CHAPTER 17

The evolution of sex-limited colour polymorphism

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Abstract

Species that exhibit colour polymorphism, the simultaneous occurrence of two or more discrete phenotypes with a genetic basis, are ideal for studying the microevolutionary forces that maintain genetic variation in nature. One very intriguing type of genetically determined polymorphism is the co-existence of several discrete morphs within only the male, or within only the female, sex. These morphs typically differ in body coloration and sometimes behaviour, with one morph often resembling the opposite sex. In males, this resemblance often allows access to receptive females, whereas in females the polymorphism appears related to avoiding excessive male sexual harassment. One might wonder why natural selection does not simply give rise to a single best male and female type for each species. Odonates are good candidate species to address this type of question because sex-limited polymorphism is widespread within the group, facilitating hypothesis testing through comparative analyses. Odonates are also widely distributed geographically and they are convenient to work with from a methodological perspective because they can be studied over their lifetime on an individual basis under either natural or artificial conditions. The phenomenon of sex-limited polymorphisms provides an important opportunity to test contemporary ideas relating to sexual selection and sexual conflict, and the diversity of polymorphisms that have arisen in odonates clearly offers one of the best natural systems for among-species comparative research.

17.1 The wheres and whys of intraspecific discrete colour variation

Variation in colour between individuals that has a genetic basis is widespread in nature, with multiple examples found in vertebrates, invertebrates, and plants (e.g. Maynard Smith 1998). Such variation is considered a polymorphism when two or more distinct and genetically determined morphs co-exist at the same time in a single interbreeding population, the least abundant of which is present in numbers too great to be due solely to recurrent mutation (Ford 1957). As Fisher (1930) argued, the existence of a permanent polymorphism often implies a selective balance (frequency-dependent selection) between the two (or more) alternative morphs, each enjoying a selective advantage when rare but also suffering some disadvantage when common. General explanations for these and other polymorphisms therefore include frequency-dependent selection, but also heterosis (where the heterozygote is fitter than either homozygote) and variable morph fitnesses in space or time. Clearly, polymorphisms are attractive model systems to explore how natural selection can work to maintain diversity. Among the two most widely known cases are the so-called massive polymorphisms seen in the land snail *Cepaea nemoralis* (e.g. Jones *et al.* 1977) and industrial melanism with light and dark morphs in the peppered moth *Biston betularia* (e.g. Majerus 2005).

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Intriguingly, there are examples where the occurrence of colour polymorphism is restricted to just to one sex, with examples seen in a wide variety of taxonomic groups including reptiles (Shine *et al.* 2001), birds (Galeotti *et al.* 2003), and insects (Forsyth and Alcock 1990). Instances of female-limited polymorphism are generally considered to have evolved in response to excessive male sexual harassment, sometimes in combination with selection to resemble unpalatable heterospecifics (Beccaloni 1997). Species with alternative male morphs often include a territorial fighter male and a 'sneaky' male that resembles the conspecific female in behaviour and phenotype and that succeeds in intercepting females for mating at the borders of territorial male's territory (Gross 1996).

These examples illustrate that, rather than selection giving rise to a single best male and female type for each species, it has instead resulted in multi-modal phenotypic diversity. An important question is how and why selection favours the co-existence of multiple morphs. To address this question it is preferable to study taxonomic groups that are both widespread and convenient to work with from a methodological perspective. A wide geographical distribution not only allows easy access to specimens, but also provides sufficient variation in biotic and abiotic conditions (e.g. density, temperature) to explore environmental influences on morph frequency. Likewise, it is useful to select a study group for which several species show the trait while others do not, thereby facilitating comparative analyses.

17.2 Generality of polymorphic species within different animal taxa

In most animal taxa, the occurrence of male- or female-limited colour polymorphisms is restricted to a few cases (see Box 17.1); for example, in birds, 25 species have been reported to show sex-limited polymorphism (Galeotti *et al.* 2003). In copepods, sex-limited polymorphism has so far been reported in only a single species (Fava 1986). Arguably, sex-limited polymorphism is only truly common (i.e. many species throughout an entire order) among female odonates (e.g. Fincke *et al.* 2005) (see Box 17.1). Indeed, female-limited polymorphism

is observed for species of both Anisoptera and Zygoptera and has been described for more than 100 species (Fincke *et al.* 2005).

