

# **Adaptive Phenotypic plasticity**

## **Dynamics of adapting plasticity**

TJM Van Dooren  
tvdooren@gmail.com

Institute of Ecology and Environmental Sciences iEES Paris

Dept. Evolutionary Ecology  
team Phenotypic Variability and Adaptation (VPA)

Similar formalisms to classical selection equations:

The nineties

Frequency-dependent selection

Mutation-limited evolution (“evolutionary” time scale)

Neglecting small terms and substituting into Equation (A6) gives the per generation change of the population average phenotype  $\bar{z}$ ,

$$\Delta \bar{z} = G_x (\partial \ln W(z; \bar{z}) / \partial z) \Big|_{z=\bar{z}} \quad (\text{A9})$$

Here we note that the coefficient  $G_x$  is the genetic variance (variance of  $x$ ) not the phenotypic variance (variance of  $z$ ).

The same argument holds for diploid organisms provided that the genetic effects are purely additive. If

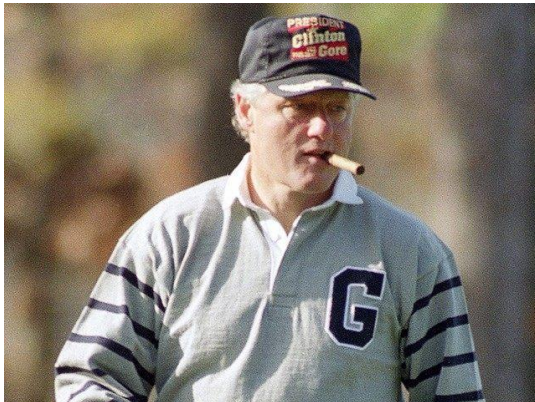
Iwasa, Pomiankowski & Nee (1991)



## The Canonical Equation of Adaptive Dynamics

$$\frac{dz}{dt} = \frac{1}{2} \mu \sigma^2 N^*(z) \frac{\partial W(z', z)}{\partial z'} \Big|_{z'=z}$$

Dieckmann and Law (1996)



The model discussed in this paper uses net reproductive rate,  $R_0$ , as the fitness measure. Thus fitness is defined as

$$R_0 = \int_x^{\infty} l(x)m(x) dx \quad (1)$$

where  $x$  denotes age,  $\alpha$  denotes age at maturity,  $l(x)$  denotes survival up to age  $x$ , and  $m(x)$  denotes fecundity at age  $x$ . To determine the optimal age at maturity we further assume 1) that growth is determinate and that 2) adult and juvenile mortality rates are independent of age and size. With these assumptions equation (1) is reduced to

$$R_0 = \frac{l(\alpha)m(\alpha)}{a} = \frac{e^{-j\alpha}m(\alpha)}{a} \quad (2)$$

where  $a$  denotes adult,  $j$  denotes juvenile mortality rate. A list of the symbols used in the formulation of the model is given in Table 1.

To find the age at maturity that maximizes fitness,  $R_0$ , we differentiate equation (2) with respect to  $\alpha$  and set the resulting equation to 0 to get

$$\frac{dm}{d\alpha} = \frac{\partial m}{\partial s} \frac{\partial s}{\partial \alpha} = jm(\alpha) \quad (3)$$

