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Colour polymorphism in odonates: females that mimic males?

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Summary

Female colour polymorphism is a widespread characteristic of many Odonata. Fifty-four per cent of the genera of European zygopterans have at least one polychromatic species, although this phenomenon is unequally distributed among families. In this paper we review the adaptive explanations that have been proposed to explain the maintenance of female polychromatism in damselflies, and the field and laboratory experiments that have been done to test these hypotheses. The available data suggest that this polymorphism is maintained by density-dependent factors in *Ischnura* species, but the maintenance of colour morphs in other genera remains poorly understood.

Introduction

In many species of Odonata, a marked polymorphism in coloration exists, restricted to the female sex. One of the female phenotypes is coloured like the conspecific male, whereas one or more additional colour morphs are very different from the male coloration. In the scientific literature male-like females have been named homeochromes, andromorphs, and *androchromotypics, in contrast to heterochromes, heteromorphs and gynochromotypics. Given that this polymorphism is based on colour and not on morphology (Hilton, 1987), we will call these females androchromes (literally, with male colour), and use gynochromes (i.e. with female colour) for those with a different coloration. This polymorphism is very common in Zygoptera. Fifty-four per cent of the genera of European zygopterans have at least one polychromatic species, although this phenomenon is unequally distributed among families (Table 1). Most European Coenagrionidae are polychromatic (65 per cent of species), particularly those of the genera *Ischnura*, *Enallagma*, *Ceriagrion* and *Pyrrhosoma* (see illustrations in Sandhall (1987) and Askew (1988)), while Lestidae are all monochromatic (although Andersson (1994: 317) indicates the opposite). In the three species so far studied, this polymorphism is controlled by a single autosomic gene (not linked to the sex chromosomes), but with expression restricted to the female sex (Johnson, 1964; Johnson, 1966; Cordero, 1990a). In some species, the great resemblance that exists between the males and the androchrome females could deceive the most expert odonatologist in a quick examination! In *Ischnura graellsii* (Rambur), a small species extremely common in wide zones of Spain, most of the mature females (about 70 per cent) have brown coloration (gynochrome *infuscans*). The androchrome female represents between 6 and 30 per cent in several populations and its mature coloration is blue as in the males. This species also has gynochrome females of the *aurantiaca* phenotype (normally 4-10 per cent) whose coloration is orange or reddish in the juvenile phases and brown in maturity. In addition, males and the three female morphs each go through several phases of coloration during their life (Cordero, 1990a). This produces an enormous variability of coloration between the adults.

Table 1. The incidence of female polychromatism in European damselflies.

		Monochromatic species whose female is:		Polymorphic species
		androchrome	gynochrome	
Calopterygidae	*Calopteryx*	-	3	1[a]
Euphaeidae	*Epallage*	1	-	-
Lestidae	*Lestes*	6	-	-
	Sympecma	2	-	-
Platycnemididae	*Platycnemis*	2	1	-
Coenagrionidae	*Pyrrhosoma*	-	-	1
	Erythromma	1[b]	1	-
	Coenagrion	4	2	5
	Cercion	-	1	-
	Enallagma	-	-	2
	Ischnura	-	-	7
	Nehalennia	-	-	1[c]
	Ceriagrion	-	-	1
	totals	16 (38%)	8 (19%)	18 (43%)

[a] *Calopteryx splendens* is polychromatic in some populations, see De Marchi (1990).

[b] In *Erythromma viridulum* two colour phenotypes exist, but we do not know if they are age-related or genetic.

[c] From the descriptions in Askew (1988) and the pictures in Sandhall (1987) we suspect that *Nehalennia speciosa* is polymorphic.