The presence of female-limited polymorphism within groups of closely related species allows us to explore associations between polymorphism and life-history traits, thereby contributing to understanding the evolution of sex-limited polymorphism in general. Robinson and Allgeyer (1996), for example, tested whether female colour polymorphism was correlated with mating-system traits for North American representatives of the genus *Ischnura*. Based on this work it was suggested that evolution from a polyandrous to a monandrous mating system was accompanied with a change in character state from polymorphic to monomorphic species. Unfortunately, a phylogeny for the genus was unavailable at the time, preventing the authors from placing the data in the proper historic context. Meanwhile, species-level-based phylogenies and higher-level relationships between odonates have been explored more intensively (e.g. Brown *et al.* 2000; Rehn 2003). Now that robust phylogenies are available it may become possible to ask whether the current presence of polymorphism results from a common ancestor or rather is the consequence of convergent evolution. Given the simple genetic system underlying polymorphism (see the next section), it is not unreasonable to suppose that recurrent mutation can facilitate the repeated evolution of this character in different species. However, we note that the presence of polymorphisms may itself create challenges for reconstructing phylogenies if polymorphy is a transient state in the process of speciation (Wiens 1999).

17.3 The genetic basis of polymorphism

For natural or sexual selection to operate on a trait it has to be heritable in some way. Simple Mendelian inheritance patterns have been found to underpin sex-limited polymorphism (e.g. Shuster and Wade 1991). Thus, in odonate species with male- or female-limited polymorphism, the proportions of colour morphs in the progeny are consistent with morph type being controlled at an autosomal locus that has sex-restricted expression, with the number

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Box 17.1 How common is sex-limited polymorphism in animals?

Three component questions are as follows.

1. In which animal taxa do we observe sex-limited polymorphism?

Co-existence of either multiple male or multiple female morphs is seen in most vertebrate phyla (such as birds, reptiles, and fish), in insects (such as dragonflies, butterflies, and beetles), and in crustaceans.

2. Are sex-limited polymorphisms equally common across animal taxa?

No, there is only example of a taxon in which sex-limited polymorphism is seen in over 100 species (Fincke *et al.* 2005).

3. Are male and female limited polymorphisms equally common?

In birds 23 species show female-limited polymorphism, whereas two species show male-limited polymorphism (Galeotti *et al.* 2003). In odonates female-limited polymorphism is observed for species of both Anisoptera and Zygoptera and has been described for more than 100 species (Fincke *et al.* 2005). By contrast, male-limited polymorphisms are relatively more rare, with examples reported in only a few families of odonates, including the Calopterygidae (e.g. Plaistow and Tsubaki 2000), the Megapodagrionidae (González-Soriano and Córdoba-Aguilar 2005), the Coenagrionidae (Polhemus and Asquith 1996), and the Amphipterygidae (Stewart 1980).

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of alleles involved equal to the number of morphs (female polymorphism, Andrés and Cordero 1999; male polymorphism, Tsubaki 2003). In the case of female-limited polymorphism it has been possible to evaluate inheritance for several species. Interestingly these species appear to differ in their hierarchy of dominance and recessiveness (see Andrés and Cordero 1999).

Over the past decade it has been possible to test for the effect of selection by comparing the rates of differentiation between the colour locus and a set of molecular markers assumed to be neutral (see Lynch and Walsh 1998). Two contrasting alternatives are possible. Negative (pro-apostatic) frequency-dependent selection may create a situation where most populations have reached equilibrium in morph frequencies; under these conditions population differentiation in morph frequencies would be expected to be significantly lower than population differentiation in neutral loci as was shown through relating differentiation based on randomly amplified polymorphic DNA (RAPD) markers (assumed to be neutral) with the degree of differentiation based on colour alleles (Andrés *et al.* 2000, 2002). Alternatively, each female morph may

exploit a slightly different ecological niche, and differences among populations may then reflect local adaptation to differing environmental conditions. Under this scenario, population differentiation in morph frequencies is expected to be significantly greater than population differentiation for neutral loci, which was indicated for a damselfly species using microsatellites (Wong *et al.* 2003).

