Male Disguised Females: Breakdown of Sexual Dimorphism in a Butterfly

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Polymorphism and natural selection

Polymorphism is defined as the presence of two or more distinct, genetically determined morphs within a single interbreeding population, the rarest of which is too frequent to be solely the result of recurrent mutation. How polymorphism provides adaptation to changing environment affords illuminating supports for the theory of evolution by natural selection (e.g. shell color in the snail *Cepea nemoralis* or melanism in the peppered moth *Biston betularia*).

Female-limited polymorphism

Color polymorphism can be expressed in one sex only, with one female morph colored like male (i.e. andromorph) while the other is dissimilar (i.e. gynomorph). Such **female-limited color polymorphism** has been documented in damselflies and in *Colias* butterflies. In *Colias*, a dominant allele codes for the white coloration of females, which is never expressed in males. In *Boloria eunomia*, we recently realized that such female-limited polymorphism exists in several Belgian populations.

The grey butterfly will be used to symbolise the gynomorph females, the orange butterfly will be used to symbolise the andromorph females.

Color polymorphism description

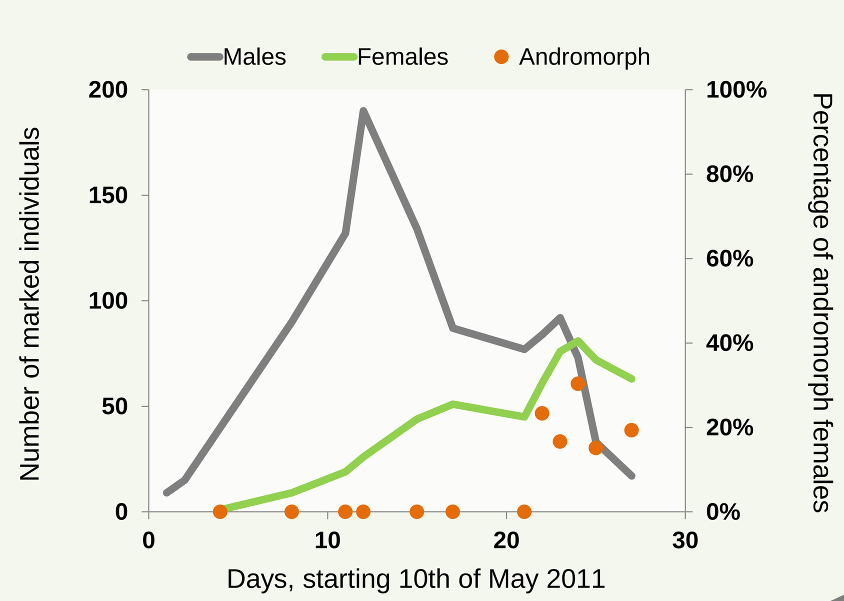
The underside of the wings of males is yellow while the underside of the wings of females can be either white (gynomorph females, on the left) or yellow as in males (andromorph females, on the right).

Objectives

To investigate the relative advantage/disadvantage of each female color morph, we performed a series of field observations and experiments to test the four hypotheses listed opposite.

Temporal variations in frequency

The temporal variation in female dimorphism frequency was investigated with a Mark-Release-Recapture study. Males appeared before females. Andromorph females were less numerous and appeared 11 days after gynomorph ones.



H0. Null hypothesis

The morph is a "neutral character whose frequency varies randomly among populations or as the result of founder effects and random genetic drift".

We expect no fitness difference between the two female morphs.

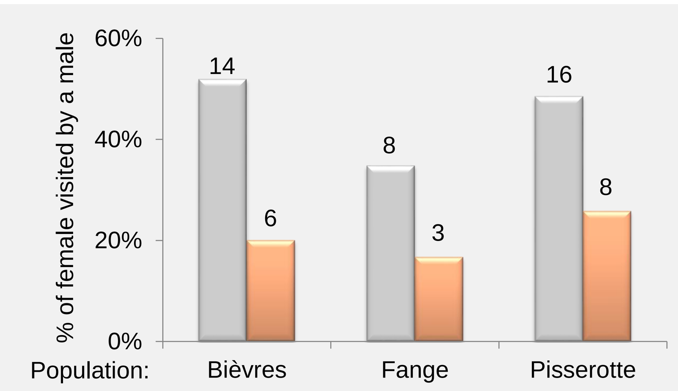
	Gynomorph		Andromorph
Potential fecundity (abdomen weight)	10.02 mg ± 0.36	<	16.79 mg ± 1.78
Daily survival (from MRR data)	0.95	>	0.62
Catchability (from MRR data)	0.32	>	0.13
Allometry	Abdomen weight increased faster with wing size in andromorphs.		

In *B. eunomia* populations, there is no spatial segregation of the morphs and no balanced polymorphism in space. **Andromorphs have a higher potential fecundity while gynomorphs have a higher daily survival.**

H1. Male mimicry (MM) & Learned mate recognition (LMR)

- MM: Gynomorphs will be more sexually harassed than andromorphs, whatever their frequency.
- LMR: Males have a biased recognition towards the most frequent morph, this morph receiving in turn a higher number of mating attempts.

We expect male harassment to be more targeted towards gynomorphs.



We followed 15 males during 10 min each in three populations. We recorded the number and morph of females that were visited and passed by two meters apart from the males' path.

