Ontogeny and Population Biology of a Sex-Limited Colour Polymorphism

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ONTOGENY AND POPULATION BIOLOGY OF A SEX-LIMITED COLOUR POLYMORPHISM

Ontogeny and population biology of a sex-limited colour polymorphism

Jessica K. Abbott

Dissertation

Lund 2006

Urban Hjärnes (1641–1724) ”dietiska regel” för sunt liv:

”*Min gosse vakta dig för 3 ting: för gamla horor, för rött vin, för nya doktorer.*”

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IV Abbott, J. K., Svensson, E. I. and Gosden, T. Adaptive morphological variation in an intraspecific mimicry system. – Manuscript. 65

V Svensson, E. I. and Abbott, J. 2005. Evolutionary dynamics and population biology of a polymorphic insect. – J. Evol. Biol. 18: 1503–1514. 81

VI Abbott, J. K., Bensch, S., Gosden, T. and Svensson, E. I. Rapid evolutionary dynamics in a polymorphic non-equilibrium system. – Manuscript. 95

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Ontogeny and population biology of a sex-limited colour polymorphism

Introduction

Having recently gone through it myself, I can say from personal experience that reproduction involves a big investment, both of time and of energy. This is especially true for females in most animal species, since they are the ones who must produce large, nutrient-rich eggs, or, as in humans and other mammals, undergo pregnancy and lactation. This implies that female reproductive capacity is limited by the amount of time and energy it takes to produce offspring, while male reproductive capacity is limited by the number of females he can mate with (Andersson, 1994). There are, of course, some exceptions to this scenario (seahorses, for example), but in a general way it is true that males should want to mate as often as possible while females should only mate as often as is necessary for fertilization. This results in a conflict between the sexes over mating rate, and females may experience substantial harassment by males attempting to induce mating (Arnqvist & Rowe, 2002). So what is a female to do? One possibility is for females to disguise themselves as males (Van Gossum *et al.*, 2001). Another is that females may come in several different types (or morphs) so that males have difficulty searching for more than one type at a time (Fincke, 2004). Or why not do both? This is what appears to be going on in the blue-tailed damselfly, *Ischnura elegans*, the study species in this thesis.

Ischnura elegans is a small annual damselfly with three female colour morphs. Males are monomorphic (Corbet, 1999). *Ischnura elegans* can be found in ponds set in open landscapes across Europe from southern Sweden to northern Spain (Askew, 1988). One of the morphs, the Androchrome, is blue and black like a male, and is considered a male mimic (Androchrome means “male-coloured”). The other two morphs, Infuscans (I) and Infuscans-obsoleta (O), are more cryptic and are olive green or brown and black (Figure 1). In this thesis, I have studied a number of populations of *I. elegans* over several years, looking at frequency changes over time, morphological differences between the sexes and the morphs, differences in growth rate and development time, differences in fecundity between the morphs, and genetic differentiation between populations. The results in this study indicate that the morphs are subject to negative frequency-dependent selection via male mating harassment, and that the differences between the morphs are part of their identity as alternative adaptive strategies.

Methods

The data in this thesis have been obtained through field work, laboratory experiments, and molecular-genetic analysis of collected damselfly specimens. Several of the chapters involve a combination of different types of data. A general theme throughout the thesis is a populational approach to the data; that is, analysis of patterns across populations and differences be-

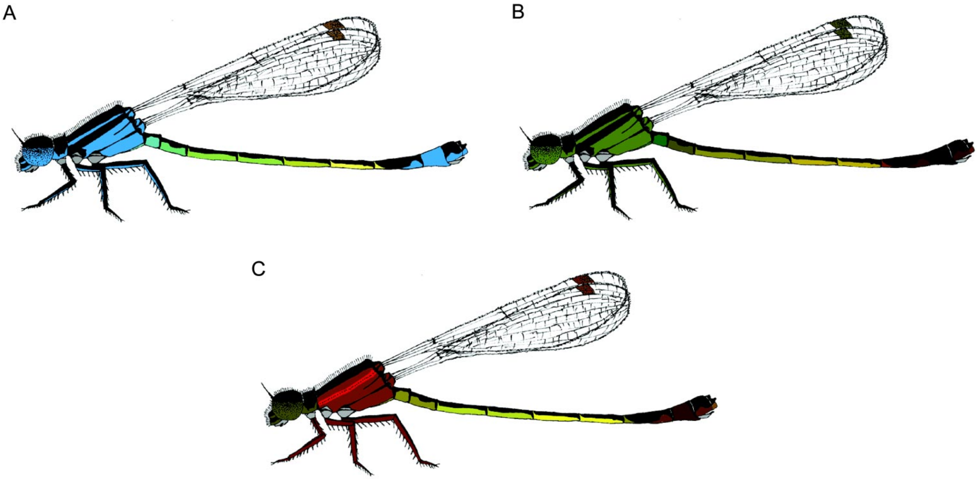

Figure 1. The three female morphs in *Ischnura elegans*. A. Androchrome female (male mimic). B. Infuscans female. C. Infuscans-obsoleta female (rarest morph).