The development of new molecular techniques that produce codominant markers, such as microsatellites, opens the door for fine-scale analysis of population differentiation and genotyping (e.g. Thompson and Watts 2006). Future advances might be made through mapping the genes involved in the expression of polymorphism, which may be particularly revealing given that there is variation across odonate species in terms of whether the polymorphism includes body colour only, or also includes body patterning or behavioural differences. It is quite possible that several genes are involved and phenomena such as pleiotropy or linkage disequilibrium may be relevant. Exploring this will allow for more powerful tests of evolutionary hypotheses on the maintenance of sex-limited colour polymorphism.

17.4 Male-limited polymorphisms: fighter males and sneaky males

As seen in other animal taxa (Gross 1996), male-limited polymorphism in odonates includes a territorial fighter male and a so-called sneaky male that resembles the conspecific female, allowing it to remain at the edge of the fighter male's territory, apparently not being recognized as a male by the territorial male while intercepting females on their way to the territorial male (e.g. Plaistow and Tsubaki 2000). Females in these species are monomorphic (Tsubaki 2003). The mating strategy of territorial males guarantees higher daily mating rates, but non-territorial males live longer and have lower costs to develop and maintain their phenotype (Plaistow and Tsubaki 2000). Despite territorial and non-territorial male morphs having contrasting life histories, lifetime reproductive success appears similar for both morphs (Tsubaki *et al.* 1997), which is what one would expect if the polymorphism were in some form of equilibrium. Although these studies support the general contention (see Gross 1996) that a territorial and a sneaky male co-exist, examples in odonates are few, not geographically widespread and no more amenable to study than examples in other animal taxa. It is noteworthy, however, that some males of Coenagrionid Hawaiian damselflies are also polymorphic (in body coloration), yet territoriality does not occur in these species (Polhemus and Asquith 1996). Therefore, different explanations may be applicable to the occurrence of male-limited polymorphism in different damselfly taxa.

17.5 Female-limited polymorphism and male sexual harassment

In cases where female limited polymorphism arises in odonates, one female morph typically resembles the male (the androchrome), while the alternative morph (or morphs) does not (the gynochrome). This polymorphism is generally assumed to have arisen as a consequence of negative frequency-dependent (pro-apostatic) selection, in which the fitness of a given morph is higher than any alternative morph when it is relatively rare in a population. Most contemporary theories have assumed that the primary

selective force generating this frequency-dependent selection is the differential harassment of female morphs by conspecific males (see Box 17.2). Male harassment is believed to affect female fitness in several ways: in particular, repeated attention by males can upset individual female time and energy budgets, and it may bring an increased likelihood of physical damage (Robertson 1985; Sirot and Brockmann 2001). Nevertheless, evidence that male harassment does reduce female fitness in damselflies is currently limited. Sirot and Brockmann (2001) indicated costs of sexual interactions to androchromes but not to gynochromes in an experimental setting only including male harassment (i.e. predation and other factors were excluded). Less directly, Svensson *et al.* (2005) applied a population-genetic model in combination with measures of female morph fecundity and field estimates on morph frequencies to support the contention that frequency- and density-dependent male harassment may drive the maintenance of female-limited polymorphism. In more recent work Gosden and Svensson (2007) show in natural populations that female morphs differ in their fecundity tolerance to matings and mating attempts.

Intuitively, if a female were seeking to avoid harassment then one might expect that it would pay more to look like something that is unprofitable to attack, rather than something which simply looked different. Mimicry is well known to generate frequency-dependent selection; indeed, the classical Batesian polymorphisms are generally explained by the diminishing effectiveness of mimicry as morph frequency increases (e.g. Ruxton *et al.* 2004). Given the morphological similarity to males and the occasional behavioural resemblance of androchromes to males (see for example Forbes *et al.* 1997; Van Gossum *et al.* 2001a), it is not surprising that male mimicry has been invoked repeatedly as the primary source of frequency dependence. Indeed, spectral reflectances have confirmed that some androchromes more closely resemble males than gynochromes (Fincke *et al.* 2007). The reasoning is simple: when androchromes are rare compared with males then they suffer less male harassment compared with gynochromes; conversely once androchromes increase in relative abundance compared with males it will become profitable for males

