

The evolution and maintenance of genetic polymorphisms in natural populations

1. How can genetic variation be maintained in natural populations?
2. Some examples of genetic polymorphisms
3. Maintenance of genetic polymorphisms through mimicry
4. Evolution and maintenance of sex-limited polymorphisms in damselflies (Odonata)



This presentation: <http://www.carleton.ca/~sherratt/teaching.htm>

The maintenance of genetic variation

1. Variation selectively neutral
2. Selection-mutation balance
3. Balance of selective forces
 - (a) Heterozygote advantage
 - (b) Frequency-dependent selection
 - (c) Fitnesses vary in space and/or time
 - (d) Selection acts differently at different levels



Genetic polymorphisms

“The occurrence together in the same locality of two or more discontinuous forms of a species in such proportions that the rarest cannot be maintained by recurrent mutation”

E.B. Ford

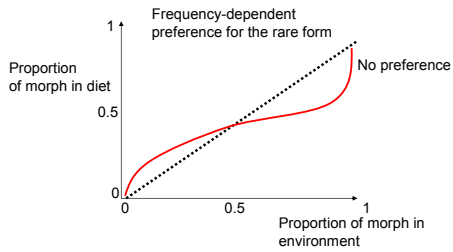
- Rules out recurrent mutation
- Focuses on phenotypes rather than genotypes – “visual polymorphisms”



Most explanations based on some form of frequency-dependent advantage whereby the relative success of one genotype is highest when it is rare (apostatic selection)

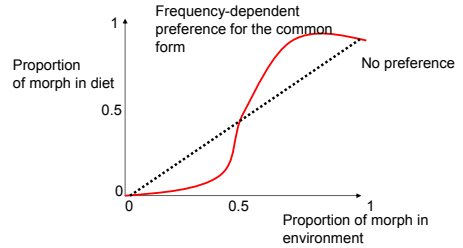


Predator behaviour may generate selection that promotes the common form over the rare form (anti-apostatic selection) – selection for uniformity



For example, greater tendency to attack prey which "stand out from the crowd"

Predator behaviour can sometimes generate selection that promotes the rare form over the common form of a species (apostatic selection) – selection for polymorphism



For example, greater tendency to approach and pursue forms that you have encountered before

Mimicry as a generator of frequency-dependent selection, hence biological diversity

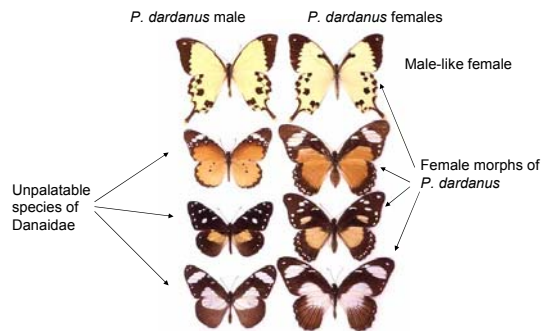


Henry Walter Bates (1825–1892).

Certain palatable (undefended) species may gain selective advantage by resembling palatable species

Greater selective advantage to mimic when it is rare (compared to the unpalatable "model")

Polymorphic mimicry in *Papilio dardanus* (African Swallowtail)



Batesian polymorphism



Volucella bombylans – a polymorphic mimetic hoverfly (Syrphidae)



Vespid wasp

Syrphid fly

Batesian mimicry

Photographs courtesy of Dr Henri Goulet, ECORC, Ottawa

Holarctic hoverflies (Syrphidae)

Bumblebee mimics



71 species

22 polymorphic

14 sex limited

Wasp mimics



157 species

0 polymorphic

4 sex limited

Data from F. Gilbert (*in press*)

Polymorphisms are common in Batesian mimetic systems, but not entirely typical



Fritz Müller

Unpalatable species may gain mutual advantage by resembling one another, thereby reducing the per capita cost of predator education

Fritz Müller

Greater selective advantage when common



Lycid beetle



Arctid moth

Müllerian mimicry

Photographs courtesy of Dr Henri Goulet, ECORC, Ottawa

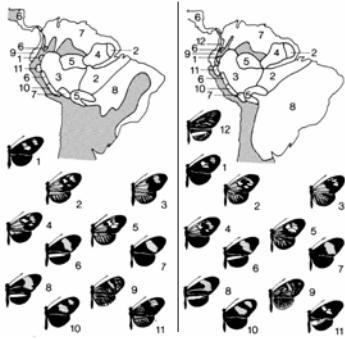
The puzzle – many Mullerian mimics are polymorphic on a regional scale

