$

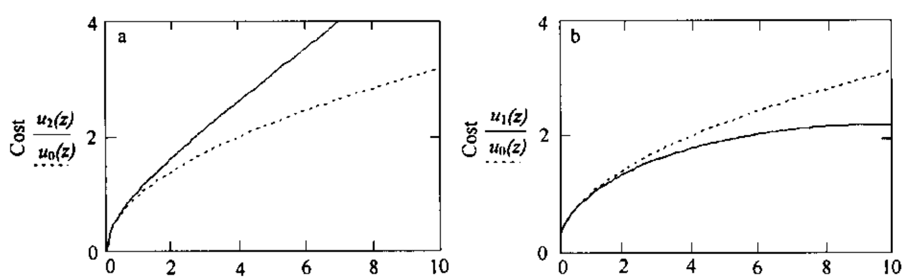

Fig.5 The curve of u_m-z based on the Eq.(11) in which $k = 1$, $c_0 = 0.2$, $c_1 = 1$

a. $u_2(z) = (z + 0.18z^2)^{1/2}$, $u_0(z) = z^{1/2}$; b. $a = -0.05$, $u_1(z) = (z - 0.05z^2)^{1/2}$, $u_2(z) = (z + 0.18z^2)^{1/2}$

Fig.5a shows the relations between u_m and z in the case of $a = 0.18$. Because after $z > 1.5$, the curve of u_m-z is a line, all tolerant species will pay high strategies (and more cost) in the high-stress environment. From Fig.5a we find that: (a) if $a > 0$, the region of low-stress which is more suitable for the intolerant species is very small. (b) the tolerant species will pay more strategies (and more cost) in the environment of $a > 0$ than that it will paid in the environment of $a = 0$.

Fig.5b shows the relations between u_m and z in the case of $a = -0.05$. Comparing with Fig.5a, we can find that the tolerant species will pay more cost but low strategies in the environment of $a < 0$ than that it will pay in the environment of $a = 0$ or $a > 0$.

Fig.6 shows the relations between the cost and the stress. In three different cases $a = 0$, $a = -0.05$

and $a = 0.18$, the intolerant species will pay nearly the same low cost in the region $z < 1.5$. But at the same environment stress z, the tolerant species will pay the highest cost in the case of $a > 0$ and the lowest cost in the cast of $a < 0$. So we consider the environment with $a > 0$ as an adverse one.

2.2 A function of dth power of press

In the above sections, we have discussed two situations about environment press: z and $z + z^2$. For this section we will study the general situation about environment press: z^d, $d > 0$, that is

$$c(u, z) = c_0 + c_1 u + \frac{kz^d}{u}, \quad u > 0, \tag{13}$$

$$u_m = (k/c_1)^{1/2} z^{d/2}, \tag{14}$$

$$c_m = c_0 + 2\sqrt{c_1 kz}^{d/2} = c_0 + 2c_1 u_m. \tag{15}$$

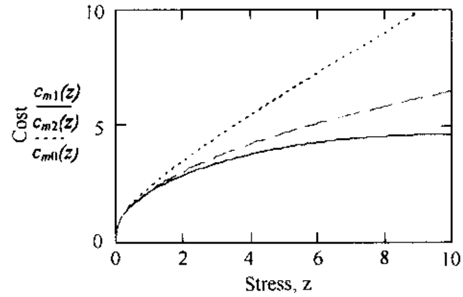

Fig.6 The curve of $c_m - z$ based on the Eq.(12) in which $k = 1, c_0 = 0.2$, $c_1 = 1$ and $a = 0$ in $c_{m0}(z)$, $a = -0.05$ in $c_{m1}(z)$ and $a = 0.18$ in $c_{m2}(z)$

Fig. 7 shows how the cost of exploiting a habitat increase with environmental stress for each of two different species that differ in their tolerance to the environmental stress in three cases: $d = 1/3$, $d = 2/3$ and $d = 3/2$.

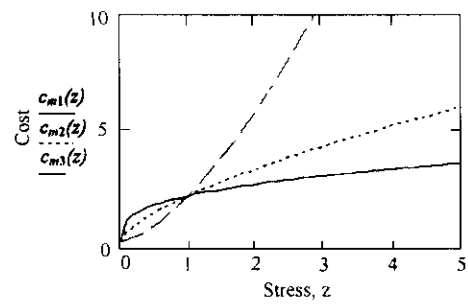

Fig.7 The comparisons of the minimum cost under the different environment press, here $k = 1$, $c_0 = 0.1$, $c_1 = 1$. The curves $c_{m1}(z)$, $c_{m2}(z)$ and $c_{m3}(z)$ correspond, respectively, to $d = 1/3$, $d = 2/3$ and $d = 3/2$