The question is, why do these different female morphs exist? The answer seems to depend on the reproductive behaviour of each species. Three main hypotheses have been proposed to explain this female polymorphism. The first of these is due to Johnson (1975), and we can term it the hypothesis of reproductive isolation. According to this author, the polymorphism is maintained because androchrome females rarely mate with males of another species (they have great reproductive isolation) while gynochromes are commonly involved in matings with heterospecific males. Obviously, this explanation assumes that polymorphic species coexist and cross-mate frequently. This advantage to the androchromes would be counterbalanced by a differential predation pressure: the androchrome females would be more attractive to predators, and this would reduce their longevity.

Robertson (1985) proposed a second explanation. In some species of *Ischnura*, mating is of very long duration (sometimes 6-7 hours). If a single sexual intercourse were enough to enable a female to fertilize all the eggs that she would lay throughout life, the androchrome coloration would be advantageous for 'deceiving' males and so avoiding unnecessary matings (these females could dedicate more time to feeding and oviposition). Males should be unable to distinguish between androchromes and other males. This is the hypothesis of intraspecific mimetism. As a balancing mechanism, Robertson proposed a more intense predation on the androchrome females, due to their more conspicuous coloration.

More recently, Hinnekint (1987) proposed a new explanation, based on density-dependence. For this author, the density of the population is the mechanism that maintains the polymorphism. At high densities (when the sex ratio is more biased toward males), the androchrome morph would have an advantage through not being disturbed by the males, but it would suffer a balancing disadvantage of reduced mating success at low male densities, and some would not be able to mate at all. The situation would be inverse for the gynochrome females. The existence of pluriannual cycles in the density of the population would permit the different morphs to achieve an evolutionary equilibrium (Hinnekint & Dumont, 1989). According to this hypothesis, the survival of the different morphs would be the same, independent of their coloration.

Interspecific matings are very rare in most species: in one population of *Ischnura graellsii* only one has been observed among 297 examined couples, and none among 435 in a second population (Cordero, 1992), and for this reason the first hypothesis is not applicable to most populations. We will therefore concentrate on the remaining two hypotheses: male mimetism and density-dependence.

Are androchromes male mimics?

If males can distinguish between androchrome females and other males, then both hypotheses are no longer applicable.

The assumption that males are unable to distinguish between androchrome females and other males has been tested by several authors using lures. Live or dead animals are presented to field males and the reponse recorded. The proportion of males trying to grasp in tandem the different models gives a measure of the sexual interest in that morph. Males of most species are rather indiscriminate in their mating attempts, but male models are not so attractive as female models. If we compare the response to the androchrome and gynochrome phenotype with that to the male model, then we can test the ability of males to identify androchromes as females. This has been done for several species (see Table 2 for references). In all *Ischnura* species so far studied, androchromes were less attractive to males than gynochromes, even in *I. denticollis* (Burmeister) where androchromes were about 50 per cent of the population (Córdoba Aguilar, 1992), and in *I. elegans* (Vander Linden), where androchromes comprised 55 per cent (Cordero *et al.*, unpublished). Mate-searching males of *Ischnura* are able to distinguish between androchromes and other males (Cordero, 1989). Fincke (1994a) indicates that among coenagrionids the proportion of the total sexual response to females that was directed towards androchromes was positively correlated with the frequency of androchromes in the population, suggesting that the commonest female morph is the most attractive to males. From Table 2 we conclude the opposite: there is not a significant correlation between the percentage of positive responses from males and the frequency of each colour morph in the population (live models: r=0.22, N=15, p=0.425 [excluding *Calopteryx*: r=0.26, N=13, P=0.390]; dead models: r=0.12, N=12, p=0.717). On the other hand, in *Ischnura graellsii*, *I. elegans* and *Ceriagrion tenellum* (Villers), there are two gynochrome female morphs, one of which is very rare but is as attractive to males as the commonest morph. Furthermore, there is a clear difference in male response to live and dead models in *I. elegans* and *C. tenellum*, which indicates that for a perfect imitation, androchromes should not only have male colours but also behave as males. Given this fact, to test the idea that males simply recognize as female the commonest morph in the population, we cannot put together in one comparison (as did Fincke (1994a)) the response

Table 2. Summary of tests of male response to different mature female morphs in polychromatic damselflies, when males are presented with one model per trial. Per cent of male sexual response per model (tandem, tandem attempt or attempted take-over of females already in tandem), excluding males that did not respond to the model (perched or flew away). The asterisk (*) indicates experiments where models were dead. Andro: androchrome, Gyno 1: type 1 gynochrome (most common), Gyno 2: type 2 gynochrome.

