

# Laws of Adaptation

A course on biological evolution in eight lectures  
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## Lecture 2

Optimization, or the “static” point of view

Wednesday October 4, 15:00-16:00

## Limitations of short term dynamics

- ❖ Most adaptations of interest in Evolutionary Ecology are intrinsically complex
- ❖ Involve characters of unknown genetics
- ❖ These characters are most likely controlled by several genes, possibly interacting in complicated pathways
- ❖ The genetically explicit models of short term dynamics cannot cope with these situations

## A solution offered by Evolutionary Ecology

- ❖ A convenient by-pass adopted in Evolutionary Ecology is to raise to the rank of a *postulate* the notion that fitness is maximized by natural selection, thereby avoiding the need of an explicit formulation of evolutionary dynamics
- ❖ Hence, to predict the solution of any given adaptive problem, faced in nature by a particular set of species, the procedure is to construct an appropriate *fitness function* that determines survival and or rates of reproduction at any given value of one or more biological traits, supposedly relevant to the problem at hand, and for any given value of environmental variables to which the species under consideration are supposed to respond adaptively
- ❖ Once the appropriate fitness function is given, the solution to the adaptive problem is obviously provided by the maxima of this function with respect to the trait values, for any given state of the environment
- ❖ This solution then, not only provides (if it agrees with empirical data) an explanation to the adaptations actually observed in nature that precipitated the analysis, but it also offers predictions concerning new adaptive possibilities in ecological situations not yet observed

## Dormant seeds of annual plants

- ❖ At the onset of the bad season (cold, dry, etc.), *annual* plants cast seeds and die.
- ❖ Seeds, protected by defensive structures, pass the bad season buried in the soil, ready to germinate and raise a new plant as the good phase of the annual cycle returns
- ❖ Not in all species of annual plants all seeds germinate immediately, at the first new cycle after their dispersal. Depending on the species, and the habitat, a fraction of seeds might remain in a dormant (quiescent) state for one or more years.
- ❖ The issue is: what determines the length (in number of years) of the dormant phase?

## Analysis of evolution of dormancy (Cohen, 1966)

- ❖ A simple life cycle model for a population of annual plants

$t \in \{0, 1, \dots\}$  : year (annual cycle starts at onset of good season, when seeds germinate)

$y(t)$  : mean number of seeds cast by a plant on year  $t$  (a random variable whose distribution is determined by the environment)

$g \in [0, 1]$  : germination rate, i.e. probability that a seed germinates at onset of new year (the evolving trait);  
 $g < 1$  in species that practice dormancy

$\mu \in (0, 1)$  : seed mortality, i.e. probability that a non-germinated seed dies during year (depends on the environment)

$S(t) \in [0, \infty)$ : seed stock alive in soil when year  $t$  begins

- ❖ Then  $S(t)$  satisfies the following recurrence equation

$$S(t+1) = [(1-g)(1-\mu) + gy(t)]S(t) \Rightarrow S(t) = \left\{ \prod_{j=0}^{t-1} [(1-g)(1-\mu) + gy(j)] \right\} S(0) \rightarrow e^{\rho(g)t} S(0) \text{ as } t \rightarrow \infty$$

where

$$\rho(g) = E \left\{ \ln [(1-g)(1-\mu) + gy(t)] \right\}$$

expectation being taken with respect to the distribution of the random variable  $y(t)$

- ❖ Hence  $\rho(g)$  may be used as the appropriate fitness associated to the trait value  $g$

## Optimal germination rate

- ❖ Notice that in order that a population subsists at all for  $0 \leq g < 1$  it is *necessary* that  $E[y(t)] > 1$ ; in fact, by the concavity of  $\ln(\cdot)$

$$\rho(g) = E \left\{ \ln \left[ (1-g)(1-\mu) + gy(t) \right] \right\} \leq \ln \left\{ (1-g)(1-\mu) + gE[y(t)] \right\} < 0 \quad \text{for } E[y(t)] \leq 1 \quad \text{when } 0 \leq g < 1$$

hence we assume that  $E[y(t)] > 1$

- ❖ Under this assumption, as it is natural, it is always advantageous to have a *positive* germination rate; in fact we have

$$\rho'(g) = \frac{d\rho(g)}{dg} = E \left\{ \frac{y(t) - (1-\mu)}{(1-g)(1-\mu) + gy(t)} \right\} \quad \text{and} \quad \rho'(0) > 0 \Leftrightarrow E[y(t)] > 1 - \mu$$

- ❖ Since the optimum germination rate,  $g^\circ$ , has to maximize  $\rho(g)$  with respect to  $g \in [0, 1]$ , in order that some dormancy is adaptive, i.e.  $0 < g^\circ < 1$ , it is sufficient that

$$\rho'(1) = 1 - (1-\mu)E \left[ \frac{1}{y(t)} \right] < 0 \quad \Leftrightarrow \quad E \left[ \frac{1}{y(t)} \right] > \frac{1}{1-\mu}$$