Box 17.2 A summary of recent explanations for female-limited polymorphism and the nature of the underlying selective forces

Theory	Frequency-dependent benefit to androchromes when rare	Frequency-dependent cost to androchromes when common	Frequency-independent cost to androchromes	Comments	Reference
Interspecific mimicry and predation	Lower harassment by heterospecific males due to male mimicry	High rate of interspecific matings, which reduce fertility	Higher predation due to higher behavioural and morphological conspicuousness		Johnson 1975
Intraspecific mimicry and predation	Lower harassment by conspecific males due to male mimicry	Breakdown of mimetic advantage when androchromes are common	Higher predation due to higher behavioural and morphological conspicuousness		Robertson 1985
Intraspecific mimicry and mate recognition	Lower male harassment due to male mimicry when populations are at high density	Androchromes are selected against when populations are low density because they are not recognized as potential mates and risk zero matings		A density-dependent theory assuming temporally varying selection; however, the nature of the frequency-dependent selection cannot in itself promote polymorphism	Hinnekint 1987
Learned mate recognition	Lower probability of male harassment on encounter	Higher probability of male harassment on encounter		Males must learn to recognize conspecific females; precise equilibrium depends on differential conspicuousness	Miller and Fincke 1999; Fincke 2004
Intraspecific mimicry and harassment	Lower probability of male harassment on encounter due to mimicry	Breakdown of mimetic advantage when androchromes are common	Higher probability of encounter by conspecific males due to higher conspicuousness		Sherratt 2001

to attempt to distinguish male-like females from males (Robertson 1985), and the benefits of male mimicry are consequently reduced (Sherratt 2001). Note that androchromes do not have to be indistinguishable from males to benefit from male mimicry: no Batesian mimic would ever pass this test. All that is required is that androchromes gain some form of fitness advantage from rarity over alternative forms through their similarity to males.

Nevertheless, there is an alternative set of hypotheses, which simply assume that males have to learn to recognize the female types: this explanation has been dubbed the learned mate-recognition hypothesis (LMR for short; Miller and Fincke 1999). Many predators exhibit a frequency-dependent preference for attacking the more common form of prey in an environment, and it is quite possible that mate-searching males exhibit an analogous response.

The reasons for this 'switching' (Murdoch 1969) are varied (see Sherratt and Harvey 1993 for review). In particular, in his classic posthumous paper, Tinbergen (1960) argued that through chance encounters with cryptic prey, predators (in the current case, male damselflies) may only gradually learn to recognize those stimuli that enable them to differentiate prey types from their surroundings (in the current case, unsuitable mates). This learning to recognize cryptic prey can readily generate higher attack rates on the more common morph, leading to polymorphisms (see for example Bond and Kamil 2002).

To distinguish between hypotheses on male mimicry and LMR (see Box 17.2) we need to study several populations of the same species over a wide range of androchrome frequencies, including contrasting populations where androchromes are the minority and the majority female morph. Male mate-choice experiments have indicated that male preference in *Ischnura elegans* correlates positively with female morph frequency (Van Gossum *et al.* 1999); that is, the more common a female morph the more it will be preferred by the male (Figure 17.1a). This positive frequency-dependent selection, when costly in terms of fitness for the more common morph, will then result in negative frequency-dependent selection, thereby supporting LMR predictions. In contrast, a review of female mating frequencies in natural populations of the same species, over a range of androchrome frequencies (8–90%), indicated that androchrome females consistently mate less often
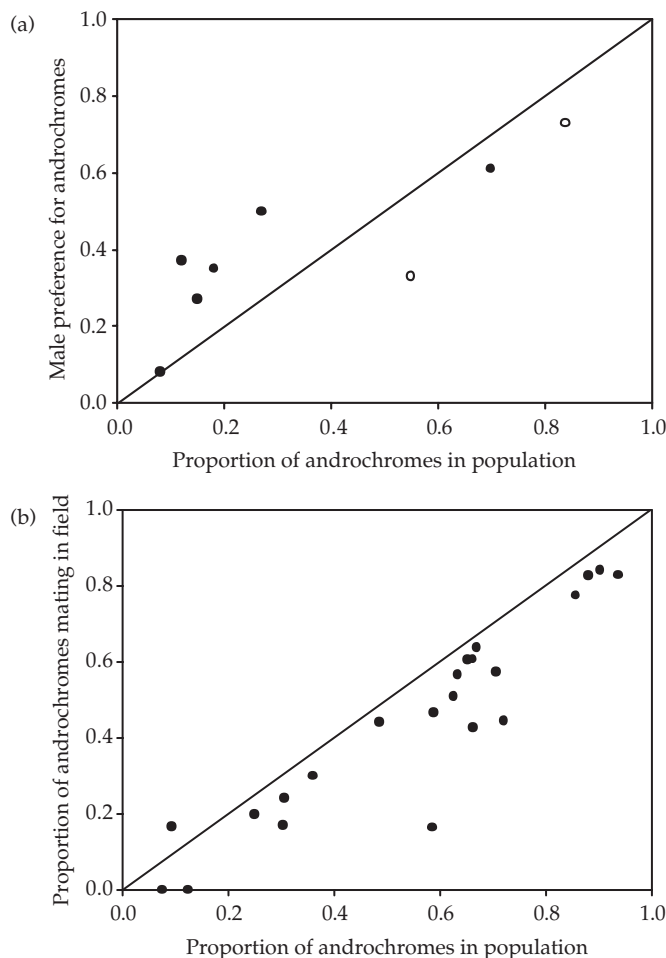