Variability in growth curves  
Between environments

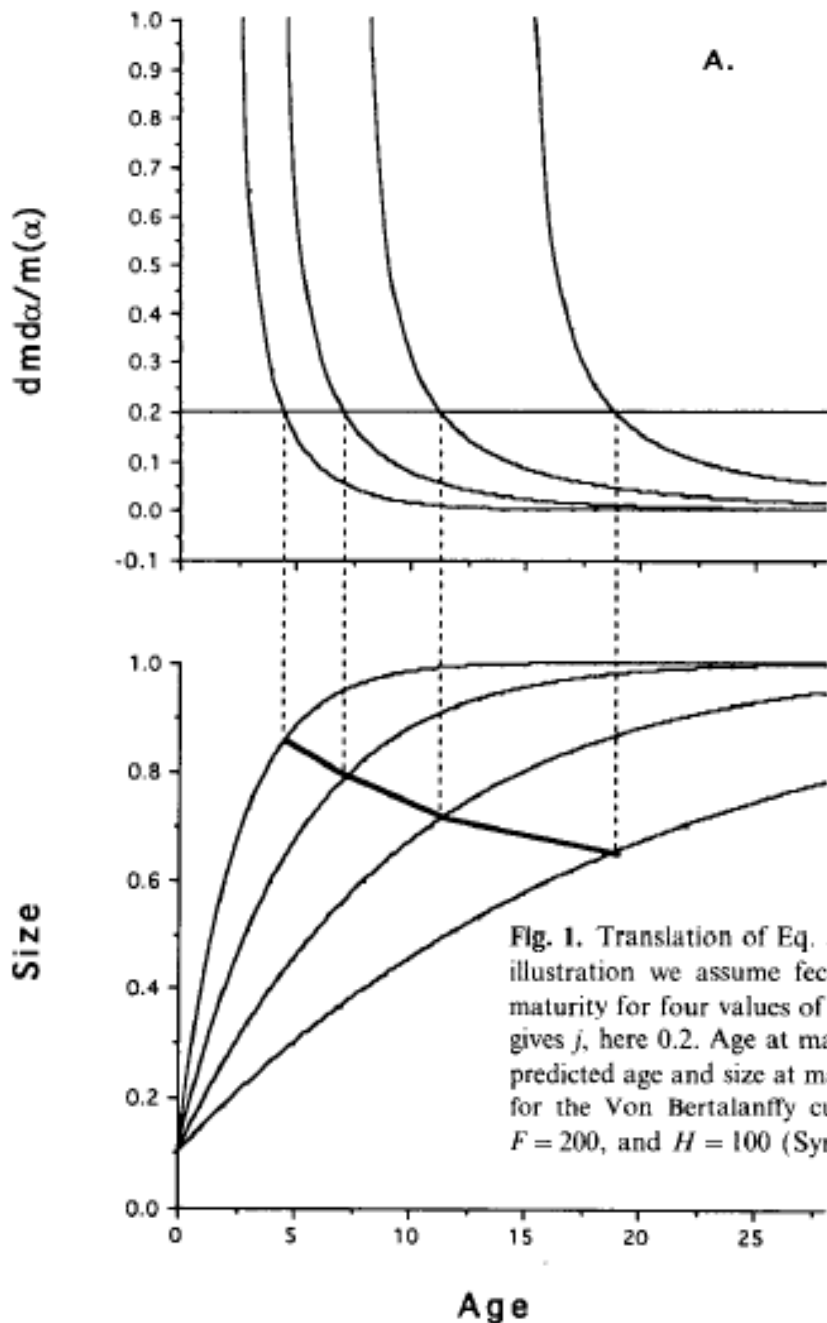
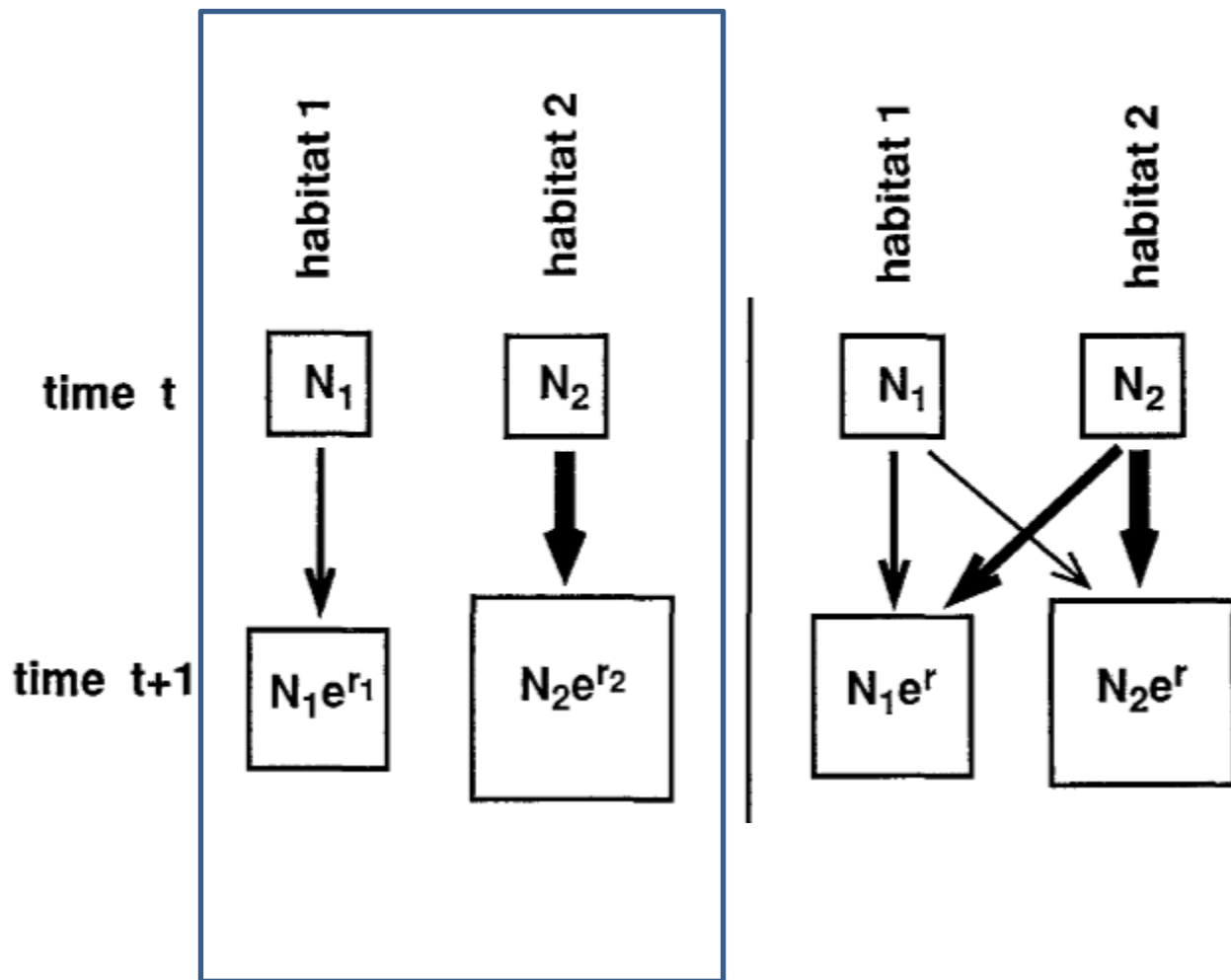