tween populations. Briefly, the methods I used were as follows:

Field work

I captured individuals in the field using hand-held nets and took morphological measurements (Chapter IV). Morph frequencies and population densities were calculated from numbers of individuals captured (Chapters I, V, and VI). I have also used capture date in the field as a proxy for date of emergence to look at differences in development time in the field (Chapter II).

Laboratory observations

I captured females in the field, brought them back to the laboratory to obtain eggs and then counted the eggs (Chapters I, IV and V). I then raised individuals from eggs laid in the laboratory and looked at development time (Chapter II). I subsequently tracked the individual growth patterns of larvae raised in lab, and looked at morphology in larval and adult stages (Chapter III). I also used data from parents and offspring to estimate quantitative genetic parameters for the morphological traits (Chapter IV)

Molecular-genetic analysis

I carried out Amplified Fragment Length Polymorphism (AFLP) analysis on individuals from different populations (Chapter VI). I then analysed population differentiation in both genetic diversity (AFLP) and morph frequency divergence (Chapter VI) using the same technique (calculation of F_{st}-values).

Frequency-dependence

Frequency-dependence occurs when the fitness of a genotype (such as the female morphs in *I. elegans*) depends on its frequency in the population. Both positive and negative frequency-dependence are possible, although negative frequency-dependence is arguably more interesting in an evolutionary perspective. In positive frequency-dependence the most common morph has a fitness advantage, which leads to fixation of locally common morphs and extinction of locally rare morphs (unless the common morph's advantage is somehow counterbalanced by a disadvantage elsewhere, Mallet & Joron, 1999). Positive frequency-dependence is therefore likely to be a transient phenomenon, and will ultimately lead to a series of monomorphic populations, each one fixed for a single morph. In contrast, negative frequency-dependence, where the most common morph has a fitness disadvantage (Sinervo & Svensson, 2002), can maintain multiple morphs indefinitely. For example, a predator that develops a search image for the most common morph is most efficient at detecting it, which leads to a decrease in the frequency of that morph (this is also known as apostatic selection; Allen, 1988). Negative frequency-dependence may produce fluctuations in the frequencies of the different morphs, and in some cases predictable cycles in morph frequencies (Sinervo & Lively, 1996).

In Chapter I, we calculated how the fecundity of each morph (a fitness component) varied according to the frequencies of itself and the other morphs in our study populations and found evidence of negative frequency-dependent selection (Table 1). Empirically estimated selection coefficients were used in a population genetic and dynamic model with environmental variation (or stochasticity). The model predicted coexistence of the three morphs, although the predicted equilibrium frequencies were different than those we have observed in our study populations (the model predicts lower Androchrome frequency and higher Infuscans frequency; Figure 2). This is interesting because it suggests that negative frequency-dependence on fecundity is sufficient to explain coexistence of the morphs. In this case, negative frequency-dependence is likely to be mediated by male harassment of the most common morph. Since copulations can be very long (Cordero *et al.*, 1998), and since the production