- ❖ Hence, dormancy is a sort of “insurance” against extreme environmental uncertainty under which very poor years – such that  $y(t) \approx 0$  – may occur, even if only occasionally

## Clutch size in animals with parental care



Eggs of Willow Flycatcher in the nest  
downloaded from [www.usgs.nau.edu](http://www.usgs.nau.edu)



A Willow Flycatcher  
downloaded from [thebirdguide.com](http://thebirdguide.com)

- ❖ Clutch size, i.e. the number of offspring born to a parent in a single batch, such as the number of eggs in birds nests, is rather constant within a species but varies among species, in animals that, as parents, have to care for their progeny for some length of time after birth, such as most birds and mammals
- ❖ Among closely related species living in different environment, clutch size varies often in correlation with biologically relevant environmental parameters
- ❖ For example in several groups of related species of birds nesting in the northern hemisphere, clutch size increases with the latitude of the breeding area of the species

## Analysis of evolution of clutch size (Lack, 1947, Charnov and Krebs, 1973)

- ❖ Clutch size appears therefore as an adaptive trait for which we could try to predict the relation to environmental properties
- ❖ The basic ideas being that: (i) in any given environment, parents can gather only a limited amount of food in the unit time, the less so in poorer environments, so that if offspring are too many their health and survival might be at risk; (ii) caring for offspring may be costly for parents, the more so in less productive environments, so that if the progeny to be looked after is too large, parents well-being might be impaired
- ❖ Consider the following simple model, mostly applicable to birds

$t \in \{0, 1, \dots\}$ : year, considered to begin at nesting time

$b \in [0, B]$ : clutch size

$s(b) \in [0, 1]$ : proportion of nestlings surviving to next year, when they will reproduce for the first time

$p(b) \in [0, 1]$ : proportion of adults surviving from one year to the next

$n(t) \in [0, \infty)$ : total number of adults alive at onset of year  $t$  in a given population

- ❖ Then,  $n(t)$  satisfies the following law of growth

$$n(t+1) = [p(b) + bs(b)]n(t)$$

- ❖ The fitness function that we assume to be maximized with respect to clutch size,  $b$ , is the growth rate of the population:

$$r(b) = p(b) + bs(b)$$

# Optimal clutch size in various situations

## ❖ General assumptions

$p(b)$ ,  $s(b)$ : non increasing with  $b$  ;  $s(B) = 0$

$r(b)$ : concave in  $b$

## ❖ Interested in

$b^\circ$ : value of  $b$  such that  $r(b^\circ) = \max_{0 \leq b \leq B} r(b)$

## ❖ **Case 1:** parent survival independent of clutch size; nestling survival dependent on environment

$b^\circ$ :  $b^\circ s(b^\circ) = \max_{0 \leq b \leq B} bs(b)$  [note:  $bs(b)$  is no. of offspring raised to adulthood]

$e \in [0, \infty)$ : environmental productivity of food resources

$s(b) = s(b, e) = \sigma\left(\frac{b}{B(e)}\right)$  ;  $B(e) \uparrow$  in  $e$  ;  $\sigma(u) \downarrow$  in  $u \in [0, 1]$  ;  $\therefore e'' > e' \Rightarrow s(b, e'') > s(b, e') \forall b \in [0, B)$

$u^\circ$ :  $u^\circ \sigma(u^\circ) = \max_{0 \leq u \leq 1} u \sigma(u) \Leftrightarrow b^\circ = b^\circ(e) = B(e)u^\circ \Rightarrow b^\circ(e) \uparrow$  in  $e$

## ❖ This result can explain increase of clutch size with latitude: as latitude increases the number of daily light hours in summer also increases and with it the amount of time available for parents to gather food for their nestlings



- ❖ **Case 2:** parent survival dependent on clutch size

$$p(b) \downarrow \text{ in } b \in [0, B]$$

$$b^\circ : r(b^\circ) = \max_{0 \leq b \leq B} r(b) = \max_{0 \leq b \leq B} [p(b) + bs(b)] \Leftrightarrow s(b^\circ) + b^\circ s'(b^\circ) = -p'(b^\circ) > 0$$

$$b^* : b^* s(b^*) = \max_{0 \leq b \leq B} bs(b) \Leftrightarrow s(b^*) + b^* s'(b^*) = 0 \quad ; \quad \therefore b^\circ < b^* \quad \text{because } s(b) + bs'(b) \downarrow \text{ in } b$$