Fig. 1. Translation of Eq. 3 into a reaction norm for age and size at maturity. For the purposes of this illustration we assume fecundity increases linearly with size. Panel A illustrates the optimal age at maturity for four values of the growth coefficient of the Von Bertalanffy equation,  $k$ . The horizontal line gives  $j$ , here 0.2. Age at maturity is on the  $x$  axis and  $(dm/dx)/m(x)$  is on the  $y$  axis. Panel B shows the predicted age and size at maturity at an evolutionary equilibrium. In this example the growth coefficients for the Von Bertalanffy curves are 0.05 (right), 0.1, 0.2, and 0.4 (left). In addition,  $A = 1$ ,  $B = 0.9$ ,  $F = 200$ , and  $H = 100$  (Symbols defined in Table 1).



where  $L(x,h)$  is the survival to age  $x$  in habitat  $h$ . The number of individuals born in a given habitat during time  $dt$  differs from the number of individuals settling in this habitat at this time because some offspring emigrate and some settlers come from other habitats. However, the total number of individuals born at a given time in the population must be the same whether they are classified by the habitat of origin (i.e. their parents' habitat) or by the habitat in which they are destined to live. Hence

$$dt \int_{\mathbf{H}} N(0,h,t) dh = dt \int_{\mathbf{H}} \left[ \int_0^{\infty} N(0,h,t-x) L(x,h) B(x,h) dx \right] dh \quad (4)$$