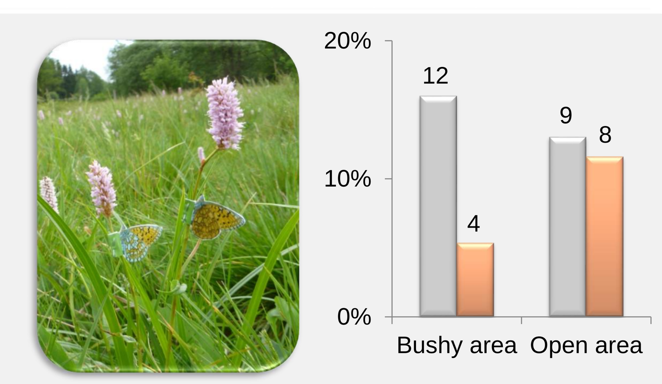
The proportion of andro- and gynomorphs encountered by males did not significantly change between populations. However, **the probability to be visited by a male was higher for gynomorphs** but did not differ between populations.

Morph effect: $X^2 = 5.8$, $P = 0.016$

H2. Density-dependent predation

Female morphs may differ in selection by predators, while the search image for the most common prey could be density-dependent. Additionally, the white gynomorphs may be more conspicuous to predators.

We expect a higher predation rate on most frequent, gynomorph females.



Printed female pictures were stapled on host leaves or stems by pairs (1 gyno- and 1 andromorph) in two habitat configurations (bushy vs. open areas). Predation marks were recorded on each of the 60 printed females, on 6 different days.

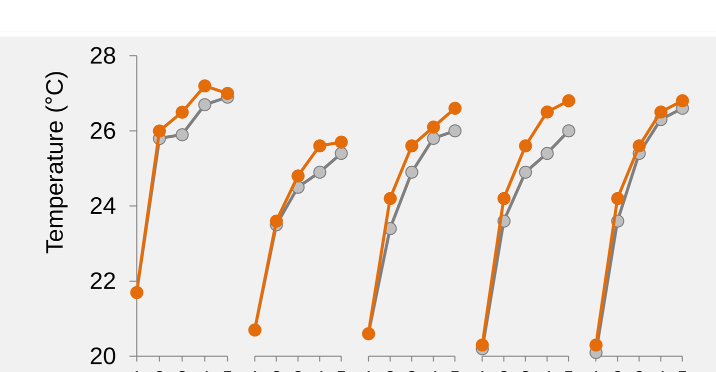
We recorded predation marks on 33 out of 288 printed pictures. Close to the bushes, the proportion of printed pictures that were attacked was significantly higher for gynomorphs than for andromorphs. This was not the case in open area.

Fisher exact one-tailed tests: $P = 0.031$ & $P = 0.50$

H3. Thermal property and wing coloration

Different wing colors have different absorption properties; darker individuals increasing their body temperature faster. As butterfly activities are governed by body temperature, faster heating up may confer fitness benefits to darker morphs by allocating more time to other activities.

We expect the darker (andromorph) females to increase faster their body temperature than lighter ones.



Female body temperature, recorded using an IR thermometer, as a function of reheating time (min) after females have been cooled down to a standardized temperature. Each panel is a size-matched pair of females (one gynomorph and one andromorph; 5 pairs tested).

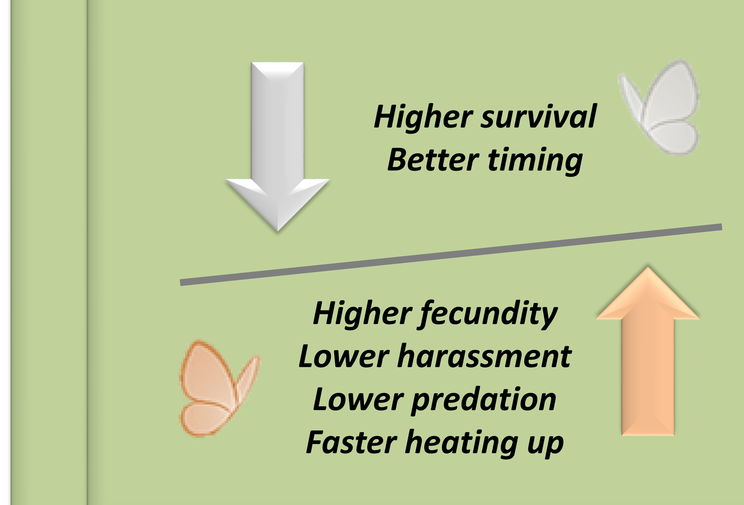
Andromorph females heated up faster than gynomorph females (positive andromorph-gynomorph temperature difference increasing with time). As body temperature reached a threshold around 5 min, the temperature difference decreased at the end of the experiment.

Linear time effect: $t_1 = 2.12$, $P = 0.046$
Quadratic time effect: $t_1 = -2.52$, $P = 0.019$

Conclusions

As we detected differences in survival, fecundity, male harassment, predation pressure and thermal properties between the two morphs, we thus **reject the null hypothesis**. However, our results match the other hypotheses; **the maintenance of the female-limited dimorphism in *B. eunomia* being linked to sexual conflict, density-dependent processes and fitness trade-offs.**

Lifestyle of both morphs is associated with different costs and benefits



Advantages in daily survival and emergence time for the gynomorphs are traded-off against a lower fecundity, higher predation risk and rate of male harassment. Indeed, andromorphs have a higher potential fecundity and are less predated and harassed by males, which should translate into a higher realized fecundity per day. But their longer development put them at risk to emerge when all males are dead and hence to be "lost in time, lonely and single".

This delay in the emergence could hence have a crucial role in the maintenance of the female-limited dimorphism in *B. eunomia*.

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