	% positive response to				Population frequency			
	Andro	Gyno 1	Gyno 2	male	Andro	Gyno 1	Gyno 2	source
Coenagrionidae								
*Argia vivida**	54	56	-	-	66[a]	34	-	Conrad & Pritchard (1989)
Ceriagrion tenellum	63	82	83	45	12	62	26	Andrés (unpubl.)
*Cerigrion tenellum**	88	88	96	90	12	62	26	Andrés (unpubl.)
*Enallagma ebrium**	96	100	-	-	07	93	-	Forbes (1994)
Enallagma hageni	40	73	-	05	26	74	-	Fincke (1994)
Ischnura denticollis	49	86	-	00	51[b]	49	-	Córdoba Aguilar (1992)
Ischnura elegans	33	60	63	37	55	27	18	Cordero *et al.* (unpubl.)
*Ischnura elegans**	83	90	93	83	55	27	18	Cordero *et al.* (unpubl.)
Ischnura graellsii	33	100	78	26	14	76	11	Cordero (1989, 1990a)
*Ischnura ramburi**	55	75	-	55	31	69	-	Robertson (1985)
Calopterygidae								
Calopteryx splendens	85	80	-	-	10	90	-	De Marchi (1990)

[a] largest sample in Conrad & Pritchard (1989)

[b] in litt. 10.2.93

Data for *Argia apicalis* by Bick & Bick (1965) and for *Enallagma boreale* by Forbes (1991) are not included because the experimental procedure was a simultaneous presentation of two female morphs.

of males to live and dead models. The correct way to test that hypothesis is to compare the degree of sexual response in populations of the same species that differ in the relative frequency of female morphs.

Is one mating enough from the female perspective?

Male odonates do not give nutrients to females during copulation. In fact, the only male contribution to reproduction is sperm. Therefore, if *copula* duration is very long, females could be selected to minimize the number of copulations. In *Ischnura graellsii*, the amount of sperm that females receive during copulation is enough to fertilize all the eggs produced during two weeks after mating (Cordero, 1990b). Given that the female lifespan is about one week, this amount of sperm is enough for lifetime egg production. The same is true for *I. verticalis* (Say) (Fincke, 1987).

Is predation phenotype-dependent?

Robertson's hypothesis assumes that male coloration is more conspicuous and therefore attracts predators. This should determine a shorter androchrome (and male) lifespan. Table 3 presents the results of measuring lifespan by means of mark-recapture methods under field conditions. Only in two cases (*I. damula* Calvert, and the 1981 data set for *Enallagma hageni* Walsh) was androchrome survival less than that of gynochromes. We conclude that survivorship is similar in all female colour morphs, probably because mortality factors are independent of female coloration. The only visual predators that regularly feed on damselflies are asilids and frogs, but asilids are not common, and we do not know if they select prey by colour, whereas frogs are very common but unselective: they attack any moving object (see Michiels & Dhondt (1990) and Rehfeldt (1992) for a description of frog predation on ovipositing dragonflies).

Is female mating rate density-dependent?

If copulation depends on the number of male-female encounters, it is easy to see that the more males there are at the mating rendezvous, the greater will be the probability that females will mate. In the low density population of *I. graellsii* studied by Cordero (1992), female mating rate was positively correlated with male numbers, but this did not occur in the high density population (Cordero *et al.*, unpublished). In one population of *I. elegans* there was a positive correlation between female mating rate and male density for androchromes but not for gynochromes (Cordero *et al.*, unpublished). In contrast, neither in *Enallagma hageni* nor in *E. boreale* Sélys, was the daily mating efficiency of females correlated with the density of males (Fincke, 1994a). Therefore, only in some populations is female mating rate density-dependent.