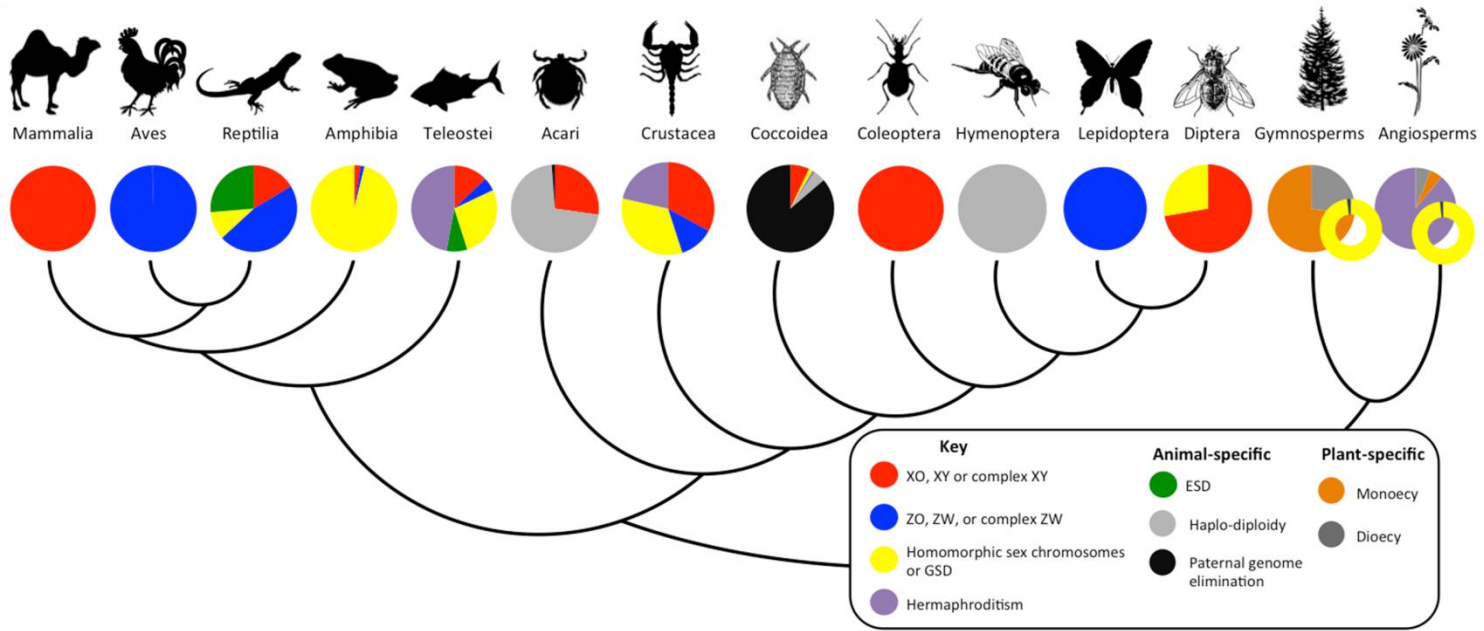
$$N(0,h,t-x) = N(0,h,t) e^{-rx} \quad (5)$$

By substituting this relation into Equation 4 and dividing both sides by the total number of individuals born during period  $dt$ , one obtains the characteristic equation:

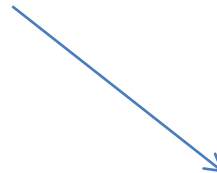
$$1 = \int_{\mathbf{H}} \left[ q(h) \int_0^{\infty} e^{-rx} L(x,h) B(x,h) dx \right] dh \quad (6)$$