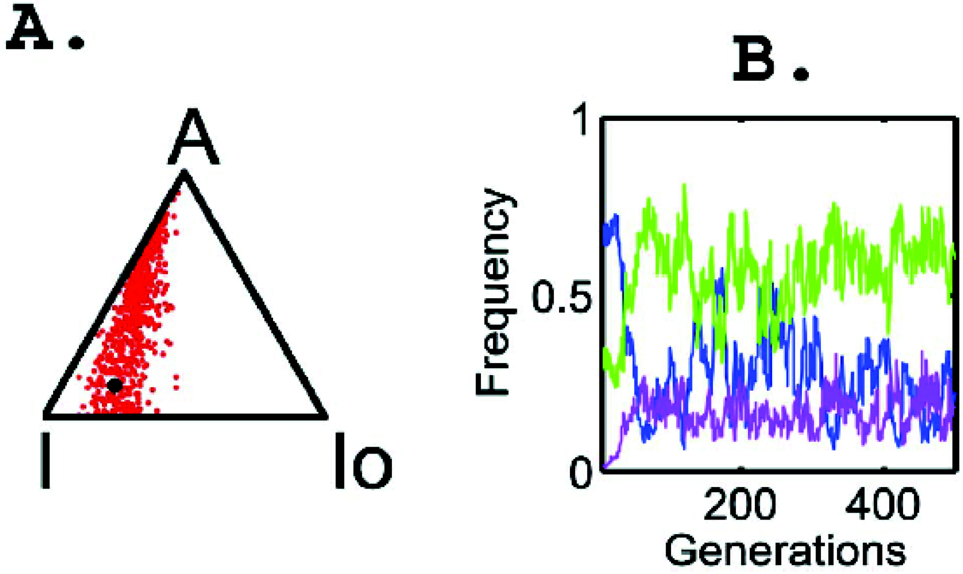

Figure 2. Results from simulations of a frequency-dependent selection model in Ischnura elegans. A. Equilibrium morph frequencies predicted from fecundity data. Any interior point in the triangle represents a frequency combination of the three colour morphs. Distances from vertices are proportional to the frequency of each morph, and the top apex represents fixation of Androchrome females ($P_A = 1$). The mean multiple regression coefficients predict coexistence of all morphs with the following proportions: Infuscans = 0.68, Infuscans-obsoleta = 0.19, Androchrome = 0.13 (black dot). To visualize the effect of variation in the regression coefficients, the red dots depict 1 000 bootstrapped equilibria, where we used empirically estimated variances to resample regression coefficients. B. Predicted frequencies of the three morphs over 500 generations, when morph fecundities are subject to environmental noise. Green = Infuscans, blue = Androchrome, purple = Infuscans-obsoleta.

Table 1. Selection coefficients for the fecundity-morph frequency relationship used in the population genetic simulation model. All coefficients are significantly different from zero.

Coefficient	S_{AA}	S_{AI}	S_{AO}	S_{IA}	S_{II}	S_{IO}	S_{OA}	S_{OI}	S_{OO}
Estimate	0.93	1.17	0.25	1.21	0.21	3.40	1.30	1.52	–1.21
SD	0.008	0.020	0.042	0.017	0.044	0.091	0.042	0.109	0.224

of fertile eggs does not seem to be positively affected by number of copulations (Sirot & Brockmann, 2001), there is little incentive for females to copulate multiple times, and there may also be direct fecundity costs of superfluous matings (T. Gosden & E. I. Svensson, unpublished data). Males appear to form a search image for the most common morph (Fincke, 2004), leading to greater harassment of that morph, and consequently, reduced fecundity. This is a similar process to apostatic selection mention above, but in this case, frequency-dependence is produced via sexual interactions rather than predation.

In Chapter V, I examined fecundity differences between the morphs and morph frequency changes over time in more detail. I found that Infuscans females had the highest fecundity but that, as expected from negative frequency-dependence, fecundity decreased with increasing frequency in the population for all three morphs. Over 4 years, Androchrome frequency declined and Infuscans frequency increased. Some of our study populations are relatively recently created wetlands, while others are either natural or created more than 20 years ago. The pattern of morph frequency changes differed between new and old populations (Figure 3), so perhaps new populations are in the process of reaching some equilibrium frequency with lower proportion of Androchromes, consistent with the population genetic modelling results (Chapter I).

Sexual dimorphism

Males and females differ physically and behaviourally in many traits, and these differences are referred to as sexual dimorphism (Andersson, 1994). Because of their different reproductive roles, it makes sense that males and females are often selected towards different optimal trait values (Andersson, 1994). A classic example is the peacock, where males have large, showy tails which females lack. This is because male fitness is increased by attracting more mates (via display of the tail), while female fitness is increased by avoiding predation (which is difficult when burdened by a large, brightly coloured tail). Some traits are more or less completely limited in expression to one sex or the other (such as lactation in female mammals) while other traits are present in both sexes, but differ in value (for instance one sex may be larger than the other). Especially in traits that are sexually dimorphic but not sex-limited, males and females may be prevented from reaching their optimal trait values by recombination and/or selection in the opposite sex (Rice, 1984; Rice & Chippindale,

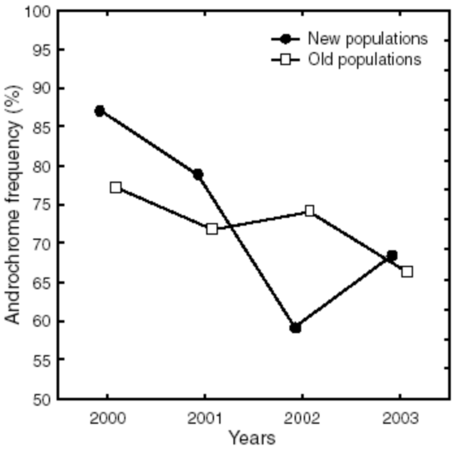

Figure 3. Percentage of Androchrome females in old (n = 4, natural wetlands or wetlands created more than 20 years ago) and new (n = 6, wetlands created between 1990 and 1999) populations across the study period 2000–2003 (four generations).