Table 3. Mean lifespan (±SE [N]) of female morphs in polychromatic damselflies. Part of the differences in longevity between species is due to the exclusion of unrecaptured individuals in some species.

	Andro	Gyno 1	Gyno 2	P	Source
Ceriagrion tenellum	2.6±0.2 (31)	2.8±0.1 (149)	2.9±0.1 (56)	0.148[a]	Andrés (unpubl.)
Coenagrion puella	3.4±0.8 (20)	3.1±0.4 (150)	-	0.815[c]	Thompson (1989)
	4.0±0.9 (31)	4.2±0.5 (178)	-	0.898[c]	Thompson (1989)
	7.9±1.6 (11)	5.4±0.3 (163)	-	0.064[c]	Thompson (1989)
Enallagma boreale	3.6±0.5 (53)	3.3±0.4 (66)	-	>0.05[c]	Fincke (1994a)
Enallagma hageni	2.2±0.3 (96)	2.2±0.2 (274)	-	>0.05[c]	Fincke (1994a)
	1.7±0.2 (51)	2.5±0.3 (115)	-	<0.05[c]	Fincke (1994a)
	7.3±1.1 (37)	8.0±1.1 (66)	-	>0.05[c]	Fincke (1994a)
Ischnura damula	3.8	10.0	-	[b]	Johnson (1975)
Ischnura elegans[d]	3.0±0.2 (319)	2.9±0.3 (168)	2.6±0.2 (158)	0.752[a]	Cordero *et al.* (unpubl.)
Ischnura graellsii	8.5±0.9 (34)	6.8±0.3 (153)	6.8±0.9 (16)	0.229[a]	Cordero (1992)
	7.2±1.5 (17)	8.2±0.5 (113)	7.4±1.0 (25)	0.506[a]	Cordero (1992)

[a] Kruskal - Wallis test.

[b] Data are expected lifespan, from estimates of daily survival rate.

[c] t-test.

[d] tenerals excluded due to the impossibility of distinguishing between androchromes and *infuscans* in this colour phase.

Table 4. Mating failure of females in polychromatic damselflies. The table shows the percentage of females that were never seen to mate. Probability after a χ^2 test.

	Sample	Andro	Gyno 1	Gyno 2	P	Source
Ceriagrion tenellum	all females	7.7	9.3	8.5	0.849	Andrés (unpubl.)
Enallagma cyathigerum	all females	30.8	18.8	-	0.379[a]	Garrison (1978)
Enallagma hageni	seen once	56.8	48.1	-	0.385	Fincke (1994a)
	seen> once	50.0	13.8	-	0.007	Fincke (1994a)
Ischnura elegans	young	58.9	20.8	74.8	<0.001	Cordero *et al.* (unpubl.)
	mature	25.7	6.6	11.1	0.003	Cordero *et al.* (unpubl.)
Ischnura graellsii	high density	32.1	41.6	47.4	0.298	Cordero *et al.* (unpubl.)
	low density	77.7	38.0	56.3	0.003	Cordero *et al.* (unpubl.)

[a] from Table 4 in Garrison (1978)

Are there differences in mating success between female morphs?

This is the main question relating to the maintenance of colour polymorphism. What is really important is not the number of matings females obtain, but the proportion of females that never mate. Several estimates of this mating failure are presented in Table 4. In one population of *Ischnura graellsii*, and another of *I. elegans*, the proportion of androchrome females that were never seen to mate was significantly higher than for gynochromes. The same was true for *Enallagma hageni* (Fincke, 1994a), but not for *E. cyathigerum* (Charpentier) (Garrison, 1978), or *Ceriagrion tenellum* (Andrés, unpublished). In *E. hageni*, the differences were probably due to the shorter lifespan of androchromes in the group of recaptured females, and not to their colour, but in *Ischnura* the failure of androchromes seems real, because they did not have a shorter lifespan (Cordero *et al.*, unpublished). In *Coenagrion puella* (L.) the lifetime number of clutches was similar for andro- and gynochromes (Thompson, 1989).