This is a characteristic equation from which an  $r$  is derived that is an appropriate fitness

# Evolution of ESD environmental sex determination

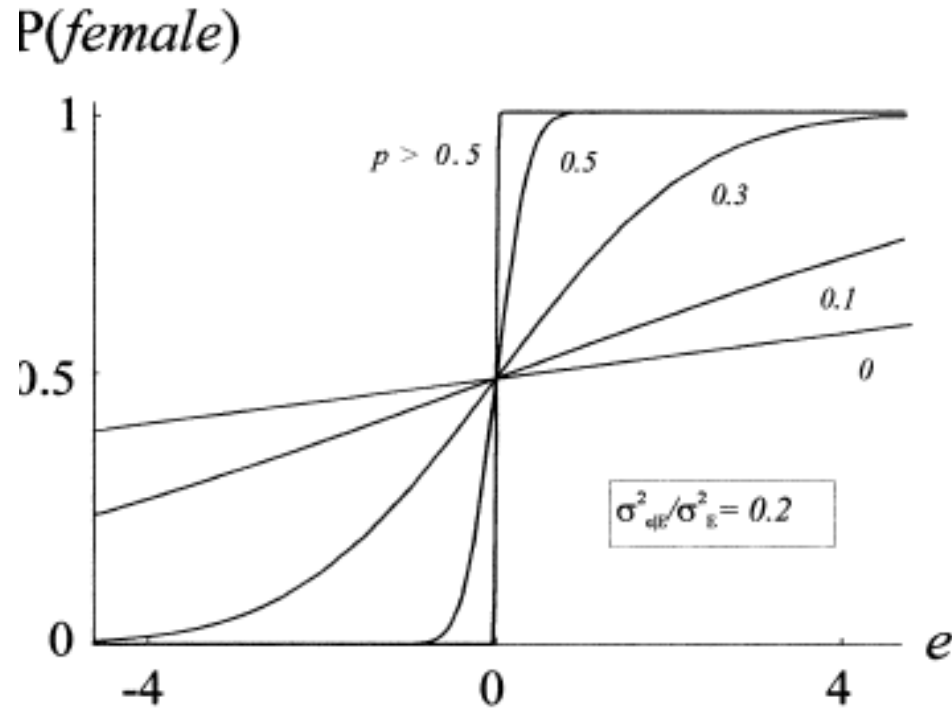


Bulmer and Bull (1982) adaptive dynamics style



Van Dooren and Leimar (2003)

# Evolution of ESD environmental sex determination





Assumptions of “adaptive dynamics” → useful simplification

Very “clean” natural selection

- Mutation - limited evolution
  - population sizes are large
  - mutations are rare and mutational steps are "small"
- evolution proceeds by invasion of mutants (and subsequent events) – use invasion fitness
- *only one genotype is common in the evolving population*
- *fitness functions and phenotype landscapes are smooth*

birth

development

competition for  
mates

Individual environment  $e$  in patch environment  $E$

Determines probability of becoming female  $x(e)$

Determines competitive ability as an adult female  $f(e)$ , male  $m(e)$

conditional probability of  $e$  with partial  
migration  $p$  between patches at moment of  
competition for mates

$$\tilde{h}(e | E) = (1 - p)h(e | E) + p \int g(V)h(e | V)dV$$

$$X(E) = \int x(e)\tilde{h}(e)de$$

and the average competitive ability among the females in the patch is

$$F(E) = \frac{1}{X(E)} \int f(e)x(e)\tilde{h}(e|E) de. \quad (3a)$$

Similarly, the average competitive ability among the males is

$$M(E) = \frac{1}{1 - X(E)} \int m(e)[1 - x(e)]\tilde{h}(e|E) de. \quad (3b)$$

There is some migration,  $p > 0$

Consider an individual using a rare mutant strategy  $x'$ . When it has developed in individual environment  $e$  and attempts to reproduce in a patch with parameter  $E$ , the expected genetic contribution of that individual to the pool of next generation zygotes will be equal to