- ❖ This result can explain the observation that in some case clutch size is less than the value that would ensure the maximum number of adult offspring
- ❖ It can be verified that also in this case, if environment affects nestling survival but not adult survival as in case 1, under the assumption of concavity of  $r(b)$ , the optimal clutch size  $b^\circ$  increases as the environment improves.
- ❖ **Case 3:** parent survival dependent on clutch size and on environment; nestling survival independent of environment

$e \in [0, \infty)$ : a measure of environmental quality for adults

$$p(b) = p(b, e) = e\pi(b) \quad ; \quad \pi(b) \downarrow \text{ in } b \in [0, B]$$

$$b^\circ(e) : s(b^\circ(e)) + b^\circ(e)s'(b^\circ(e)) + e\pi'(b^\circ(e)) = 0 \quad \forall e \in [0, \infty)$$

$$e_2 > e_1 \Rightarrow 0 = s(b^\circ(e_1)) + b^\circ(e_1)s'(b^\circ(e_1)) + e_1\pi'(b^\circ(e_1)) > s(b^\circ(e_1)) + b^\circ(e_1)s'(b^\circ(e_1)) + e_2\pi'(b^\circ(e_1))$$

$$\therefore b^\circ(e_2) < b^\circ(e_1)$$

- ❖ Thus influences of the environment on nestling survival and on parent survival have just opposite consequences for the optimal clutch size: when the environment is improved the optimal clutch size increases in the former case, decreases in the latter

## Conflicts between individuals



Spanish Ibex males fighting  
photographer joanna korman peter arnold, inc  
downloaded from [www.painetworks.com](http://www.painetworks.com)

- ❖ In many ecological contexts, reproductive success of individuals depends on the outcome of interactions with other members of the population. For example, this is the case of conflicts for the possession of an important resource, such as a food item, a territory, or a mate
- ❖ The outcome of such interactions depends not only on the qualities and the behavior of the subject, but also on the characteristics of his adversary. For example, in a situation of potential fight, a very aggressive individual might do very well with a submissive adversary but not equally well with one as aggressive as himself
- ❖ Whenever this is the case, fitness associated to any trait or behavior which is relevant to the interaction is *frequency dependent*, i.e. it depends on the composition of the population with respect to the variation of such trait
- ❖ If fitness of a trait is frequency dependent, there might not exist an “optimal” value of this trait, a value that maximizes fitness in all possible population states: an alternative notion to “optimality” is required
- ❖ A solution is provided by the framework of *Game Theory*

## The “Hawk-Dove” population game

- ❖ *Situation*: contests among two individuals for the possession of a valuable resource; in these situations many animals start by displaying, thenceforth may escalate or retreat
- ❖ *Strategies*: (i) “Hawks”, who always escalate till succumb or win; (ii) “Doves”, who always retreat as soon as opponent escalates
- ❖ *Payoffs* (relative to resource value – additive contribution to fitness of contest’s outcome):

$v(X,Y)$  = payoff to individual playing X when opponent plays Y

		opponent	
		H	D
subject	H	$(1-c)/2$	1
	D	0	$1/2$

- ❖ Assume: (i) an infinite population where a proportion  $p$  of the individuals play H and the rest play D; (ii) pairs of interacting individuals meet at random

$$\text{fitness of H: } W(H) = W_0 + p v(H,H) + (1-p) v(H,D) = W_0 + 1 - \frac{1+c}{2} p$$

$$\text{fitness of D: } W(D) = W_0 + p v(D,H) + (1-p) v(D,D) = W_0 + \frac{1-p}{2}$$

- ❖ Then, if  $c > 1$ :  $p \approx 0 \Rightarrow W(H) > W(D)$  while  $p \approx 1 \Rightarrow W(D) > W(H)$

## Evolutionarily Stable Strategies (Maynard Smith and Price, 1973)

- ❖ The notion of ESS is related to that of “Nash Equilibrium”, but is adapted to a biological and evolutionary context to replace the notion of “Optimality” when selection is frequency dependent
- ❖ A strategy  $X^\circ$  is an ESS if, when it is sufficiently abundant in a population containing also a minority strategy  $X$ , its fitness is greater than that of  $X$ , for all possible  $X \neq X^\circ$
- ❖ The underlying *assumption* – exactly as in the optimality approach – being that, since  $X^\circ$  has a superior fitness when it prevails in a population, any mutant strategy, introduced in small number, will be eliminated through natural selection, so that no further evolutionary change can take place in the population
- ❖ *Condition for an ESS*: suppose that  $X^\circ$  is an ESS, adopted in a population by a proportion  $p$  of individuals, while the others follow an alternative  $X$ ; then

$$W(X^\circ) = W_0 + pv(X^\circ, X^\circ) + (1-p)v(X^\circ, X) \quad , \quad W(X) = W_0 + pv(X, X^\circ) + (1-p)v(X, X)$$