2001). This deviation from the optimum for each sex can be so costly that it could explain sex-specific differences in mortality/longevity, and even the evolution of ageing (or senescence, Promislow, 2003).

I have examined several different aspects of sexual dimorphism. I found that males emerge earlier than females in the laboratory (Chapter II, Figure 4), a process which is known as protandry (Morbey & Ydenberg, 2001). I also found that females had a higher growth rate than males (Chapter III, Figure 5) and that they were larger in the adult stage (Chapters III and IV, Figure 6A). This means that sexual size dimorphism (SSD) is produced in *I. elegans* by a combination of development time and development rate acting in concert (Badyaev, 2002). Protandry is often explained by different selection pressures acting on the sexes. For males, it is more important to emerge early in order to gain access to females first (but not so early that there are no females present, of course), while for females, it is more important to be large since this increases fecundity, even if growing large takes longer (Morbey & Ydenberg, 2001). This appears to be the case in *I. elegans* since females both take longer to develop and have a higher growth rate than males. Females and males also differed in body shape (Chapters III and IV); males had relatively longer and narrower abdomens and shorter wings than females (Figure 6B). This is probably related to the positions of the sexes during mating and the presence of the ovaries in the female abdomen. The degree of sexual dimorphism in size and shape varied between populations (Chapter IV), which could be a result of differential sensitivity of the sexes to different abiotic or biotic environmental conditions between populations (Badyaev, 2002).

Differences between female colour morphs

A main focus of the research in this thesis is genetic polymorphism. Morphs are variant forms within a species and can be either environmentally determined, genetic with an environmental switch point, or entirely genetically determined (Via & Lande, 1985; Leimar, 2005). An example of an environmentally determined morph is a phenotypically plastic defence, which is only produced in the presence of predators, such as can be found in Crucian carp (*Carassius carassius*, Brönmark & Miner, 1992). Some butterfly caterpillars can be either melanic (dark-coloured) or not depending on environmental conditions (Wilson *et al.*, 2001). Since melanin is important for disease resistance, which morph is produced depends on population density during development, and the densities at which different genotypes switch are genetically determined and vary between families or populations (Wilson *et al.*, 2001).

The female morphs in *I. elegans* are pure genetic morphs, and it has been shown that they

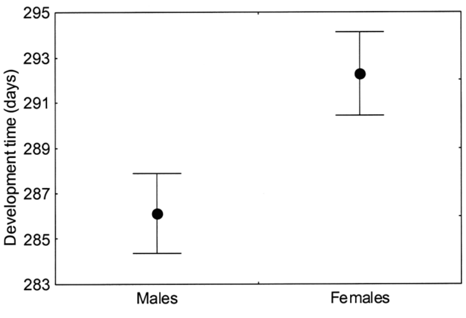

Figure 4. Development time (days±SE) in the laboratory in relation to sex. Males had a significantly shorter development time than females ($P < 0.0001$).

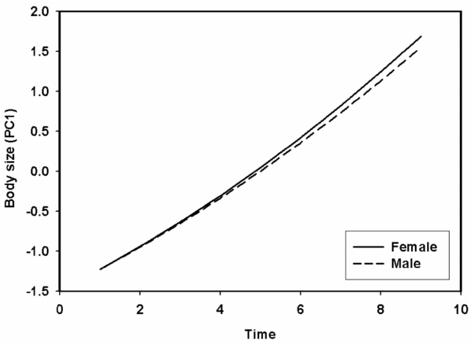

Figure 5. The effect of sex on body size in the larval stage. Females have a higher growth rate than males.

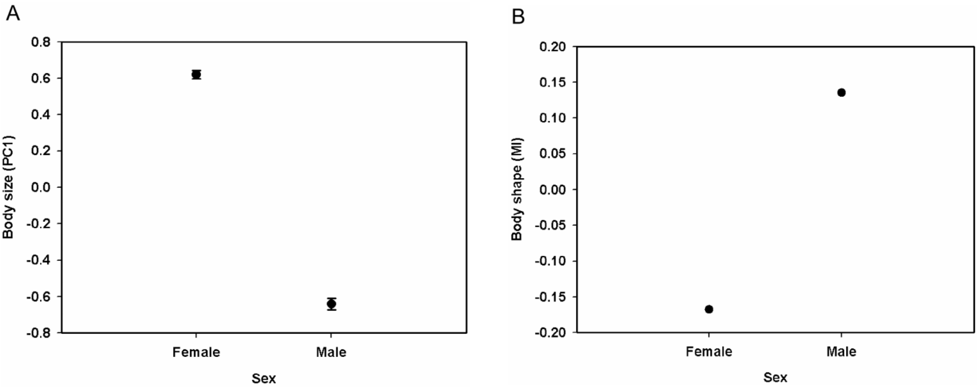

Figure 6. Sexual dimorphism in the field in A. Body size (PC1). Females are significantly larger than males ($P < 0.0001$). B. Body shape ("maleness index", or MI). Error bars overlap with points and are therefore not shown. Females have relatively shorter but wider abdomens ($P < 0.0001$).