$$R(x', x | e, E) = \frac{1}{2} \left\{ x'(e) \frac{f(e)}{F(E)} \frac{1}{X(E)} + [1 - x'(e)] \frac{m(e)}{M(E)} \frac{1}{1 - X(E)} \right\}. \quad (4)$$

$$R(x', x | E) = \int R(x', x | e, E) \tilde{h}(e | E) de = \frac{1}{2} \left\{ \frac{F'(E)X'(E)}{F(E)X(E)} + \frac{M'(E)[1 - X'(E)]}{M(E)[1 - X(E)]} \right\}. \quad (5)$$

$$R(x', x) = \int R(x', x | E) g(E) dE. \quad (8)$$

## SPECIAL WHEN THERE IS ONE RESIDENT REACTION NORM

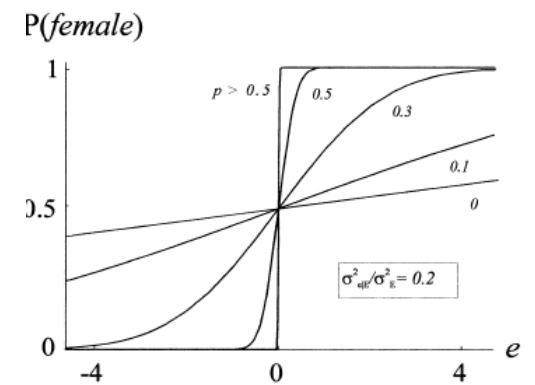
Evolution maximizes

$$P(x) = \frac{1}{2} \int \log\{F(E)X(E)M(E)[1 - X(E)]\}g(E) dE, \quad (12)$$

since one readily verifies that

$$s_c = \frac{\partial P(x)}{\partial c}. \quad (13)$$

$c$  a parameter that characterizes the reaction norm



We modeled sex-determination phenotypes using a family of sigmoid functions,  $x_{a,b}(e)$ , of the individual environmental variable  $e$ , and with two genotypic parameters,  $a$  and  $b$ . These give the value ( $a$ ) of the environmental variable where the probability of becoming a female equals one-half, and the slope ( $b$ ) of the reaction norm at that point (see Fig. 1 for some examples). As sigmoid functions with these properties, we used

$$x_{a,b}(e) = \Phi[\sqrt{2\pi}b(e - a)], \quad (14)$$

where  $\Phi(z)$  is the cumulative distribution of a standard normal variate. We can interpret equation (14) as a threshold trait with discrete developmental responses to a continuously varying liability (Lynch and Walsh 1998). Thus, we can re-