Body size

Body size is a phenotypic variable that has an important influence on female fecundity. In most animals, larger females produce more eggs (Labarbera, 1989) and this is also true for damselflies (Gribbin & Thompson, 1990; Cordero, 1991). Table 5 presents body size comparisons between female phenotypes in the species that have been studied to date. In most species, all phenotypes have similar body size, but in one population of *I. graellsii* and another of *I. elegans*, androchromes were larger than gynochromes. However, longevity is a complicating factor in the size/fecundity relationship (Leather, 1988). Longevity, and the factors affecting it, seems to be the single most important influence on damselfly fecundity: 70 per cent of variance in female reproductive success in *Coenagrion puella* was due to differences in survival (Banks & Thompson, 1987).

Table 5. Body size comparisons (mean ±SE (N) in mm) of female morphs in polychromatic damselflies. When several values are presented for one species, averages refer to different samples, either from different populations or from different sets from the same population. P after a t-test.

	Andro	Gyno 1	Gyno 2	P (andro-gyno)	Source
Ceriagrion tenellum [a]	32.67±0.13 (53)	32.56±0.15 (242)	32.77±0.09 (85)	0.856	Andrés (unpubl.)
Coenagrion puella [b]	22.73±0.12 (20)	22.74±0.05 (150)	-	0.931	Thompson (1989)
	22.58±0.09 (31)	22.73±0.05 (178)	-	0.215	Thompson (1989)
	22.27±0.25 (11)	21.98±0.05 (163)	-	0.142	Thompson (1989)
Enallagma boreale [b]	19.96±0.2 (25)	19.53±0.2 (19)	-	>0.05	Fincke (1994a)
	12.4±0.08 (31)	12.5±0.12 (23)	-	0.70	Forbes (1994a)
Enallagma hageni [b]	18.26±0.1 (77)	18.21±0.04 (228)	-	>0.05	Fincke (1994a)
Ischnura elegans [a]	29.96±0.13 (270)	29.57±0.17 (120)	29.67±0.19 (146)	0.007	Cordero *et al.* (unpubl.)
Ischnura graellsii [a]	27.84±0.11 (84)	27.47±0.05 (452)	27.50±0.17 (62)	0.007	Cordero (1992)
	28.33±0.11 (98)	28.23±0.07 (297)	28.02±0.15 (55)	0.304	Cordero (1992)
	28.73±0.22 (21)	28.53±0.10 (79)	28.99±0.14 (20)	0.607	Cordero (1992)

[a] body length

[b] wing length

Conrad & Pritchard (1989) compared wing length between 11 androchromes and 11 gynochromes of *Argia vivida*, and they did not find significant differences, but averages were not presented.

Discussion

The results of investigations carried out in several natural populations suggest that the density-dependent hypothesis is the most likely explanation for the maintenance of female colour polymorphism in *Ischnura graellsii* and *I. elegans*. We therefore conclude that, at least in these species, the male coloration of androchromes confers some advantages under conditions of high male density. If this explanation is correct, then we should find a higher proportion of androchrome females in populations of high density than in populations of low density. The comparison of the frequencies of the different types of females in five natural populations of *I. graellsii*, supports this interpretation (Cordero, 1990a): the androchrome females represented only seven per cent in a population of low density and 18–30 per cent at high density. A similar result has been found in *Nehalennia irene* Hagen, where frequency of androchromes in several natural populations was positively correlated with an index of male density (Forbes *et al.*, 1995).