Figure 17.1 (a) Relationship between the proportion of androchrome females in a population (androchromes/all females) and male preference for the androchrome female in an experimental setting. Filled circles refer to binary choice experiments where males were offered the choice between an androchrome and a gynochrome female; open circles refer to trials where males were confronted with only androchromes and male sexual interest for this female morphs was scored. (b) Relationship between the proportion of androchrome females in a population (androchromes/all females) and the proportion of androchrome females found mating in the field. Data for these graphs were derived from Cordero and Andrés (1996); Van Gossum *et al.* (1999, 2001b); Cordero-Rivera and Sánchez-Guillén (2007).

than expected from their population frequency, with no element of frequency dependence based on relative frequencies of females (Cordero-Rivera and Sánchez-Guillén 2007) (Figure 17.1b). These contrasting results offer insight into the difficulty to test predictions on male mimicry or LMR. One likely explanation is that choice experiments measure mainly male preference (i.e. exclude most female behaviour), whereas field surveys are the combined result of male preference, morph conspicuousness, and female avoidance of male harassment.

In many damselflies, males search continuously for females, but females are not passive objects of male attention. It seems that morphs may sometimes differ in their response to male attention and also more generally in their behavioural patterns. For example, androchrome female *I. elegans* are more aggressive towards approaching males than gynochromes (Van Gossum *et al.* 2001a). Also, androchromes of *I. elegans* use more open habitat and fly less than gynochromes, which reside more within vegetation and fly longer distances (Van Gossum *et al.* 2001a). Female morphs therefore not only have contrasting coloration, but also show different behaviour. Consequently, manipulative experiments in which female behaviour is excluded or restricted may not adequately provide insights in the interaction between males and females in the field. It is interesting, in this context, that where sexual interactions among free-ranging individuals in natural populations have been studied, contrary to LMR predictions, it was found that the rarer morph (gynochrome) was more likely to receive male harassment (e.g. Sirot *et al.* 2003). Clearly, more studies following male–female interactions over a range of androchrome frequencies are needed.

17.6 Conspicuous or cryptic morphs: risks of being eaten?

As we have seen, sex-limited morphs have different phenotypes, and this appears relevant in the context of sexual selection. Two further questions are relevant: (1) do morphs differ in phenotypic traits other than colour, pattern or behaviour and (2) do phenotypic differences between morphs have additional consequences beyond those relating to reproductive success? At least for examples

where polymorphism is not restricted to only one sex, it has been shown that different colour morphs may differ in traits as diverse as development, fecundity and disease resistance (e.g. Svensson *et al.* 2002; True 2003). Where morphs differ in other traits, then selection on these traits potentially can result in a correlated response in morph frequencies. Furthermore, if morphs differ not only with respect to reproductive success, but are differentially affected by other selective pressures, these may help explain how polymorphism is maintained. Although a variety of mechanisms are possible, the possibility of differential predation on the morphs has been discussed most frequently (see Box 17.2). For example, it is interesting that examples of Batesian mimicry and related polymorphisms are sometimes restricted only to females and one leading explanation is that females of these species are more exposed to predators than males (Stamps and Gon 1983; Ruxton *et al.* 2004).