are the product of three alleles in a dominance hierarchy at a single locus (Sánchez-Guillén *et al.*, 2005). Genetic polymorphism is of general interest since, as I discuss in several of the chapters in this thesis, it can be either the first step on the path to speciation or, conversely, can be an alternative outcome to speciation by disruptive selection (Bolnick & Doebeli, 2003). Morphs which differ in colour can also differ in several other traits and they may in some cases be integrated alternative adaptive strategies. For example, the two female morphs in the side-blotched lizard *Uta stansburiana* differ in aggressiveness, fecundity, egg size, and immune function. This is related to their respective r-type (many offspring of lower quality) and K-type (fewer offspring of better quality) strategies (Svensson *et al.*, 2001).

Another interesting aspect of the genetic polymorphism in *I. elegans* is that of intraspecific mimicry. Androchrome females have similar colouration and patterning to males, which has lead to the assumption that they are male mimics (Cordero *et al.*, 1998). I therefore set out to determine if the female morphs did differ other ways than simply colouration, and if these differences were consistent with biologically meaningful alternative adaptive strategies.

In Chapter II, I investigated differences in development time between the morphs both in the laboratory and in the field and found that in the field, Infuscans-obsoleta females emerge first and Infuscans females later (Figure 7A). The same pattern is also observed in the laboratory, although here it is the offspring of Infuscans-obsoleta females which emerge first and the offspring of Infuscans females which emerge last (Figure 7B). Differences in development time between morphs could thus result in change in morph frequencies in the field as a correlated response to selection on development time. I also investigated differences in growth rates (Chapter III), and I found that growth rate was highest in offspring of Infuscans-obsoleta females (Figure 8). This fits in well with the results on development time in Chapter II since Infuscans-obsoleta females and their offspring are not any smaller in the adult stage. Instead, they reach same size in shorter time. Thus, regarding the size of the female morphs in the laboratory, the effects of growth rate and development time cancel each other out (as compared to SSD, where they reinforce each other).

I also examined morphological differences between the morphs both in the laboratory (Chapter III) and the field (Chapter IV). In the field Androchromes had the most male-like body shape overall, Infuscans females had the least male-like body shape, and the body shape of Infuscans-obsoleta females varied between populations (Figure 9). They were similar to Infuscans females in some populations, and had even more male-like morphology than Androchromes in other populations. This suggests

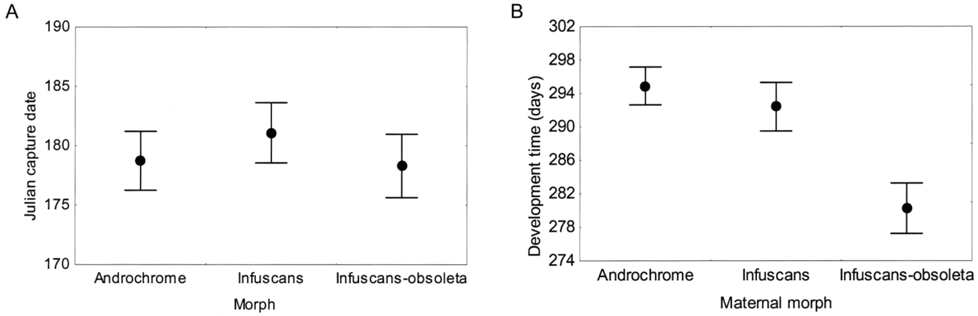

Figure 7. Differences in development time between the three morphs in the field and in the laboratory. A. Capture date (julian day±SE) in the field is used as a proxy for development time. Infuscans females were captured significantly later than either of the two other morphs ($P < 0.05$). B. Development time (days±SE) in the laboratory for offspring of the three female morphs. Offspring of Infuscans-obsoleta females had a significantly shorter development time than the offspring of the other two morphs ($P < 0.01$).

that morphology in Infuscans-obsoleta females may be more sensitive to environmental conditions than the other morphs, or that they are subject to correlated evolutionary responses to selection on morphology in the other morphs.