Fig.7 shows that: (1) in the region of $z < 1$ (low-stress), the cost of exploiting a habitat paid by species in the case of $d = 3/2$, is the lowest. So, the great the stress of the environment is, or the more complex the environment is, the lower cost the intolerant species will pay in the region of $z < 1$. (2) The cost will increase rapidly in the high stress region in the cases of $d = 3/2$, the high-stress region is almost not suitable for the majority of species. Obviously, in order to exist or to evolve from an environment of high-stress, the organisms must possess a higher u, or a better means of mitigating of the stress of environment. (3) In the region $d > 1$, when d decrease, the intolerant species will pays more lower cost of exploiting a habitat in the low-stress environment while the tolerant one will pays more lower cost in the high-stress environment. This means that scale d describes the selection character of the species system in the evolution process, the small the d ($d < 1$) is, the better the selection or the mitigation the system will possesses. Because the resource density in each habitat z will be set by the species that pays the lowest cost in that habitat (Mitchell, 2000), it is possible for the intolerant species to reduce resource density in low-stress habitats to a level that is unprofitable for the tolerant species while the tolerant species will exclude intolerant species from high-stress habitats.

3 Discussion

First we study a simple evolution trade-off function, the cost function which was studied by Mitchell (Mitchell, 2000):

$$c(u, z) = c_0 + c_1 u + \frac{zk}{1 + u},$$

we find that the minimum z of the point tangency of the cost line is 3.9, not 0 which was showed in Mitchell's Fig.1 (Mitchell, 2000). In order to make the cost function can be used in the general situation which the minimum z of the point tangency of the cost line is 0, we put up two revised drafts. Our revised functions show: (1)the less the unit energy cost(c_1) is, the bigger the cost and the evolutionary strategy will paid; (2)the bigger the strategy is, the less different will be in the costs of different stresses.

Considering the complex of the environment, or the nonlinear interaction of the environment, we put up a new cost function:

$$c(u,z) = c_0 + c_1 u + \frac{k(z + az^2)}{u}, \quad u > 0.$$

In the adverse environment($a > 0$), the region of low-stress which is more suitable for the intolerant species is very small, and at the same environment stress z, the tolerant species will pay the more cost than it will paid in the normal environment. However the tolerant species will pay more cost but low strategies in the environment of $a < 0$ than that it will paid in the environment of $a = 0$ or $a > 0$.

Lastly, we study the general situation about environment press:

$$c(u,z) = c_0 + c_1 u + \frac{kz^d}{u}, \quad u > 0, d > 0.$$

The results showed that the greater the stress of the environment is, or the more complex the environment is, the lower cost the intolerant species will pay in the region of $z < 1$. In order to exist or to evolve from an environment of high-stress, the organisms must possess a higher u, or a better means of mitigating of the stress of environment. Meanwhile in the region $d > 1$, when d decrease, the intolerant species will pays more lower cost of exploiting a habitat in the low-stress environment while the tolerant one will pays more lower cost in the high-stress environment. This means that scale d describes the selection character of the species system in the evolution process, the small the d($d < 1$) is, the better the selection or the mitigation the system will possesses. Because the resource density in each habitat z will be set by the species that pays the lowest cost in that habitat (Mitchell, 2000), it is possible for the intolerant species to reduce resource density in low-stress habitats to a level that is unprofitable for the tolerant species while the tolerant species will exclude intolerant species from high-stress habitats.

References:

Abrams P A, Matsuda H, Harada Y, 1993. Evolutionarily unstable fitness maximum and stable fitness minima of continuous traits[J]. Evol Ecol, 7: 465—487.

Abramsky Z, 1988. The role of habitat and productivity in structuring desert rodent communities[J]. Oikos, 52: 107—114.

Brown J H, Marquet P A, Taper M L, 1994. Evolution of body size: Consequences of an energetic definition of fitness[J]. Am Nat, 142: 573—584.

Brown J S, 1990. Habitat selection as an evolutionary game[J]. Evolution, 133: 168—182.

Brown J S, 1996. Habitat selection as an evolutionary game[J]. Oikos, 75: 193—206.

Eshel I, 1983. Evolutionary and continuous stability[J]. J Theor Biol, 103: 99—101.

Holt R D, 1985. Population dynamics in two-patch environments: Some anomalous consequences of an optimal habitat distribution[J]. Theor Pop Biol, 28: 181—208.

Keitt T H, H E Stanley, 1998. Dynamics of North American breeding bird populations [J]. Nature, 393: 257—260.

Lin Z-S, 1993. The nonlinear dynamics in the atmospheric sciences[M]. Nanjing: Nanjing University Press.

Lin Z-S, 1999. The study of the behaviors of the climatic system[M]. Beijing: China Meteorology Press.

Mitchell W A, 2000. Limits to species richness in a continuum of habitat heterogeneity: An ESS approach[J]. Evolu Eco Res, 2: 293—316.

Rosenzweig M L, 1981. A theory of habitat selection[J]. Ecology, 62: 327—335.

Rosenzweig M L, 1987. Habitat selection as a source of biological diversity[J]. Evol Ecol, 1: 315—330.

Rosenzweig M L, 1995. Species diversity in space and time[M]. Cambridge: Cambridge University Press.

(Received for review June 28, 2001. Accepted October 22, 2001)