It has been argued (e.g. Robertson 1985), but not formally shown, that both territorial males and male-like females in odonates are more conspicuous than the alternative morph and as a consequence are more prone to predation by visual hunters such as birds and dragonflies (see Box 17.2). To start addressing this question information is required on morph spectra, backgrounds, environmental light conditions, and also predator visual sensitivities. This research remains to be done.

Clearly if androchromes do suffer higher predation then this source of mortality could offset any benefit that androchromes would have in avoiding male harassment (e.g. Robertson 1985). Little is known, but where female morphs have been compared for mature daily survivorship using capture–mark–recapture data, female morphs did not differ (e.g. Fincke 1994; Cordero *et al.* 1998). Also, if predators preferentially attack conspicuous individuals, then males (and androchromes) should have lower survival rate than gynochrome females (all else being equal), yet males tend to have higher survival rates than females in the Coenagrionidae, one of the most polymorphic groups of damselflies (see Chapter 2 in this volume). Further, it appears that gynochromes, possibly as a consequence of behaviour, were far more likely to end up and die in spider webs than androchromes (Van Gossum *et al.*

2004). In addition, birds are important predators on newly emerged odonates that have difficulty flying, but these immature damselflies frequently do not show their mature coloration. Together, empirical support for predators favouring the relatively more conspicuous morph remains absent.

17.7 Conclusion and future avenues of research

The wide distribution of female-limited polymorphisms in odonates provides researchers with the opportunity to evaluate the validity, and generality, of proposed hypotheses for certain species by applying it to others with rather different life histories. Furthermore, given that several of these odonate species are widespread and common, research can be conducted in contrasting environments. However, one disadvantage of using odonates to study polymorphisms is (within insects at least) the relatively long generation time, making laboratory based multi-generational studies extremely laborious. Field experiments in which the relative densities of androchromes and gynochromes are manipulated are also challenging because of the typically high abundance of species and their ability to disperse, so that, in a few hours, populations can return to the pre-treatment density (Moore 1962). Experiments in which artificial enclosures are used offer one potential solution (see for example Van Gossum *et al.* 2005) and in the future we may see more of this type of experiment. With female-limited polymorphism so common among odonates and phylogenies appearing regularly in the literature, phylogenetically controlled analyses of the correlates of sex-limited polymorphism will also be forthcoming.

Several aspects of female-limited polymorphism in odonates deserve future attention. Most research has focused on selection acting on mature individuals; however, selection may also act on immature individuals or even on the much longer-lasting (in terms of time) larval stages (e.g. Abbott and Svensson 2007). This sort of research may be accelerated if the genes involved in the polymorphism could be better characterized, leading to diagnostic tests of morph identity at any stage in the life cycle. There are also several key gaps when it comes to researching mature adults. For example, there is a continued need for more detailed studies on the behaviour and success of female morphs in populations where androchromes are the majority female morph, since the main contending explanations are best distinguished under these conditions. It is also important to note that different morphs may differ in microhabitat use (e.g. Van Gossum *et al.* 2001a) and microhabitat use may relate to thermoregulation (e.g. Watanabe 1991), so more work is needed to elucidate the role of temperature in mediating morph frequency. As seen in vertebrates (e.g. Miles *et al.* 2007) morphs may differ in endocrine levels, which shape behaviour, physiology, and performance, and this research angle also remains unexplored in studying female-limited polymorphism in odonates.

Finally, we note that polymorphism is not only of interest in its own right, but may represent be a transient stage in sympatric speciation, particularly where assortative mating arises (Gray and McKinnon 2007). The case of the dragonflies *Palpopleura lucia* and *Palpopleura portia*, for more than 200 years considered two forms of the same species (see for example Tarboton and Tarboton 2002), but recently identified as good species using molecular techniques (Mitchell and Samways 2005), is a possible example of a colour polymorphism that predates speciation.

Acknowledgements

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