Although I did not carry out any studies of differences in colouration between Androchromes and males, I did find that in both the laboratory and the field Androchromes had the most male-like body shape. In addition, male-like body shape in Androchromes did not have a negative effect on fecundity, in contrast to Infuscans-obsoleta females. Quantitative genetic parameters for morphological traits showed that an evolutionary response to selection on body shape is possible, and the traits with the greatest potential for a response (highest evolvabilities and coefficients of additive genetic variance) were abdomen width (S4) and total length. The morphological data presented here, in combination with previous studies that have shown that Androchromes have more male-like behaviour (Van Gossum *et al.*, 2001), suggest that Androchromes are in fact male mimics. My results on the differences between the morphs indicate the presence of phenotypic integration between the morph locus and other traits such as morphology, growth rate, and fecundity, and that the morphs may therefore be alternative adaptive strategies. Harassment by males may select for different phenotypic female optima, so that a female can avoid such harassment by either becoming a more or less perfect male mimic (i. e. Androchromes) or by becoming so different that it falls outside the usual range of female phenotypes encountered by males (i. e. Infuscans-obsoleta).

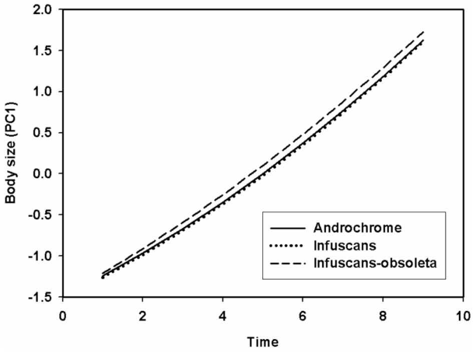

Figure 8. The effect of Maternal morph on body size in the larval stage. Offspring of Infuscans-obsoleta females have a higher growth rate than offspring of the other morphs.

Indirect inferences about selection

The amount of genetic differences between populations can be measured using the F_{st}-value, which is an estimate of the amount of differentiation among populations relative to the amount of differentiation within populations.

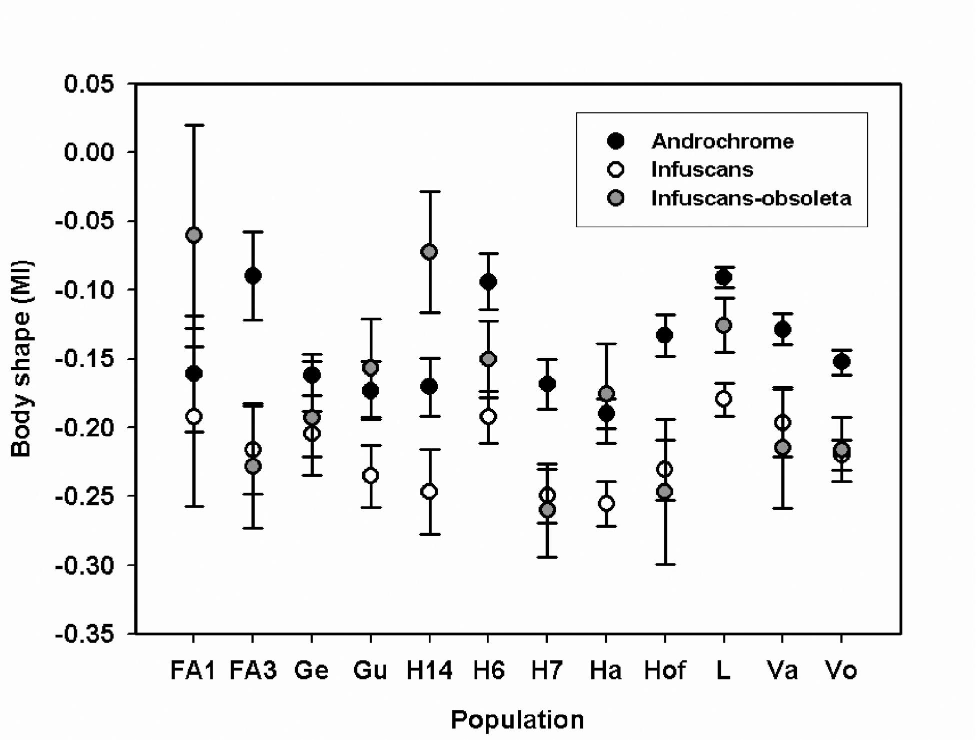

Figure 9. Differences in body shape ("maleness index", or MI) between the female morphs between populations. Androchromes are most male-like overall, and Infuscans females are least male-like, but the morphology of Infuscans-obsoleta females is very variable between populations.