thus

$$W(X^\circ) - W(X) = p[v(X^\circ, X^\circ) - v(X, X^\circ)] + (1-p)[v(X^\circ, X) - v(X, X)] > 0 \text{ for } p \approx 1$$

if and only if

$$v(X^\circ, X^\circ) > v(X, X^\circ)$$

or

$$v(X^\circ, X^\circ) = v(X, X^\circ) \text{ and } v(X^\circ, X) > v(X, X)$$

## Mixed strategies

- ❖ In the “Hawk-Dove” game we have explicitly mentioned only the two strategies H, D, by which an individual behaves always the same. These are *pure* strategies
- ❖ But, in addition, for any  $u \in (0,1)$ , a *mixed* strategy can be defined by which an individual plays H with probability  $u$  and plays D with probability  $(1-u)$
- ❖ In general, if the set of possible pure strategies is  $\Delta = \{D_1, \dots, D_k\}$ , to any probability vector  $\mathbf{u} = (u_1, \dots, u_k)^T$  there corresponds a mixed strategy  $S(\mathbf{u})$ , by which an individual plays  $D_i$  with probability  $u_i$ , for  $i=1, \dots, k$ . The subset of  $\Delta$  of the pure strategies  $D_i$  for which, in  $S(\mathbf{u})$ ,  $u_i > 0$ , is called the support of  $S(\mathbf{u})$
- ❖ The payoff for a strategy  $S(\mathbf{u})$ , when played against  $S(\mathbf{v})$ , naturally is

$$v(S(\mathbf{u}), S(\mathbf{v})) = \sum_{ij} u_i v_j v(D_i, D_j)$$

- ❖ The *Bishop-Cannings* theorem (Bishop and Cannings, 1978): if the mixed strategy  $S(\mathbf{u}^\circ)$  is an ESS then, for each of the pure strategies  $D_i$  in its support

$$v(D_i, S(\mathbf{u}^\circ)) = v(S(\mathbf{u}^\circ), S(\mathbf{u}^\circ))$$

*Proof:* there cannot be a  $D_i$  such that  $v(D_i, S(\mathbf{u}^\circ)) > v(S(\mathbf{u}^\circ), S(\mathbf{u}^\circ))$ , otherwise  $S(\mathbf{u}^\circ)$  would not be an ESS. Suppose now that the reverse inequality is strictly true for a particular  $D_i$  in the support of  $S(\mathbf{u}^\circ)$ . Then, if  $\mathbf{v}^\circ$  denotes the conditional probability distribution implied by  $\mathbf{u}^\circ$  given that  $D_i$  is *not* played, it would follow that

$$v(S(\mathbf{u}^\circ), S(\mathbf{u}^\circ)) = u_i v(D_i, S(\mathbf{u}^\circ)) + (1 - u_i) v(S(\mathbf{v}^\circ), S(\mathbf{u}^\circ)) < v(S(\mathbf{v}^\circ), S(\mathbf{u}^\circ))$$

which is impossible because  $S(\mathbf{u}^\circ)$  is an ESS.

## ESS in the “Hawk-Dove” population game (Maynard Smith, 1982)

- ❖ D cannot be an ESS because  $v(H,D) > v(D,D)$
- ❖ If escalation does not cost much ( $c < 1$ ), H is an ESS because  $v(D,H) < v(H,H)$ , but when the cost of escalation is great compared to the value of the contended resource ( $c > 1$ ) even H cannot be an ESS
- ❖ Are there mixed ESS? These can be identified by the aid of the Bishop-Cannings theorem: a mixed strategy S could be an ESS if  $v(H,S) = v(D,S)$
- ❖ If  $u \in (0,1)$  is the probability of playing H in S, this gives the equation in u:

$$u[v(H,H) - v(D,H)] + (1 - u)[v(H,D) - v(D,D)] = 0$$

- ❖ If  $c < 1$ , when H is an ESS, there is no solution in  $(0,1)$  to this equation, but if  $c > 1$  the solution is

$$u = u^\circ = \frac{1}{c}$$

- ❖ That  $u^\circ$  actually produces an ESS,  $S^\circ$ , must yet be verified by checking the second part of the ESS condition, namely that, for any strategy  $S \neq S^\circ$ ,  $v(S^\circ, S) > v(S, S)$ ; which is indeed the case
- ❖ The biological conclusion therefore is quite reasonable: unremitting escalation in animal conflicts is adaptive only when the associated costs are small relative to the value of the contended resource; if instead these costs are high, the most adaptive behavior would be a mix of escalation and defection, with a decreasing propensity to escalate as costs increase

	H	D
H	$(1-c)/2$	1
D	0	1/2