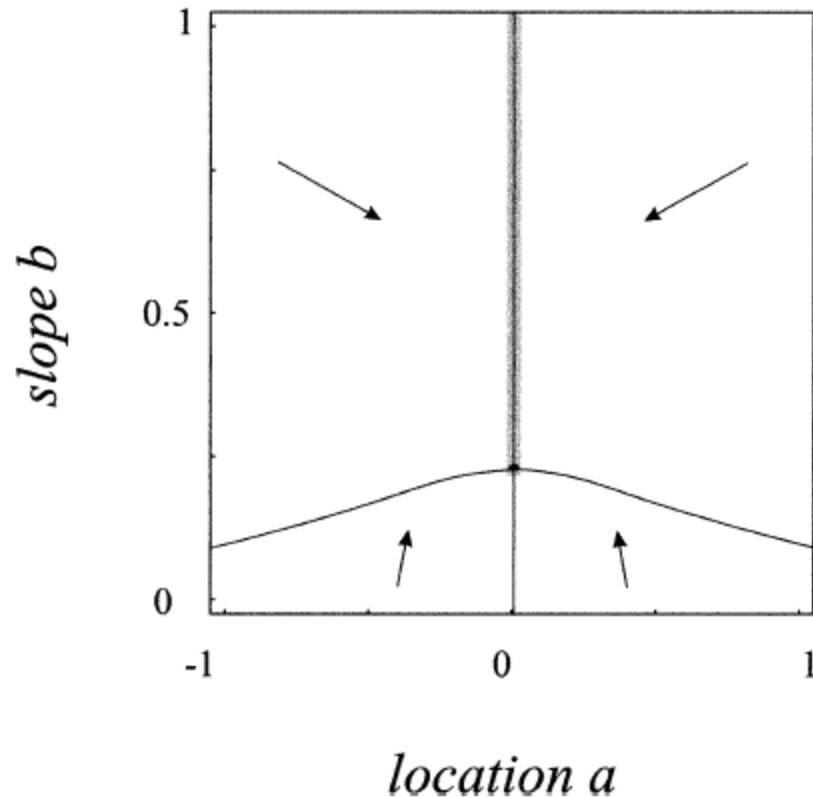
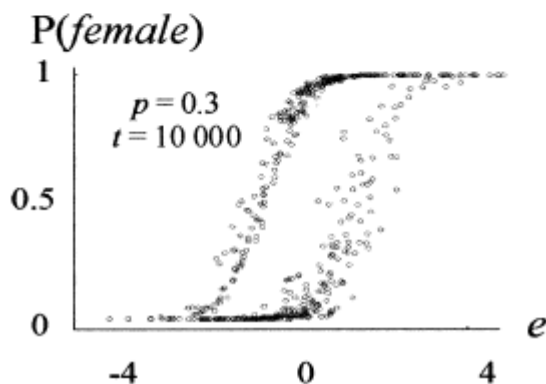
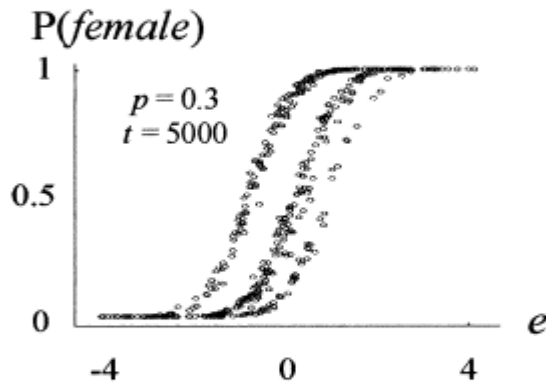
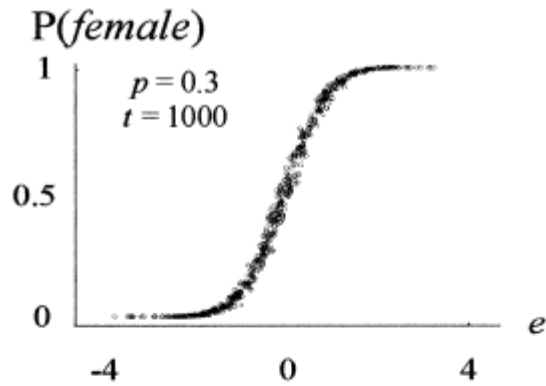


FIG. 2. Pattern of invasion fitness in the space of trait parameters  $(a, b)$ . Gradual evolution can either increase or decrease trait values, depending on the resident values of  $a$  and  $b$ . Regions with different directions of evolution are separated by lines and the main direction within each region is indicated by an arrow. Gradual evolutionary change in  $a$  and  $b$  leads to a convergence stable strategy  $(a^*, b^*) = (0.0, 0.22)$ , indicated by a dot. In the shaded interval of the line  $a = a^* = 0$ , invasion fitness shows disruptive selection on the location parameter  $a$ . Selection is weakly disruptive at  $(a^*, b^*)$ . Parameter values for the competitive abilities and environmental variables are as in Figure 1A and the migration rate  $m$  equals 0.3.



When we parameterize the reaction norm by  $a$  and slope  $b$

and constrain the evolution of  $b$

we can get disruptive selection on  $a$  for very long and the evolution of GSD

**WATCH OUT WHEN USING**

**few parameters**

**arbitrary chosen speeds of evolution**