These values range between 0 and 1; 0 indicates no genetic differentiation between populations, 1 indicates that the populations are completely genetically different. Typical F_{st}-values for populations within the same species are about 0.02–0.40 (Merilä & Crnokrak, 2001). In Chapter VI, I investigated population differentiation in both neutral loci and in morph frequencies. Neutral data provide genetic information about the expected population differentiation when loci are not under selection. This can be either non-coding (sometimes called "junk") DNA, or synonymous changes in coding DNA. Changes in neutral DNA are expected to accumulate over time, so the more isolated from each other two populations are, and the longer they have been isolated, the more genetically different they will be (Page & Holmes, 1998).

One can get an idea of the existence and scale of selection on morph frequencies by comparing F_{st}-values for morph frequency differentiation with F_{st}-values for neutral genetic data (Lynch & Walsh, 1998). If there is no difference between the amount of neutral differentiation and differentiation in morph frequencies, then changes in morph frequencies are probably random, and population differentiation in morph frequencies is indistinguishable from what would be expected under genetic drift alone. If F_{st}(neutral) > F_{st}(morph frequencies) then morph frequencies are less different between populations than expected from random genetic drift. This means that selection is probably acting over a large scale to keep morph frequencies the same across populations, for instance via large-scale climatic factors. If F_{st}(neutral) < F_{st}(morph frequencies) then morph frequencies are more different than expected from random drift. This suggests that there is differential local adaptation, and that divergent selection has pushed the different populations apart. I found that whether morph frequencies were more or less divergent than neutral data varied over time, so the scale of selection had apparently changed (Figure 10). The amount of differentiation in morph frequencies was initially larger than differentiation in neutral data but only two years later morph frequency differentiation was significantly smaller than neutral differentiation. This result is consistent with our other observational data (Chapter V) and modelling results (Chapter I) that population morph frequencies may be in the process of reaching equilibrium. Alternatively, populations of *I. elegans* may be perturbed so often that the system is (at least in Sweden) constantly in a non-equilibrium state, and differentiation in morph frequencies may regularly fluctuate above and below the amount of neutral differentiation.

I also investigated if there was any evidence for Isolation by Distance (IBD) in chapter VI. This is when populations are more genetically different the farther they are from each other (Schemske & Bierzychudek, 2001). However, I