Recently Fincke (1994a) has analysed the maintenance of female polymorphism in *Enallagma hageni* and *E. boreale*, and arrived at the conclusion that there are no fitness differences between the two types of females of these species. This means that it has not been possible to reject the null hypothesis (i.e. that this colour polymorphism is maintained by chance) and the fact that a female has blue or brown coloration does not matter. The problem with this interpretation is that the available hypotheses are not valid for *Enallagma*, and Fincke tested them without testing their assumptions. In fact, androchrome *Enallagma* are not a perfect mimic of conspecific males and so cannot avoid male interest: males of *Enallagma* do distinguish between androchromes and other males (Fincke, 1994a; Forbes & Teather, 1994). Also, and more important, due to underwater oviposition in this genus, additional matings are advantageous for all female morphs, because females benefit from male help in escaping from the surface film (Fincke, 1986; Miller, 1990). Therefore, avoiding additional matings (as androchrome *Ischnura* females seem to do) does not confer any benefit on androchrome *Enallagma* females.

Robinson & Allgeyer (in press) reviewed the life-histories of seventeen *Ischnura* species from North America, Europe and Asia and found that these species can be grouped into three categories: small monandrous species, large polyandrous species without tandem guarding and polyandrous species with tandem oviposition. Of these seventeen species, all but four are polychromatic, and all four monochromatic species belong to the monandrous group. This fact suggests a relationship between the degree of polygamy and female polychromatism. They propose that the evolution of female monandry neutralized the selective advantage of colour patterns and for this reason fixation has occurred in this group (two of the monochromatic species have only androchrome females and the remaining two species only gynochrome females). The existence of polychromatic females in all polyandrous species supports the view that this polychromatism is not neutral, because if female morphs were maintained only by random factors, at least in some populations fixation should have occurred (Golding, 1992). In our experience all populations of *I. graellsii* and *I. elegans* are polychromatic, although some populations of *I. pumilio* (Charpentier) (the only European *Ischnura* whose androchromes are not a perfect mimic of males) have only gynochrome females (e.g. in Britain, Corbet *et al.* (1960: 23)).

Two facts remain unexplained: the larger body size of androchromes in some populations and the existence of more than one gynochrome morph in many species. Cordero (1992) proposed that the individuals bearing the androchrome allele could be more aggressive during their larval stages, defending the best feeding sites and therefore achieving greater size. It is also possible that such a small body size difference as was detected among female morphs in *I. graellsii* and *I. elegans* does not have any important evolutionary effect. A study of more populations is required.

New explanations are needed for the existence of two (or even three) different gynochrome females in some species. We propose the following ideas: differential survivorship or competitive abilities during the larval or immature stages, differential habitat selection either by larvae or adults, differential dispersal tendencies (one morph could be better at finding new habitats), differential fecundity, and, of course, the neutral hypothesis.

Polymorphism of coloration has been a classic example of the action of natural selection; the case of industrial melanism in the Peppered Moth (*Biston betularia*) has been widely used as an example in biology text books. This emphasis on characters with great visual impact could lead to an erroneous interpretation and produce the generalization that all polymorphisms of coloration are maintained by the action of natural selection (Oxford, 1993). Several cases exist where colour polymorphism seems to be maintained by factors that have nothing to do with natural selection, such as random changes in the frequencies of the genes controlling the character in question, migration from populations with different gene frequencies, and so on. Even in *Ischnura graellsii*, the species that has been studied most intensively from the point of view of its polymorphic coloration, the situation is not fully clear, and perhaps, after all, random factors are the most important in the maintenance of the polymorphism, as Fincke (1994b) suggests. Certainly, this interesting topic will continue to inspire new studies until it is possible to determine the advantages and disadvantages of each coloration with greater precision. This intriguing phenomenon will be clarified only after the study of a greater number of species - we suggest *Pyrrhosoma nymphula* (Sulzer) as a good candidate.

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