Mimicry in *Heliconius*



Other Mullerian mimic species

Turner (1981) Ann Rev Ecol Syst



Heliconius melpomene

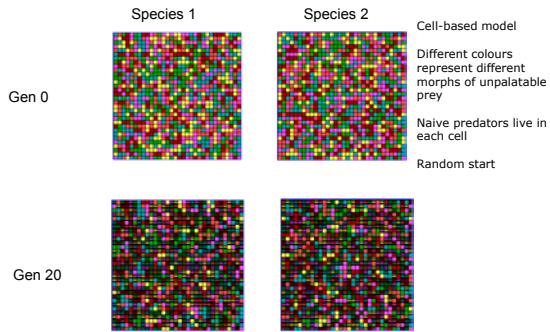
Heliconius erato

Dendrobatid imitator on top

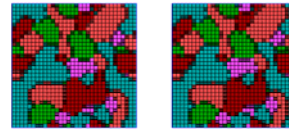


Symula et al. Proceedings B (2001)

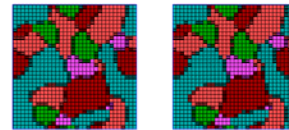
Understanding how polymorphism can be maintained when there is strong selection for uniformity



Gen 500



Gen 1000



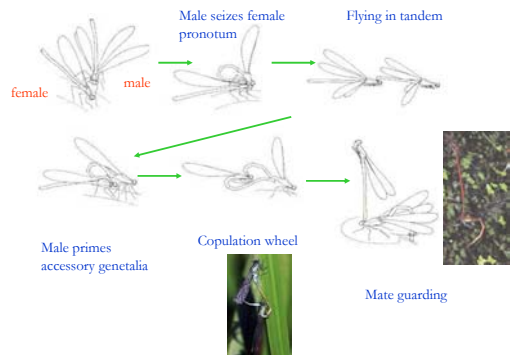
Selection for uniformity in unpalatable prey promotes homogeneity, but it can also preserve regional heterogeneity once local differences have arisen by some other means

Sex-limited polymorphism in damselflies (Odonata)

1. Odonate ecology
2. The phenomenon of sex-limited polymorphism
3. A theory, and some evidence



Typical mating behaviour of damselflies



Polymorphism in *Enallagma cyathigerum*



Gynomorph female

Andromorph female

Male

Xanthocnemis zealandica



Gynomorph



Andromorph

Polymorphism in *Ischnura elegans*



Gynomorph females
(rufescens-obsolata)

(infuscans)

Andromorph female

Male

Female-limited polymorphism in damselflies: a few facts and figures



Common (occurs in $\approx 1/2$ European genera)

One form resembles the male (**andromorph**), while one or more do not (**gynomorph(s)**)

Crossing experiments indicate genotypic ratios consistent with **genetic variation at a single locus** with sex-limited expression

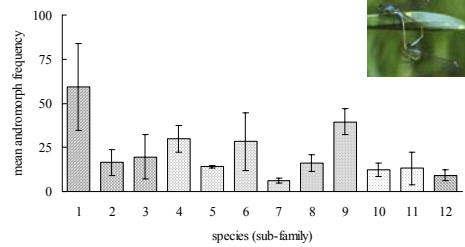
Analogous female-limited polymorphisms occur in some species of **butterfly** and **hummingbird**



Several field studies have found no difference in survivorship between morphs, or life-time reproductive success (e.g. Thompson 1989, Cordero 1992, Fincke 1994).



McKee et al. (in prep)



Mean andromorph frequency of twelve species of coenagrionid damselflies, arranged in sub-family groups: 1 *Argia vivida* (Argiinae); 2 *Coenagrion mercuriale* (Coenagrioninae); 3 *Coenagrion puella* (Coenagrioninae); 4 *Enallagma hageni* (Ischnurinae); 5 *Ischnura damula* (Ischnurinae); 6 *Ischnura elegans* (Ischnurinae); 7 *Ischnura fluviatilis* (Ischnurinae); 8 *Ischnura graellsii* (Ischnurinae); 9 *Ischnura ramburi* (Ischnurinae); 10 *Cenagrion tenellum* (Nehalenninae); 11 *Nehalonia irene* (Nehalenninae); 12 *Xanthocnemis zealandica* (Pseudagrioninae).

Is it mimicry ?

Sometimes only differentiable on close inspection

Often behavioural as well as morphological similarity
(Robertson 1985, Forbes *et al.* 1991)



Different forms not arbitrary: - there is always one form that resembles the male



It looks likely that its mimicry, but **intra-specific** rather than **inter-specific** (and a rather unusual case of females resembling males.....)



Male mimicry may have evolved in females to avoid excessive harassment by males

Even if females can reject male advances it can still result in physical injury and upset energy budgets.

But if mimicry were so good, why isn't there selection for all females to become mimetic?

A formal theory for the evolution and maintenance of polymorphism in odonates

Andromorphs gain a frequency-dependent advantage by avoiding harassment through mimicry, but pay the frequency-independent cost of being encountered more by conspecific males.