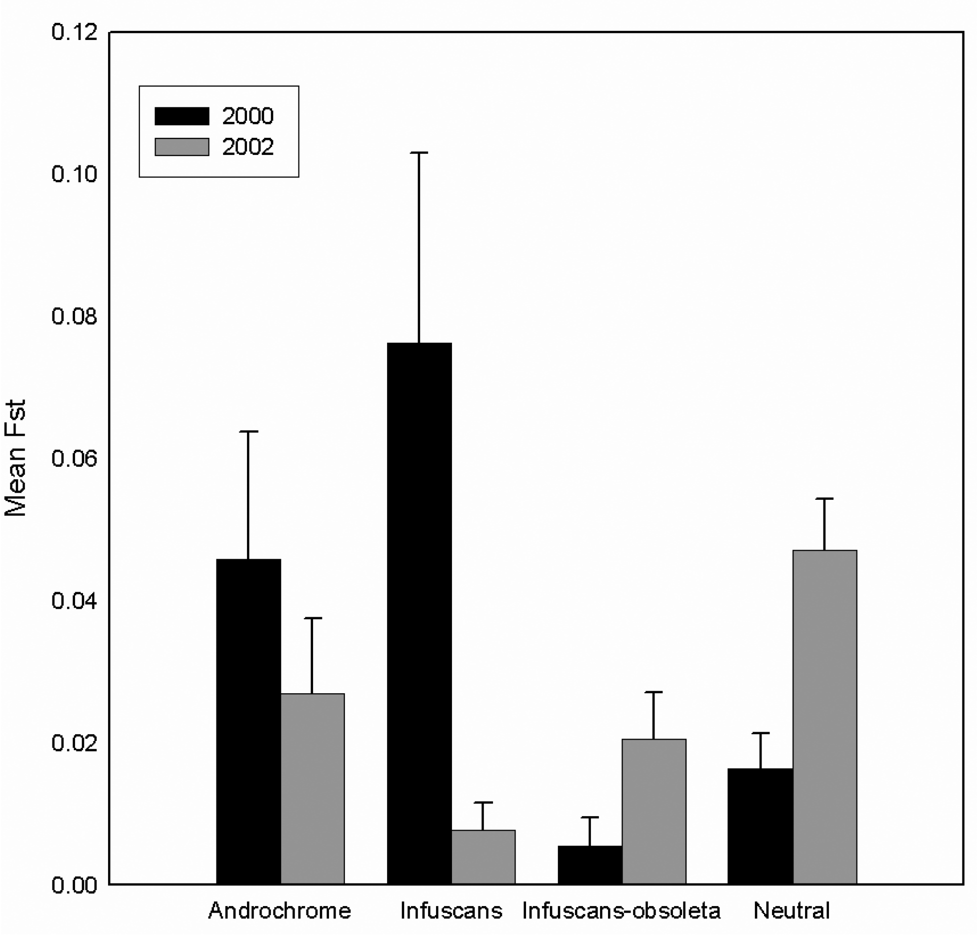

Figure 10. Mean F_{st} values (with 95% confidence limits shown) for morph frequencies and neutral data for years 2000 and 2002. F_{st} values of Androchrome and Infuscans frequency are significantly higher than neutral F_{st} values in 2000, and significantly lower than neutral F_{st} values in 2002. F_{st} values of Infuscans-obsoleta frequency are significantly lower than neutral F_{st} values in both years

did not find any such pattern, which is expected in a non-equilibrium system. Instead, it appears that diversity is influenced by wind direction. Prevailing winds in Skåne are in an East-West direction, and we found that diversity is lower in an East-West direction than in a North-South direction (Figure 11). The more genetic exchange between two populations, the more similar they will be, so this is what is expected if migration between populations is more likely to occur in the same direction as the prevailing winds.

Conclusions and future directions

There are many aspects of this system which still remain to be investigated. For instance, though I have demonstrated correlated morphological and developmental differences between the morphs, it is still unclear what causes these differences. Maternal effects (non-genetic effects of the mother), pleiotropy of the morph locus (when the gene for morph also produces other differences as a side-effect), or linkage disequilibrium (when several traits are usually found in combination, often as a result of physical linkage between genes; blonde hair and blue eyes in combination in humans is an example) are all possible explanations. To determine whether populations are reaching some sort of equilibrium morph frequencies, or if cycling of frequencies is occurring, long-term data following our study populations is necessary. More detailed ecological and experimental investigations of male-female interactions in the field are currently underway.

Finally, I would like to end on a personal note. Doing a PhD project is similar to reproduction in that they both require a substantial investment of time and energy. But (just like my own experience with reproduction) I'm pleased with the result and feel that it was worth it.

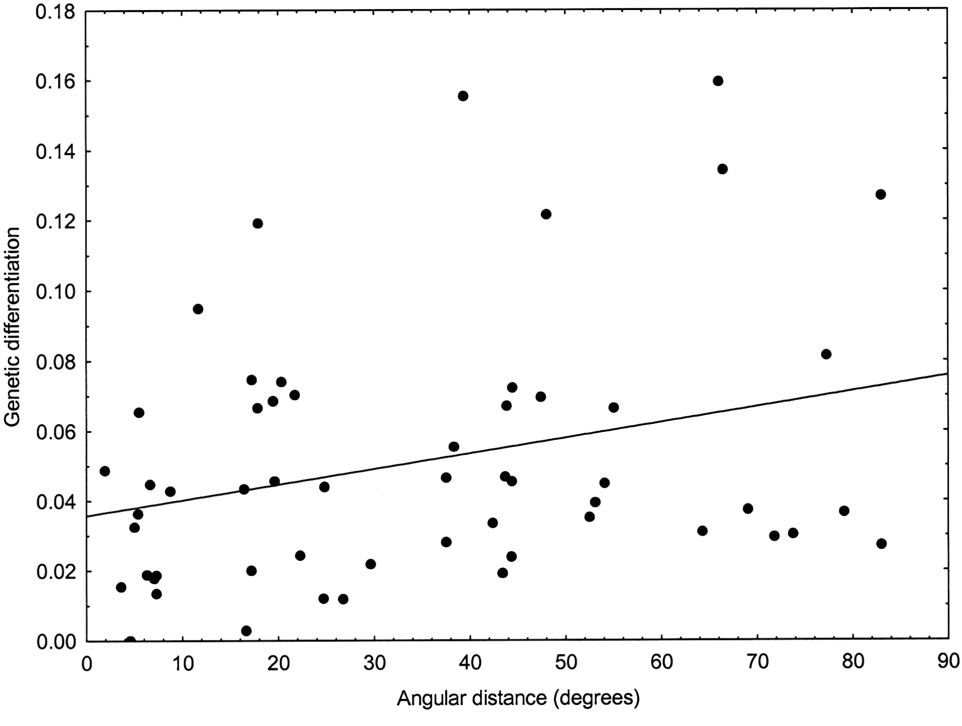

Figure 11. Scatterplot of pairwise F_{st} values vs. angular distance from E-W (E-W = 0°, N-S = 90°). Populations that lie east or west of each other have lower genetic differentiation than those that lie to the north or south, and this relationship is significant (r = 0.291, *P* = 0.032).

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