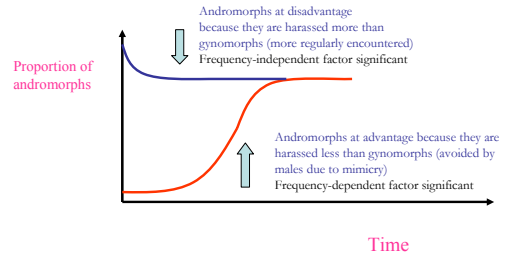
Andromorphs are likely to be encountered more frequently by males than gynomorphs because:

- (a) They are more conspicuous
- (b) They tend to be less concealed, in order to mimic males behaviourally

Sherratt (2001) Ecol. Letts.

Verbal model

Mimicry of males is a double-edged sword




Quantitative model

The males perspective...



Payoffs

True identity	Attempt to Mate ?	
	No	Yes
Andromorph	0	Benefit B
Another male	0	Cost C



Determining the optimal strategy for the male: model parameters

A - density of andromorphs

M - density of males

p - probability that a male attempts to mate given that it has encountered an andromorph

q - probability that a male attempts to mate given that it has encountered another male

Derived variables as consequences of actions

Net payoff to male proportional to:

$$A p B - M q C \quad (1)$$

Signal detection theory

Attack probabilities p (andromorph) and q (male) are related. How different p and q are depends on the *perfection of mimicry*

[$p = 1, q = 0$: no mimicry ; $p = q$: perfect mimicry]

$$p = q^s \quad (2)$$

($0 < s < 1$) $s = 0 \Rightarrow$ no mimicry, $s = 1 \Rightarrow$ perfect mimicry

Staddon & Gendron (1983) Am Nat

(2) in (1) yields:

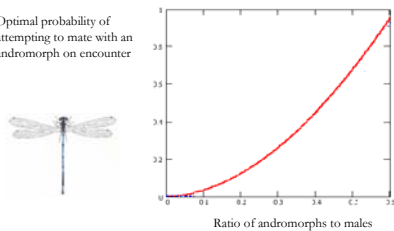
$$\text{Net payoff to male} \propto A p B - M p^{(1/s)} C$$

which is maximised by attacking andromorphs with probability p^* when encountered, where:

$$p^* = \left(\frac{A B s}{M C} \right)^{\frac{s}{(1-s)}} \quad (3)$$

Optimal attack probability for andromorphs rises with ratio of andromorphs / males

Optimal probability of attempting to mate with an andromorph on encounter



At *equilibrium* both morphs should be *equally harassed*. If andromorphs encounter males more frequently than gynomorphs, then:

$$\text{Proportion of andromorphic females (f*)} = R (C / s B) (a_G / a_A)^{(1-s)/s} \quad (4)$$

a_A, a_G - per capita encounter rates of andromorphs and gynomorphs with males ($a_A > a_G$)

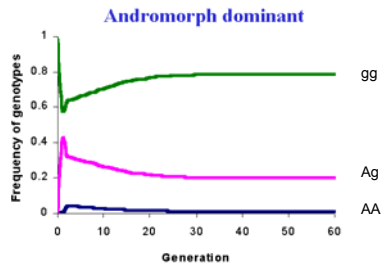
R - operational sex ratio (males / females)

*This condition provides the balance such that andromorphs are more harassed than gynomorphs if they exceed f^**

This model dealt with phenotypes rather than genotypes...

but the “phenotypic gambit” pays off....!

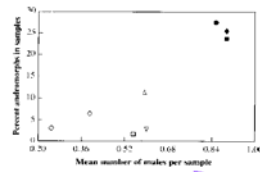
$B = 1, C = 0.1, R = 2, s = 0.7, a_A/a_G = 2 \Rightarrow 21.2\%$ andromorphs at equilibrium.



Equilibrium conditions....

$$\text{Proportion of andromorphic females} = R(C/sB)(a_G/a_A)^{(1-s)/s}$$

Nehalennia irene

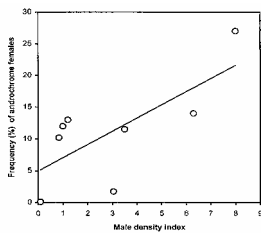


Forbes et al. 1995

Highly significantly correlated with sex ratio



Andres et al. (2002) Anim. Behav.



Ceriatrion tenellum



Summary

There are many ways in which genetic variation can be maintained in natural populations

Discrete visual polymorphisms are amongst the most eye-catching and curious

Most (but by no means all) explanations of discrete polymorphisms depend on some form of frequency-dependent selection

Most experiment and theory has been based on phenotypes rather than genotypes, but the emphasis is beginning to change

Mimicry is intrinsically a frequency-dependent phenomenon, capable of generating discrete polymorphisms

You have seen one application of mimicry theory to begin to understand polymorphisms in damselflies and help generate testable predictions

